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**Phylogenetic Studies of
North American Minnows, with
Emphasis on the Genus *Cyprinella*
(Teleostei: Cypriniformes)**

By

Richard L. Mayden

UNIVERSITY OF KANSAS
LAWRENCE

June 1, 1989

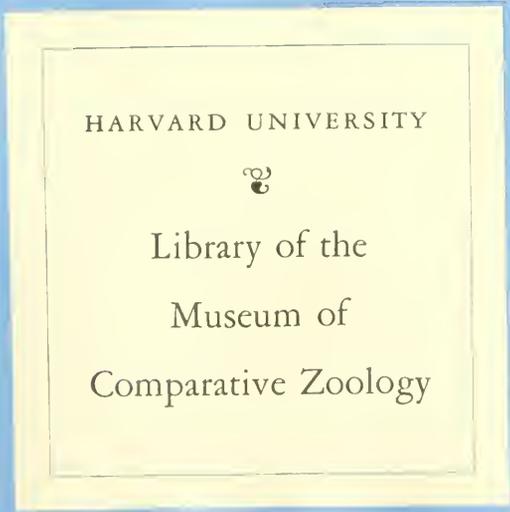
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BY

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INTRODUCTION

The North American cyprinid fauna is diverse, comprising nearly 30 percent of the total fish diversity north of Mexico. Our understanding of cyprinid diversity is reasonably complete, but cyprinids are poorly known phylogenetically. The present status of the systematics of this group has not changed appreciably since 1977, when Carl L. Hubbs and Robert R. Miller stated "It is abundantly obvious that much of the generic placement in American cyprinids is in a chaotic state . . ." (Hubbs and Miller, 1977, p. 275). Many important studies of cyprinid species variation have been published in North America, again aiding our understanding of species diversity, but not necessarily improving our knowledge of genealogical relationships. Only a few studies have developed hypotheses of species relationships. Many have concentrated on *Notropis*, the largest of the North American genera. Sutkus (1950) examined the subgenus *Pteronotropis*, Gilbert (1964), Rainboth and Whitt (1974), Buth (1978), Buth and Mayden (1981), Menzel (1976, 1977), Dowling and Moore (1984), and Mayden (1988) dealt with the subgenus *Luxilus*, Snelson (1972) and Stein et al. (1985) with *Lythrurus*, Swift (1970) with *Hydrophlox*, *Alburnops*, and other species groups, and Gibbs (1955, 1957a) and Contreras-Balderas (1975, 1978) with *Cyprinella*. Our knowledge of *Notropis* diversity and systematics has been greatly aided by studies by Contreras-Balderas (1975, 1978), Hubbs and Miller (1978), Chernoff and Miller (1981, 1982, 1986), and Chernoff et al. (1982). In these revisionary studies hypotheses or statements of relationships may be present.

Systematic studies of other North American genera include Hubbs and Black (1947) and Niazi (1960) for *Pimephales*; Illick (1956) for many cyprinids; Sisk (1961) for *Notropis*, Uyeno (1961) for *Gila*; Reno (1966, 1969) for some *Notropis* and *Hybopsis*; Barbour and Miller (1978) and Jensen and Barbour (1981) for *Algansea*; Buhan (1970) for the genera *Richardsonius*, *Clinostomus*, and *Semotilus*;

Jenkins and Lachner (1971) for *Nocomis* and *Hybopsis*; Buth and Burr (1978) for *Camposotoma*; Coad (1975) for many North American and Eurasian cyprinids; and Hubbs and Miller (1977) for the genus *Dionda*. In all of the above studies statements of relationship are generally presented.

Coad (1975) and McAllister and Coad (1978) were among the first to examine higher relationships of North American cyprinids, but some problems remain. Because the genus *Notropis* is so diverse, it was considered the most primitive and was used to determine character polarities. This technique may seem sound, but character evaluation may be flawed given that *Notropis* may in fact be an ingroup. In the latter study hybridization frequency data were used as an indication of genealogical relatedness. Although innovative, this methodology is suspect because reproductive compatibility may be a retained primitive characteristic (Rosen, 1979), and like any primitive morphological or genetic character, is not indicative of a close relationship. Further, frequency of opportunity to participate in hybridization was not considered. Not until the late 1970's was the philosophy of phylogenetic systematics (*sensu* Hennig, 1966) applied to species relationships of North American cyprinids. Barbour and Miller's (1978) and Jensen and Barbour's (1981) study of *Algansea*, Buth's (1978) analysis of *Luxilus*, and Coburn's (1982) analysis of the subgenus *Notropis*, as well as other species of this genus and other North American genera, were pioneering efforts into the systematics of North American minnows.

Cyprinella is one of many recognizably monophyletic (*sensu* Hennig) groups of the North American cyprinid fauna. Presently *Cyprinella* contains 27 species, distributed on the Atlantic Slope from the St. Lawrence River south to the Gulf Coast, west to the Great Plains, and southwest to the Rio Nazas of central Mexico. Previous systematic works on the group were mainly alpha in level, with the

exception of Gibbs, who supported species or species group relationships with characters. Species level problems have been reasonably well resolved through efforts by Bailey and Gibbs (1956), Gibbs (1955, 1957a, 1957b, 1957c, 1961, 1963), and Howell and Williams (1971) for eastern members of this group, herein regarded as the *whipplei* clade. The southwestern U. S. and Mexico clade, herein referred to as the *lutrensis* clade, has been thoroughly studied by Contreras-Balderas (1975, 1978), Minckley and Lytle (1969), Lytle (1972), Hubbs and Miller (1978), Chernoff and Miller (1982), and Matthews (1987).

In spite of these efforts, some taxonomic problems remain in *Cyprinella*. Within the wide-ranging red shiner, *Cyprinella lutrensis*, several Mexican forms referred to by Contreras-Balderas (1975, 1978) as subspecies of *C. lutrensis* are better recognized as separate species and some may represent undescribed forms. *Cyprinella lepida* of the Edwards Plateau of Texas is considered a distinct species and the number of forms of *Cyprinella lutrensis* present in drainages in the U. S. deserves additional investigation. Although a first attempt at the latter problem has been made by Matthews (1987), additional study is recommended. In the primarily eastern *whipplei* clade interesting questions remain concerning the specific status of the present subspecies of *spiloptera* and *venusta*, and the species *analostana* and *chloristia*. All of these species have very narrow regions of hypothesized introgression

between species (*analostana* and *chloristia*) or subspecies (*venusta* and *spiloptera*) or none at all. Whether these narrow areas of introgression reflect conspecificity remains to be tested.

The present study is a review of the genus *Cyprinella*, with osteological descriptions of the included species and hypotheses of their phylogenetic relationships. Further, the relationships of *Cyprinella* to other North American cyprinids are presented. In doing this, some previously recognized subgenera of the large and unnatural genus *Notropis* are elevated to generic rank. These changes and others are done so that species relationships are consistent with formal classification. Because of a growing interest in the ichthyological community to recognize *Cyprinella* as a distinct genus rather than a subgenus of *Notropis*, and the necessity to insure that the classification is consistent with the phylogenetic relationships of the species, I have recognized *Cyprinella* as a distinct genus. In doing so, *Luxilus*, *Lythrurus*, and *Pteronotropis* are also recognized as distinct genera because of their sister or close relationships to the genus *Cyprinella*. Relationships presented here are hypotheses that remain to be tested with additional, and perhaps different data sets. Further, some of the above listed areas of concern in the genus *Cyprinella* could not be addressed in this analysis. These areas of concern, as well as others, should be investigated independently to corroborate or falsify hypotheses presented here.

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METHODS

The phylogenetic techniques used in this analysis to determine species relationships follow Hennig (1966) and Wiley (1981). Determination of character polarity involved outgroup comparison and ontogeny, where possible. When two characters occurred within *Cyprinella* the character found in outgroups was considered primitive within *Cyprinella*. The alternate character was considered derived and used to determine species relationships. The primary outgroups used in determining species relationships within the genus *Cyprinella* included species of the genera *Luxilus* and *Lythrurus*. Justifications for using these subgenera as outgroups are provided below.

Characters used in this analysis included osteology, tuberculation, and body and fin pigmentation patterns. Osteological characters were taken from cleared and double stained specimens and disarticulated materials prepared with methods outlined by Dingerkus and Uhler (1977) and Mayden and Wiley (1984). Osteological characters were drawn with the aid of a camera lucida. Whenever possible, interspecific comparisons of morphologies were made between individuals of similar standard length to avoid possible problems associated with allometry. All body lengths referred to in the text and figures are standard lengths (SL). Tuberculation characters were taken from breeding males with maximum tubercle development. Males early in tubercle development were also examined to assess ontogenetic characters in tubercle patterns. Coloration characters were taken from freshly collected specimens or color photographs of freshly preserved individuals in breeding condition.

Within species accounts, meristic and morphometric data presented follow methods

outlined by Hubbs and Lagler (1964), Contreras-Balderas (1975), Howell and Williams (1971), Hubbs and Miller (1978), and Chernoff and Miller (1982). In some accounts, data are summarized from some of these publications. Precaudal and caudal vertebrae were distinguished on the basis of haemal spines. The first caudal element was the first element with a well-developed haemal spine. The precaudal vertebra at the dorsal fin insertion was that element below the anterior extent of the first pterygiophore. In each account pore counts presented for cephalic-lateralis canals are for one side of the head; numbers listed in parentheses for meristic characters represent modes. Peak or high males in discussions of tuberculation patterns and development of tubercles refers to breeding males with maximum tubercle development. Gut coiling terminology follows Kafuku (1958). Where scale counts are presented numbers refer to the number of scale rows; modes are in parentheses.

Terminologies and origins of bones follow Harrington (1955), Patterson (1977), and Coburn (1982). Nomenclature of the caudal skeleton follows Nybelin (1963) and Buhan (1972). Exceptions include: the urodermals of the latter two authors are here considered uroneurals, following Patterson (1968); lateral process of the parhypural in Buhan (1972) and Gosline (1960) is considered the hypurapophysis after Nursall (1963). The following anatomical abbreviations are used throughout the text and in illustrations for identification of structures:

A1T, tubercle of maxilla for insertion of A1 branch of *adductor mandibulae* muscle
 ABHL, anterior basihyal ligament
 ACH, anterior ceratohyal
 AP, ascending process of premaxilla

APT, autopterotic	KE, kinethmoid
ART, anguloarticular	LA, lacrymal
ASP, ascending process of maxilla	LE, lateral ethmoid
BB, basibranchial	LG, lacrymal groove
BH, basihyal	LOF, lateral occipital foramen
BO, basioccipital	LP, lateral process
BPT, basipterygium	M, mentomeckelian
BR, branchiostegal	MC, Meckel's cartilage
CB, ceratobranchial	MCO, mesocoracoid
CH, ceratohyal	ME, mesethmoid
CL, cleithrum	MP, median process
CLA, claustrum	MPT, metapterygoid
COR, coracoid	MX, maxilla
CP, coronoid process	MXM, premaxillary process of maxilla
DBHL, dorsal basihyal ligament	N, nasal
DE, dentary	NA, neural arch
DF, dilator fossa	NC, neural crest
DHH, dorsal hypohyal	NPU, compound centrum
DP, dorsal process of epibranchial 4	NS, neural spine
DPT, dermopterotic	OF, olfactory foramen
EB, epibranchial	OP, operculum
ECP, ectopterygoid	ORS, orbitosphenoid
ENP, endopterygoid	OS, os suspensorium
EOC, exoccipital	PA, parietal
EP, epural	PAL, palatine
EPB, epiphyseal bar	PBR, pharyngobranchial
EPO, epiotic	PCH, posterior ceratohyal
FIC, carotid foramen	PCL, postcleithrum
FM, foramen magnum	PDB, predorsal bone
FR, frontal	PE, preethmoid
FV, trigeminal foramen	PET, planum ethmoidale
FVII, facial foramen	PG, palatine groove
H, hypural	PH, parahypural
HA, haemal arch	PMO, posterior myodome opening
HB, hypobranchial	PMX, premaxilla
HH, hypohyal	POP, preoperculum
HN, hyomandibular notch	PPBO, pharyngeal process of basioccipital
HS, haemal spine	PPD, pharyngeal pad
HYF, hyoideal foramen	PR, posterior ramus of premaxilla
HYO, hyomandibular	PRO, prootic
IC, cavum sinus impar	PS, parasphenoid
ICA, intercalarium	PSOC, palatine socket
IH, interhyal	PTF, posttemporal fossa
IMB, intermuscular bone	PTS, pterosphenoïd
IO, infraorbital bone	PTT, posttemporal
IOP, interoperculum	PU, preural
ISC, ischiac process	QA, quadrate
IST, isthmus of maxilla	R, rib

RA, retroarticular	STF, subtemporal fossa
RAD, radial	SY, symplectic
RPM, rostral process of maxilla	TRP, tripus
SA, sesamoid articular	UN, uroneural
SCA, scapula	UO, urohyal
SCL, supracleithrum	UOL, urohyal ligament
SCM, scaphium	UP, uncinat process
SE, supraethmoid	V, vertebra
SEP, supraethmoid process of palatine	VBHL, ventral basihyal ligament
SO, supraorbital	VHH, ventral hypophyal
SOC, supraoccipital	VO, vomer
SOP, suboperculum	VP, vomer process of palatine
SPH, sphenotic	

MATERIALS EXAMINED

The following specimens were examined in this revision. For each species the museum acronym and number is listed first, followed by the number of specimens in parentheses. For some collections both cleared and double-stained and alcoholic specimens were examined from a single collection. Cleared and stained specimens are identified with the abbreviation CS. Institutional acronyms are identified in acknowledgments.

Agosia chrysogaster KU 8084 (5:3CS), 8085 (24:6CS). *Azteculea sallei* KU 5433 (3); UMMZ 108625 (6CS), 182346 (6), 191695 (6CS), 192368 (6). *Campostoma anomalum* KU 3946 (1:4CS), 12581 (2CS), 13200 (3CS). *C. oligolepis* KU 7583 (17CS), 12502 (1CS), 12520 (2CS). *C. ornatum* KU 3251 (15). *Clinostomus elongatus* KU 11322 (2CS). *C. funduloides* INHS 86752 (10CS); KU 3262 (38), 10697 (4:6CS). *Couesius plumbeus* KU 18881 (6:8CS). *Cyprinella analostana* INHS 74347 (15CS), 77855 (3CS); KU 5446 (1), 15367 (26), 19785 (10), 20400 (20); TU 25867 (31). *C. bocagrande* KU 20399 (1CS); UMMZ 208250 (1CS), 208265 (5). *C. caerulea* INHS 74805 (9CS); KU 18978 (2:8CS), 19666 (13); LACM 38942-1 (10CS). *C. callisema* KU 8830 (11), 8836 (9CS), 8842 (28:11CS), 19653 (24); TU 26173 (17). *C. callistia* KU 5293 (1), 8777 (2), 16900 (10), 18848 (14:11CS), 18888 (20), 19697 (15), 20166 (12CS), 20265 (3), 20282 (2), 20483 (36). *C. callitaenia* AUM

6828 (8); KU 8809 (23), 19232 (10:5CS); TU 23637 (42), 92770 (9:11CS). *C. camura* KU 12112 (2CS), 12215 (15), 12231 (9), 16019 (14CS), 15734 (10), 15792 (10CS), 19715 (3CS), 20591 (20); LACM 39815-1 (10CS). *C. chloristia* KU 5267 (1), 5274 (4), 8882 (15:12CS), 8894 (2), 20041 (13CS); TU 28224 (5). *C. formosa* ASU 64-0820 (4); KU 8307 (47), 8399 (42:15CS), 8391 (15CS). *C. galactura* KU 10937 (10), 10882 (50), 10839 (49), 9512 (9), 7866 (9), 11225 (9), 5205 (2), 7727 (7), 7765 (15), 9512 (9CS), 16461 (2CS), 9512 (19), 19732 (13), 10882 (50), 14966 (14), 16461 (2), 19732 (13), 12029 (12CS). *C. garmani* FMNH 4368 (30); KU 5416 (17:8CS), 20164 (51:10CS). *C. gibbsi* KU 8790 (44), 15331 (10), 16904 (10), 18892 (3:12CS), 20266 (25), 20284 (152), 20472 (38), 20285 (47); TU 40670 (32). *C. leedsii* KU 18985 (13CS); UAIC 3127.01 (6); UF 8515 (15), 14535 (12), 29099 (30). *C. lepida* TNHC 5279 (63), 5634 (2), 7572 (50); TU 55189 (5:10CS); WJM 375 (13). *C. lutrensis* KU 8388 (72), 10451 (5CS), 15595 (274), 17293 (9), 17297 (10), 18779 (50), 19431 (8CS), 20592 (147); LACM 39833-1 (8CS); TNHC 1400 (15). *C. nivea* INHS 76888 (8CS); KU 5353 (1), 8883 (14), 18987 (3:12CS); TU 29483 (6), 38616 (3). *C. ornata* ASU 9629 (6); INHS 84079 (10); KU 4997 (45:10CS), 8405 (29:6CS). *C. panarcys* ASU 64-0853 (6); KU 4991 (5), 5404 (4), 5439 (3); TNHC 4341 (33); UMMZ 208212 (14CS). *C.*

- proserpina* ASU 3600 (5); KU 18852 (15:10CS); TNHC 3262 (10:10CS), 9771 (170). *C. pyrrhomelas* INHS 76839 (4:16CS), 76978 (3CS); KU 5276 (21), 18989 (15); UAIC 2550.05 (10). *C. rutila* ASU 5982 (5:9CS), 64-0264 (12:10CS), 64-0913 (5); KU 7347 (64). *C. spiloptera* KU 8628 (87), 3595 (17), 10088 (11), 10353 (50), 10599 (8), 11356 (17:3CS), 14561 (6CS), 17776 (10CS); LACM 39819-1 (10CS). *C. trichroistia* KU 5292 (4), 18853 (10CS), 20450 (31); LACM 39851-1 (12CS); UAIC 5550.04 (84), 5526.04 (36), 5528.04 (148), 5557.04 (290), 5554.06 (238), 5551.04 (199), 5559.03 (237), 5559.07 (340), 5527.06 (190), 5556.06 (562), 5525.02 (41), 5534.06 (242), 5536.06 (349), 5532.05 (203). *C. venusta* KU 8800 (118), 8810 (10CS), 9413 (115), 9570 (89), 16318 (227), 17835 (28), 17869 (9), 17591 (27), 19674 (2), 19698 (57); LACM 39831-1 (10CS); RDS 3374 (1CS), 3375 (1CS). *C. whipplei* KU 9040 (37), 11357 (40), 14211 (15CS); LACM 39820-2 (10CS). *C. xaenura* KU 8823 (8), 18994 (3:12CS), 19655 (8CS); TU 29458 (3). *C. xanthicara* ASU 3642 (18:9CS), 5102 (6); INHS 84062 (2CS); UMMZ 179205 (25), 179827 (15), 179878 (6). *Cyprinus carpio* KU 12440 (1CS). *Dionda episcopa* INHS 83145 (15CS); KU 7427 (5:7CS), 16891 (5CS). *D. ipni* INHS 75342 (3), 75359 (3), 75369 (7). *Ericymba buccata* KU 17764 (4:8CS). *Erimystax cahni* KU 19614 (3CS); REJ 737 (2). *E. dissimilis* KU 15159 (1CS), 17235 (3CS); REJ 552 (2). *E. insignis* INHS 83108 (1:9CS); REJ 916 (20). *E. monacha* KU 19615 (9CS); KFW 1102 (32); NB 783 (3); REJ uncat. (10); UL 7712 (19); UT 44.1031 (2CS). *E. x-punctata* KU 2583 (3), 11279 (7), 16385 (1CS), 18439 (6CS). *Exoglossum laurae* KU 18922 (2CS), 18923 (5CS). *E. maxillingua* KU 18925 (3:12CS). *Extrarius aestivalis* KU 9654 (1), 2311 (10), 12110 (8CS), 14217 (10), 17035 (2CS). *Gila atraria* KU 11922 (1CS). *G. caerulea* KU 18904 (15CS). *G. conspersa* INHS 75307 (12CS). *G. copei* KU 11819 (1CS). *G. orcutti* INHS 76640 (19). *G. robusta* KU 3249 (5). *Hemitrema flammea* KU 18884 (10CS), 18931 (14). *Hesperoleucus symmetricus* KU 18917 (15CS). *Hybognathus nuchalis* KU 14123 (1CS). *H. placitus* KU 9766 (5CS), 12597 (3CS). *Hybopsis alborus* INHS 75078 (6CS); KU 18973 (2:10CS). *H. amblops* KU 6318 (10CS), 16556 (6CS); TU 25401 (2CS). *H. amnis* KU 18847 (10CS); TU 34008 (2CS). *H. bifrenatus* KU 18977 (12CS). *H. boucardi* TU 55376 (3CS); UMMZ 191686 (7:8CS). *H. calientis* RDS 3408 (2CS); TU 30695 (5:15CS). *H. dorsalis* KU 4670 (98), 5382 (47), 12223 (111), 16132 (103), 16237 (15CS). *H. hypsinotus* KU 18968 (8CS), 20034 (4CS); REJ 1113 (1); REJ uncat. (20). *H. labrosa* KU 10922 (37); INHS 88319 (4:6CS); KU 20035 (2CS). *H. sp. cf. labrosa* KU 20037 (3CS). *H. lineapunctata* KU 18885 (2:8CS). *H. longirostris* KU 16871 (109), 17965 (10:15CS); LACM 39853-1 (10CS); RDS 3272 (1CS). *H. rubrifrons* KU 8829 (1:8CS); TU 26159 (2CS). *H. sabiniae* KU 6237 (32:10CS), 9480 (24), 19673 (6). *H. winchelli* KU 16896 (25); TU 3031 (2CS), 39705 (2CS); RDS 3384 (1CS). *H. zanema* INHS 76841 (6CS), 88320 (15CS); KU 20036 (4CS). *Iotichthys phlegethontis* KU 11935 (5CS). *Lepidomeda mollispinis* KU 11937 (3CS). *Luxilus albeolus* INHS 27231 (5:15CS); KU 3266 (5), 18972 (10); UAIC 4144.04 (58). *L. cardinalis* KU 12295 (48), 14418 (147), 15015 (85), 15281 (13CS), 16247 (16), 20737 (23), 20963 (1). *L. cerasinus* INHS 83520 (1); KU 3281 (26:14CS); UAIC 4144.07 (147). *L. chrysocephalus* KU 7868 (113), 12654 (10CS), 18440 (1); LACM 39808-1 (5CS). *L. coccogenis* INHS 75417 (1), 79254 (4CS); KU 8898 (7CS), 11468 (15CS), 12020 (26); UAIC 6238.05 (26). *L. cornutus* KU 4035 (9CS), 7296 (26), 8686 (11CS), 12942 (38); LACM 39844-1 (3CS). *L. pilsbryi* KU 13009 (5CS). *L. zonatus* KU 12648 (123:10CS), 21197 (1CS). *L. zonistius* INHS 75135 (15CS); KU 18995 (5:10CS); UAIC 2553.03 (111). *Lythrurus ardens* KU 4136 (27:15CS), 5718 (40), 11557 (7); UAIC 5115.02 (3). *L. atrapiculus* KU 18887 (10CS), 18976 (3CS). *L. bellus* KU 14511 (15CS), 17377 (18); LACM 39811-1 (10CS). *L. fumeus* INHS 87307 (10CS); KU 6244 (8CS). *L. lirus* INHS 75410 (20); KU 18933 (15CS), 18986 (15); UAIC

- 647.07 (18), 653.05 (16), 4757.08 (14). *L. roseipinnis* KU 16857 (63:12CS), 16909 (50). *L. umbratilis* KU 7790 (78), 9547 (4CS), 11275 (28), 15521 (15CS), 15550 (32), 15736 (9). *Macrhybopsis gelida* KU 6862 (1), 9687 (2CS), 8111 (1CS), 1888 (2CS), 17360 (5), 19775 (1CS). *M. meeki* KU 7326 (1CS), 9688 (3CS). *M. storeriana* KU 2173 (4CS), 12104 (5CS), 12126 (1CS), 14218 (14), 19896 (8CS); TU 42770 (2CS), 45301 (2CS). *Nocomis biguttatus* KU 7295 (21). *N. effusus* KU 18932 (10CS). *N. leptocephalus* KU 12740 (1CS), 18858 (3:9CS). *N. platyrhynchus* KU 18926 (15CS). *N. raneyi* INHS 74357 (5CS); KU 19616 (5:4CS). *Notemigonus crysoleucus* KU 1357 (2:4CS), 10775 (1CS), 13101 (4), 18938 (1CS), 19632 (4). *Notropis aguirrepequenoi* INHS 75330 (6CS); UMMZ 97399 (15:10CS). *N. altipinnis* INHS 86955 (6CS); KU 18974 (12CS), 19783 (10), 20040 (5CS); LACM 39837-1 (6CS), 39837-3 (4CS); TU 7343 (163). *N. amabilis* KU 6008 (35), 15444 (12), 17023 (15:15CS). *N. amoenus* INHS 77856 (5:15CS); KU 18975 (15), 19784 (2CS). *N. anogenus* UMMZ 183967 (5CS). *N. asperifrons* KU 18886 (11:20CS), 20165 (1); LACM 39843-1 (9CS); TU 32744 (29). *N. atherinoides* KU 4138 (7CS), 10996 (4), 16494 (7), 18935 (56:15CS); LACM 39836-1 (12CS); RDS 4471 (4CS). *N. atrocaudalis* INHS 76980 (8), 87782 (4); KU 6106 (2:12CS), 6073 (26), 6061 (4), 20195 (14). *N. baileyi* KU 14510 (15CS), 17375 (12); LACM 39849-1 (6CS). *N. bairdi* KU 18473 (166), 18474 (34:11CS). *N. blennioides* KU 5130 (1CS), 8242 (36), 9640 (22), 9665 (32), 16045 (15CS). *N. boops* KU 6169 (18CS), 14424 (115), 15873 (7), 19680 (10), 21195 (1); LACM 39820-1 (12CS), 39820-3 (3CS). *N. braytoni* TNHC 4457 (5:15CS); TU 87158 (15). *N. buccula* KU 14286 (8:12CS). *N. buechanani* KU 2313 (15), 3084 (4), 15031 (23). *N. candidus* KU 18889 (10:10CS); TU 80042 (8:12CS). *N. chalybaeus* KU 9405 (58:15CS), 9568 (46), 19689 (4); LACM 39822-1-6 (26CS), 39829-1 (10CS), 39855-1 (8CS). *N. chihuahua* KU 4999 (17CS), 8406 (17). *N. chiliticus* INHS 74150 (7); KU 16902 (10), 18981 (3:12CS); LACM 39847-2 (10CS). *N. chlorocephalus* INHS 75049 (3:16CS); KU 18440 (1), 18982 (15). *N. chrosomus* KU 16903 (10), 18849 (10CS), 18890 (15); UAIC 2574.01 (8), 4946.07 (7). *N. cummingsae* KU 5258 (25:15CS); LACM 39832-1 (10CS); UAIC 1618.02 (111). *N. edwardraneyi* KU 18891 (16CS). *N. emiliae* KU 14316 (18), 18855 (15:10CS), 18984 (12CS); LACM 39835-2 (3CS); RDS 4471 (2CS). *N. girardi* KU 3245 (127), 3959 (124), 8039 (14CS), 8572 (174). *N. greenei* KU 10085 (114), 10766 (3), 12986 (15CS). *N. harperi* KU 16849 (18), 19690 (1CS); LACM 39812-1 (12CS); TU 2316 (3:12CS), 38202 (2CS); UAIC 941.08 (37). *N. heterodon* KU 4590 (43), 10320 (1), 14255 (15CS); LACM 39850-1 (6CS). *N. heterolepis* KU 3436 (17), 11296 (14CS), 12275 (3), 18626 (12). *N. hubbsi* KU 19039 (2CS), 19350 (6CS). *N. hudsonius* KU 14257 (15CS), 20042 (4CS). *N. hypsilepis* KU 8807 (7:3CS); LACM 39845-1 (7CS); UAIC 1235.04 (35). *N. jemezianus* KU 8066 (14:12CS), 8073 (88), 8364 (10); TU 11334 (85). *N. leuciodus* KU 12022 (1), 18850 (10CS); LACM 39809-1 (10CS); UAIC 5998.05 (27), 6000.04 (7). *N. lutipinnis* KU 5314 (15CS); LACM 39818-1 (14CS), 39851-1 (2CS), 39852-2 (2CS), 39852-3 (2CS). *N. maculatus* KU 15511 (13:12CS), 16906 (25); LACM 39846-1 (10CS); UAIC 1599.01 (93). *N. mekistocholas* KU 20043 (1CS). *N. nazas* INHS 84099 (5:15CS). *N. nubilus* KU 7286 (14CS), 17189 (14), 19089 (16). *N. ortenburgeri* KU 12962 (5:10CS). *N. oxyrhynchus* KU 2316 (32), 6028 (3:15CS), 14288 (9); TU 19687 (8), 20228 (13). *N. ozarcanus* KU 7664 (9CS), 7725 (28), 12656 (9), 15163 (16). *N. perpallidus* INHS 81047 (6CS). *N. petersoni* KU 14072 (56), 17161 (131:15CS), 17886 (9); LACM 39825-1 (2CS), 39825-2 (8CS), 39838-1 (10CS), 39841-1 (6CS). *N. photogenis* INHS 77121 (5:15CS); KU 5805 (6). *N. potteri* KU 14222 (302:20CS); LACM 39839-1 (10CS). *N. procne* INHS 77857 (5:15CS); KU 16907 (5), 18877 (25). *N. rubellus* KU 7888 (53), 11030 (15CS), 12086 (35), 21196 (3); LACM 39834-1 (9CS), 39835-1 (5CS). *N. rubricroceus* KU 3290 (7CS); UAIC 5990.01 (10). *N. saladonis* FMNH 62160 (11). *N. scab-*

riceps KU 16911 (5), 18862 (2:13CS), 18990 (5:10CS). *N. szepticus* INHS 76886 (18CS); KU 5268 (6); LACM 39837-2 (10CS). *N. semperasper* INHS 27260 (4CS); KU 18992 (1:9CS), 19617 (4CS). *N. shumardi* KU 9623 (4), 14290 (14CS). *N. simus* KU 8067 (57:16CS); UMMZ 125064 (4CS). *N. spectrunculus* KU 5473 (9CS); TU 29229 (5), 32807 (69); UAIC 2557.06 (8). *N. sp. cf. spectrunculus* SIUC 3536. (2); UAIC 2973.14 (48). *N. stilbius* KU 8770 (6:10CS), 16912 (5). *N. stramineus* KU 8582 (233), 12288 (17), 19011 (7CS), 21073 (12CS). *N. telescopus* KU 11505 (1), 12653 (54), 15231 (19CS). *N. texanus* KU 9612 (34), 17977 (69:15CS); LACM39826-1 (3CS), 39826-2 (8CS), 39840-1 (6CS); RDS 4471 (3CS). *N. topeka* KU 4198 (50), 18682 (19), 12289 (17), 13136 (7), 18759 (6), 19033 (15CS); UMMZ 163223 (1). *N. tropicus* TU 43597 (3:12CS). *N. uranoscopus* KU 18894 (18CS); TU 29893 (93). *N. volucellus* KU 8456 (33), 9462 (16), 17025 (16CS); RDS 4471 (6CS). *N. xaenocephalus* KU 18854 (10:10CS), 18896 (20); LACM39830-1 (2CS), 39830-2 (8CS), 39848-1 (10CS); TU 25956 (11). *Oregonichthys crameri* KU 18905 (3CS), 18906 (4CS), 18907 (3CS). *Phenacobius catostomus* KU 18897 (7CS), 18898 (5CS); REJ uncat. (2). *P. crassilabrum* KU 19618 (2CS); REJ 466 (2). *P. mirabilis* KU 7918 (5CS), 15151 (3CS), 16387 (1CS). *P. teretulus* KU

18929 (11:6CS), 18930 (2); REJ 971 (1); NB 746 (1). *P. uranops* KU 19619 (2CS); REJ 982 (2). *Phoxinus cumberlandensis* KU 18934 (8CS). *P. eos* KU 12255 (10CS). *P. erythrogaster* KU 5539 (36), 13198 (3CS). *P. neogaeus* KU 18882 (12CS). *P. oreas* KU 3259 (6CS), 3275 (14). *Pimephales notatus* KU 8003 (5CS), 12579 (3CS). *P. promelas* KU 12106 (4CS). *P. tenellus* KU 12127 (1CS). *P. vigilax* KU 16388 (1CS). *Plagopterus argentissimus* KU 11932 (3CS). *Platygobio gracilis* KU 3409 (5CS), 8351 (13CS), 11950 (1CS), 14595 (35), 17146 (5CS). *Pteronotropis euryzonus* KU 19233 (10CS). *P. hypselopterus* KU 16905 (10), 17401 (10CS), 19691 (5); LACM39814-1 (12CS). *P. signipinnis* KU 16858 (59:15CS). *P. welaka* INHS 79413 (5:15CS); KU 16913 (5CS), 18895 (10CS); LACM39817-1 (10CS); TU 25785 (368). *Ptychocheilus grandis* KU 18920 (12CS). *P. umpquae* KU 18908 (2:8CS). *Rhinichthys atratulus* KU 2779 (6), 4145 (2). *R. cataractae* KU 11845 (16), 12264 (21). *R. evermanni* KU 18910 (15CS). *R. falcatus* KU 18911 (3CS), 18912 (8CS). *Richardsonius egregius* KU 11788 (3CS), 12442 (23). *Semotilus atromaculatus* KU 12094 (3CS), 12442 (23), 12094 (3), 16527 (6), 18921 (2CS). *S. corporalis* KU 18856 (10CS). *S. margarita* INHS 83643 (5CS), 19000 (10CS). *Yuriria alta* INHS 75315 (20CS).

MONOPHYLY OF *CYPRINELLA* AND RELATIONSHIPS TO OTHER NORTH AMERICAN CYPRINIDS

Based on results of this study and those of Coburn (1982, 1983), many eastern North American cyprinids belong to a single monophyletic group, all sharing the derived character of an open posterior myodome (Fig. 1, Suite 1). The genus *Cyprinella* is embedded in this clade. Within this large group of cyprinids with an open myodome is a large polytomy of species and monophyletic groups. Included are species of *Notropis* (except *Azteculea sallei*), and the genera *Cyprinella*, *Luxilus*, *Lythrurus*, *Pteronotropis*, *Oregonichthys*, *Clinostomus*, *Richardsonius*, *Yuriria*, and three

other large monophyletic groups (Fig. 1). One clade (Fig. 1, Suite 2) includes the genera *Hybognathus*, *Exoglossum*, *Dionda*, *Campostoma*, *Nocomis*, *Platygobio*, *Macrhybopsis*, *Extrarius*, *Phenacobius*, and *Erimystax* (Figs. 1–3). A second clade (Fig. 1, Suite 4) includes species of the genus *Hybopsis*, *Ericymba buccata*, and species previously referred to *Notropis*: *H. boucardi*, *H. calientis*, *H. dorsalis*, *H. longirostris*, *H. sabiniae*, *H. alborus*, and *H. bifrenatus* (Figs. 1, 4). The third clade (Fig. 1, Suite 5) includes the genera *Pteronotropis*, *Cyprinella*, *Luxilus*, *Lythrurus*,

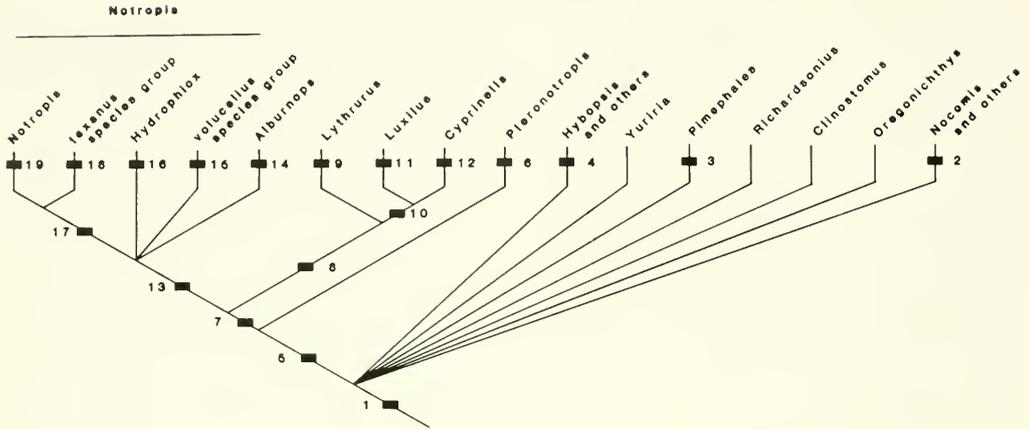


Fig. 1. Hypothesized phylogenetic relationships of North American cyprinids with an open posterior myodome. Other cyprinids examined in this study are not included in this clade. Numbered characters suites are discussed in text.

and *Notropis*. Within this third clade, the genus *Pteronotropis* forms the sister group to the remaining species and species groups (Fig. 1, Suite 7). Above *Pteronotropis*, a clade composed of the genera *Lythrurus*, *Luxilus*, and *Cyprinella* forms the sister group to the *Notropis* clade, composed here of four major groups whose interrelationships are unresolved at this time. These groups include the subgenus *Al-*

burnops (Fig. 5), the *Notropis volucellus* species group (Fig. 6), the subgenus *Hydrophlox*, and a monophyletic group inclusive of the subgenus *Notropis* and the *Notropis texanus* species group.

Species of uncertain relationships and involved in this multichotomy between character Suites 1 and 5 in Fig. 1, but not illustrated are *Notropis topeka*, *N. atrocaudalis*, *N.*

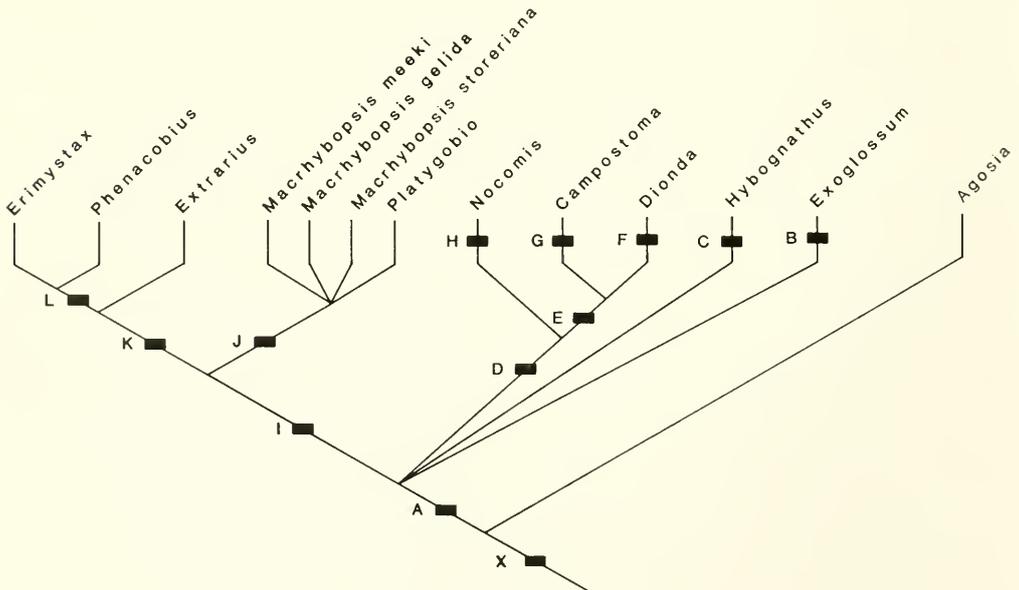


Fig. 2. Hypothesized phylogenetic relationships of North American chubs defined by suite 2 in Figure 1. Lettered character suites are discussed in text.

stramineus, *N. chihuahua*, *N. procne*, and *N. mekistocholas*. All of these species have an open myodome, but lack the derived characters for stem 5 (Suite 5).

Justifications for these particular statements of relationship and the numbered character suites presented in Fig. 1 are outlined below. Because European and some North American species were not included in the present study, and because these results and those of Coburn (1982, 1983) represent some of the first attempts at revealing higher relationships of these cyprinids, only a few formal taxonomic changes are proposed. However, in some cases the existing classification is a poor representation of our knowledge of cyprinid interrelationships, and necessitates change. For example, the obviously unnatural genera *Notropis* and *Hybopsis* are each broken up into separate genera, elevating subgeneric names to generic level. Relationships of some species of *Notropis* remain problematical. For now, these species are retained in "*Notropis*" but with unknown affinities.

CYPRINIDS WITH AN OPEN POSTERIOR MYODOME

(FIG. 1, SUITE 1).

The open floor of the posterior myodome (Fig. 7), first noted and discussed by Coburn (1982, 1983), is unique to this group of cyprinids and is considered a synapomorphy of these species. The opening is oval to elongate and slitlike and is bounded by both the parasphenoid and basioccipital. Most species of this group have the opening as juveniles and adults. However, in the genera *Nocomis*, *Campostoma*, and *Dionda* and in the species *Platygobio gracilis*, *Hybopsis boucardi*, and *H. bifrenatus* the opening exists only in juveniles and is fused shut in adults (Fig. 8). Only occasionally will an adult of these species retain the opening. The secondary closure of this opening is considered derived, occurring independently in *Platygobio*, *Hybopsis boucardi*, *H. bifrenatus*, and the *Nocomis-Campostoma-Dionda* clade. Other North American cyprinids examined apparently never develop this opening in the posterior myodome as juveniles or adults (Fig. 7A).

A similar opening in the posterior myod-

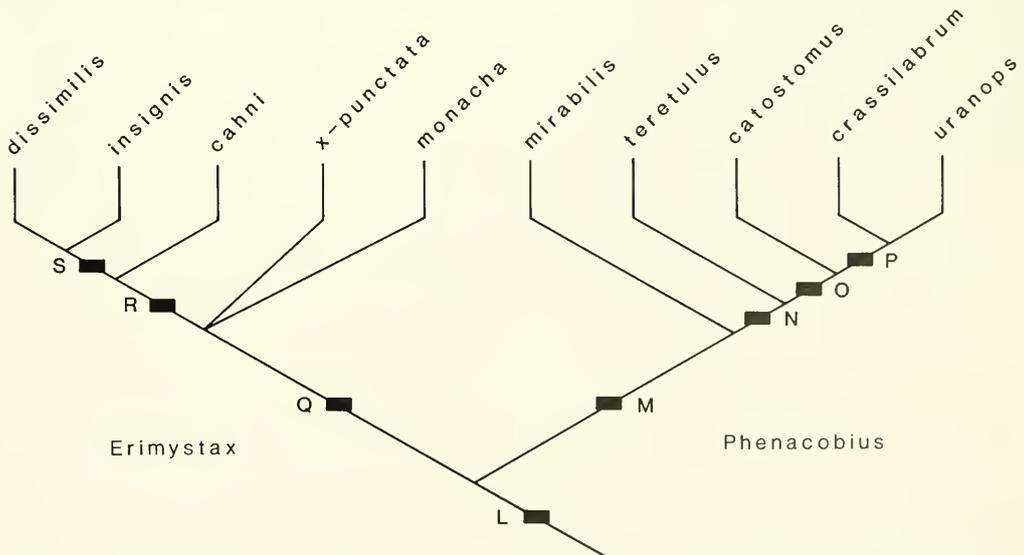


Fig. 3. Hypothesized phylogenetic relationships of species in the North American chub genera *Erimystax* and *Phenacobius*. Lettered character suites are discussed in text. Suite L corresponds to L in Figure 2.

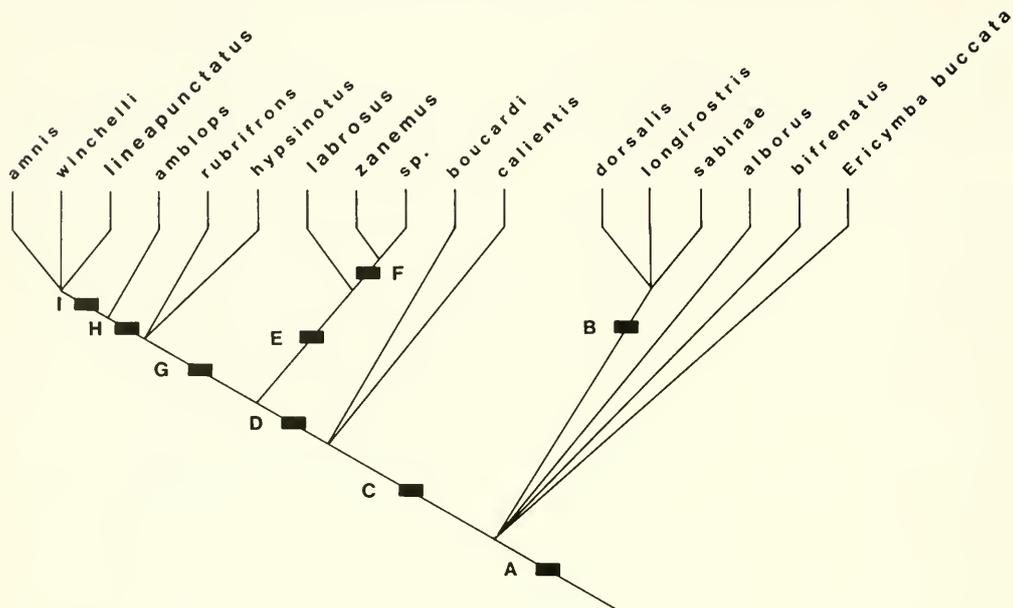


Fig. 4. Hypothesized phylogenetic relationships of species in the North American genus *Hybopsis* and the related genus *Ericymba*. Lettered character suites are discussed in text. This clade corresponds to group defined by suite 4 in Figure 1.

ome was noted by Howes (1980) for the baril-
ine group of minnows. The open condition ob-
served by Howes (1980: figs. 21, 22, 23), how-

ever, does not appear to be homologous with
that found in the clade of eastern North Ameri-
can minnows. In barilene cyprinids the open-

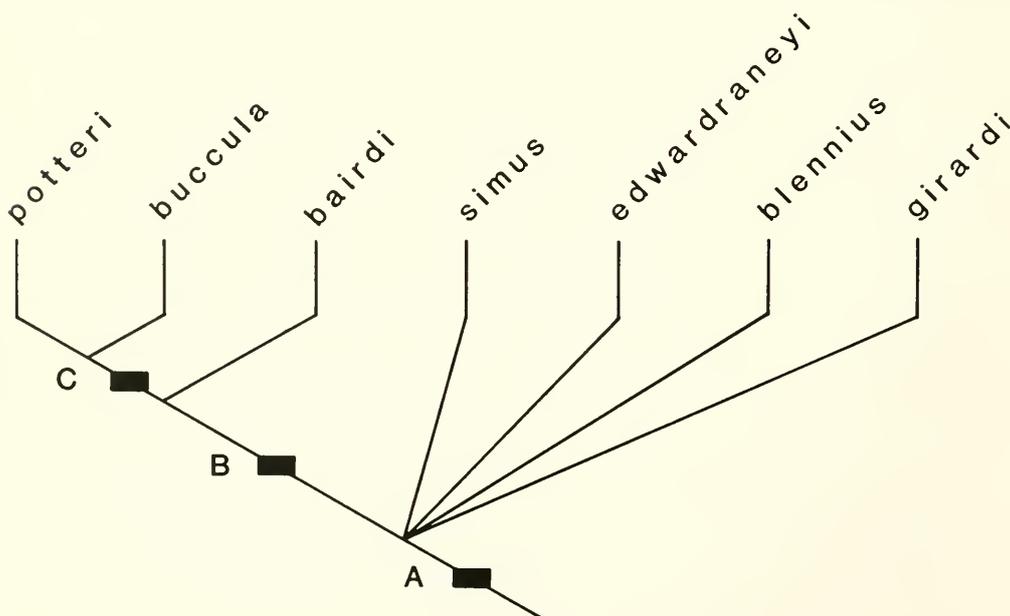


Fig. 5. Hypothesized phylogenetic relationships of shiner species in the subgenus *Alburnops* (genus *Notropis*). Lettered character suites are discussed in text.

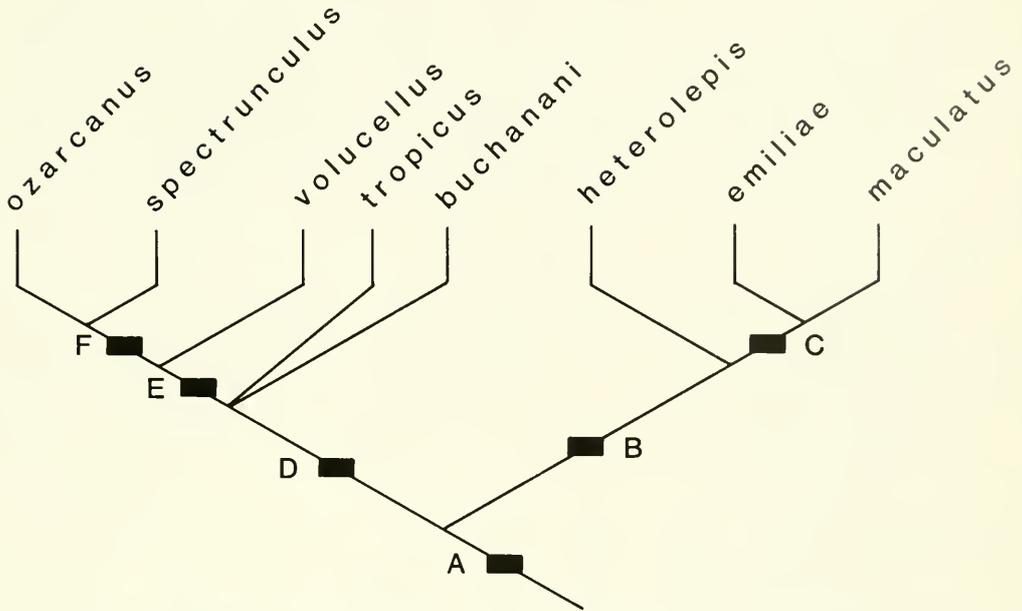


Fig. 6. Hypothesized phylogenetic relationships of minnows in the *Notropis volucellus* species group. Lettered character suites are discussed in text.

ing is located posteriorly in the myodome and is not bounded by the basioccipital posteriorly. The opening is only contained anteriorly by the parasphenoid. In the eastern North American cyprinids with the opening in the posterior

myodome the opening is located centrally in the floor of the myodome and is bounded both by the basioccipital posteriorly and parasphenoid anteriorly.

Chub clade (Fig. 1, Suite 2). Included in

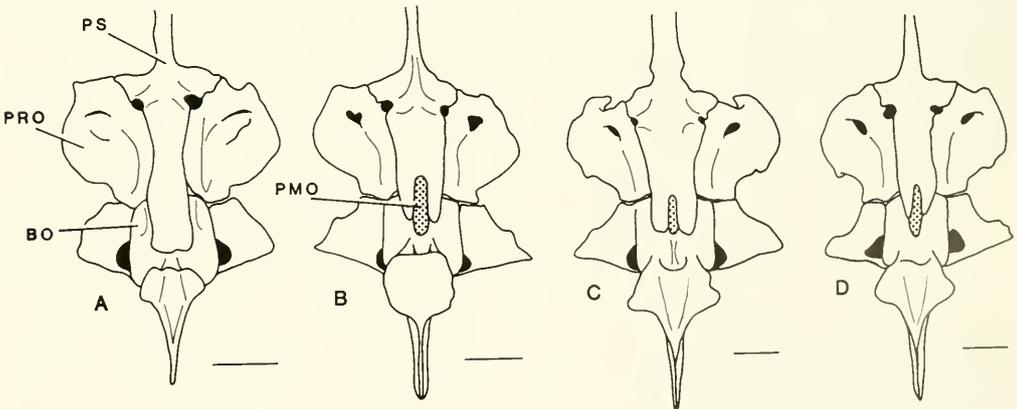


Fig. 7. Basicranial region in some North American cyprinids illustrating open posterior myodome in some taxa. A) *Iotichthys phlegathantis*, 33 mm, KU 11935. B) *Pimephales notatus*, 43 mm, KU 8003. C) *Macrhybopsis storeriana*, 48 mm, KU 12104. D) *Cyprinella galactura*, 57 mm, KU 12029. Open posterior myodome designated by stippled pattern. Horizontal bar equals 1 mm.

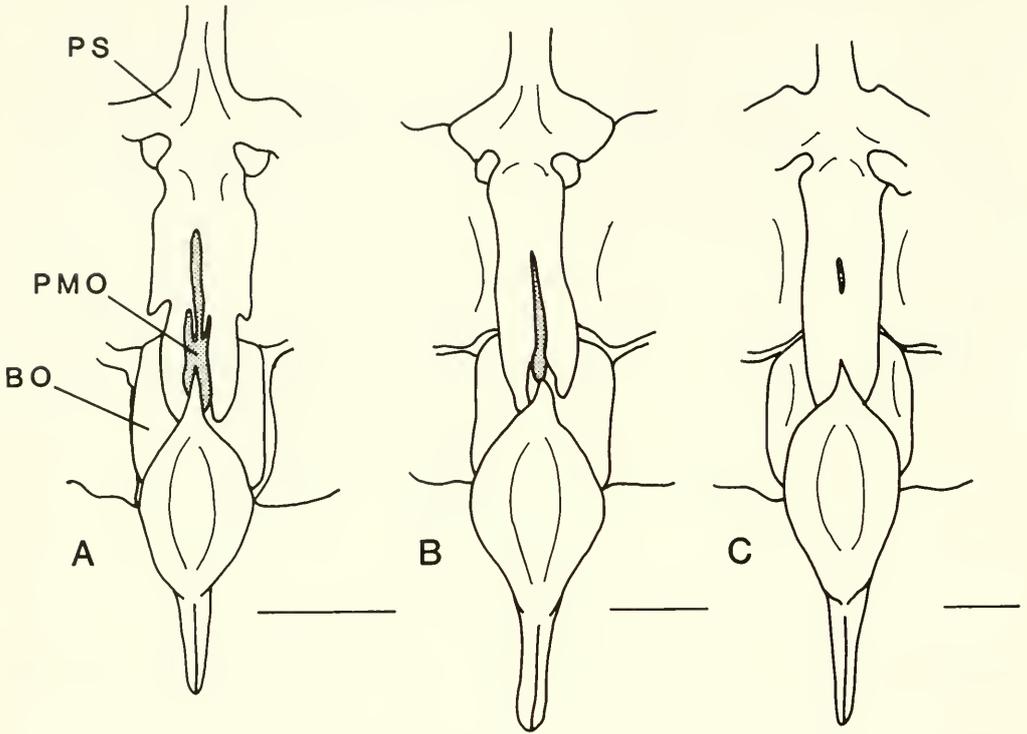


Fig. 8. Developmental closure of the open posterior myodome in *Campostoma anomalum*. A) 26 mm, KU 3946. B) 43 mm, KU 3946. C) 70 mm, KU 13200. Distribution of opening in posterior myodome designated by stippled pattern. Horizontal bar equals 1 mm.

this group are the genera and species *Agosia*, *Hybognathus*, *Exoglossum*, *Nocomis*, *Campostoma*, *Dionda*, *Platygobio*, *Macrhybopsis meeki*, *M. gelida*, *M. storeriana*, *Extrarius aestivalis*, *Phenacobius*, and *Erimystax* (Fig. 2). All of these species share two derived characters of the palatine and one of the urohyal. Three types of maxillary processes of the palatine were noted among the cyprinids examined. In the primitive condition the maxillary process is directed laterally, perpendicular to the anteroposterior axis of the palatine (Fig. 10E); this morphology occurs in most species with an open myodome and in all outgroups. In the species listed above the maxillary process of the palatine is elongate, straight, and directed anteriorly (Fig. 9A–T).

The second derived characteristic of the palatine for the chub clade involves the anteromesial socket for articulation with the

preethmoid. The primitive preethmoid-palatine articular surface on the palatine is a simple and well-developed socket developed anteromesially (Fig. 10A, B) into which fits the preethmoids. In the chub clade, the articular surface is a groove that extends anteroventrally to posterodorsally. It is unrestricted both anteriorly and posteriorly (Fig. 9A–T).

Primitively the horizontal plate of the urohyal is forked posteriorly (Fig. 11A). In all taxa of the chub clade the posterior margin of the urohyal is oval and smooth (Fig. 11E–H).

Two derived characters support the monophyly of all members of this chub clade, exclusive of *Agosia* (Fig. 2, Suite A). In all species except *Agosia*, the endopterygoid and metapterygoid are laterally convex (Fig. 12A). The laterally convex endopterygoid and metapterygoid are unique to this group of cyprinids. In all outgroups examined these bones

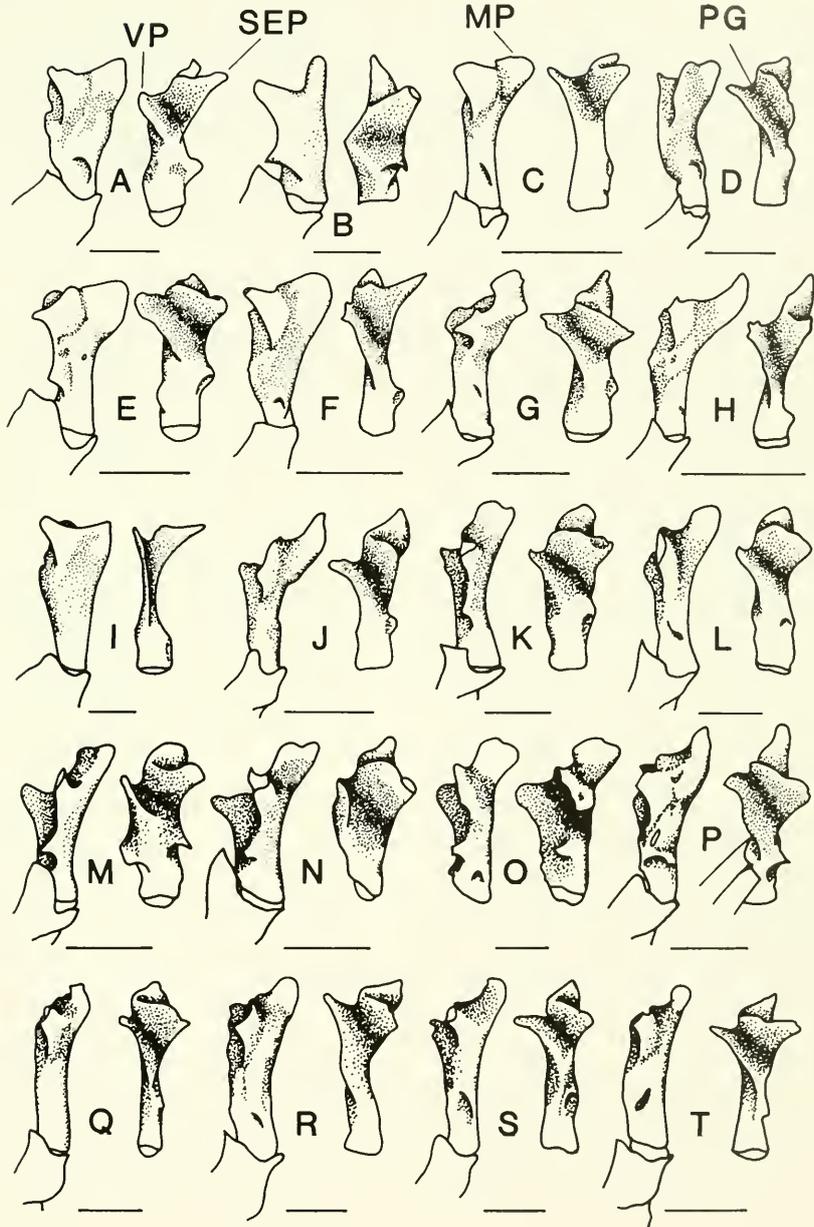


Fig. 9. Dorsal (left) and mesial (right) views of palatines of some North American cyprinids with a derived anterior preethmoid articular morphology. Up is anterior. A) *Agosia chrysoaster*, 65 mm, KU 8084. B) *Exoglossum laurae*, 56 mm, KU 18922. C) *Nocomis effusus*, 36 mm, KU 18932. D) *Campostoma anomalum*, 64 mm, KU 13200. E) *Aztecula sallei*, 56 mm, UMMZ 191695. F) *Hybognathus placitus*, 51 mm, KU 12597. G) *Dionda episcopa*, 57 mm, KU 16891. H) *Extrarius aestivalis*, 32 mm, KU 12110. I) *Platygobio gracilis*, 75 mm, KU 17146. J) *Macrhybopsis storeriana*, 46 mm, KU 12104. K) *Phenacobius mirabilis*, 61 mm, KU 16387. L) *P. teretulus*, 68 mm, KU 18929. M) *P. catostomus*, 55 mm, KU 18897. N) *P. crassilabrum*, 53 mm, KU 19618. O) *P. uranops*, 86 mm, KU 19619. P) *Erimystax monacha*, 66 mm, UT 44.1031. Q) *E. cahni*, 61 mm, KU 19614. R) *E. x-punctata*, 70 mm, KU 16385. S) *E. insignis*, 73 mm, INHS 83108. T) *E. dissimilis*, 55 mm, KU 17235. Horizontal bar equals 1 mm.

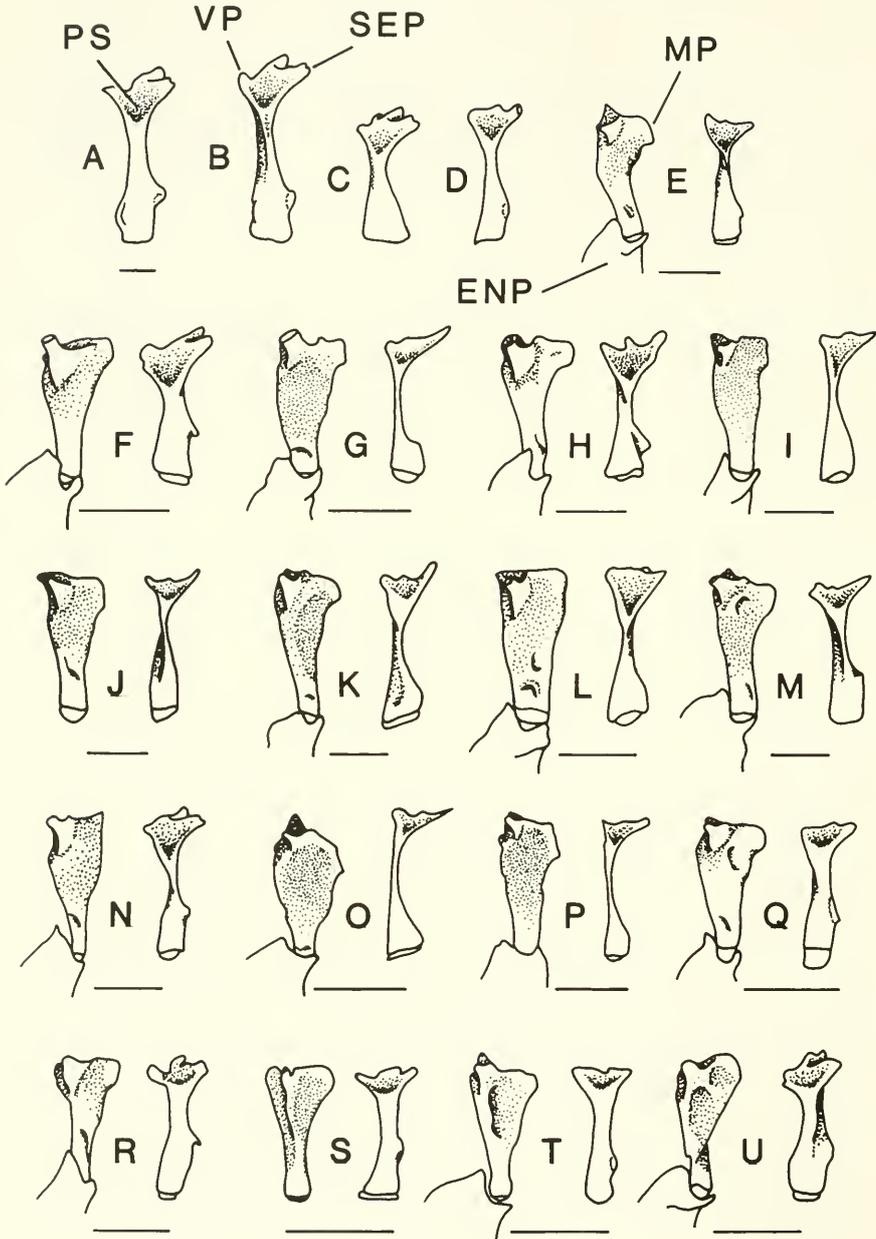


Fig. 10. Morphological variation in palatines of some North American cyprinids. Up is anterior. A) *Notropis potteri* (medial view), 50 mm, KU 14222. B) *N. bairdi* (medial view), 54 mm, KU 18474. C) *N. chihuahua*, 51 mm, KU 8406. D) *N. leuciodus*, 62 mm, KU 18850. E) Dorsal (left) and medial (right) views of palatine of *N. boops*, 56 mm, KU 6169. F) *N. braytoni*, 47 mm, TNHC 4457. G) *N. shurnardi*, 52 mm, KU 14290. H) *N. candidus*, 68 mm, KU 18889. I) *N. stilbius*, 57 mm, KU 8770. J) *N. photogenis*, 63 mm, INHS 77121. K) *N. scabriceps*, 67 mm, KU 18862. L) *N. amoenus*, 60 mm, INHS 77856. M) *N. szepticus*, 65 mm, INHS 76886. N) *N. hypselepis*, 53 mm, KU 8807. O) *N. jemezianus*, 48 mm, KU 8066. P) *N. oxyrhynchus*, 46 mm, KU 6028. Q) *N. altipinnis*, 45 mm, KU 18974. R) *Pteronotropis signipinnis*, 50 mm, KU 16858. S) *P. eurizonus*, 48 mm, KU 19233. T) *P. hypselopterus*, 45 mm, KU 17401. U) *P. pelaka*, 50 mm, KU 18895. Horizontal bar beneath A is 1 mm for A–D. Bars beneath other species represent 1 mm.

are strongly concave laterally, being dished-out posterior to the palatine-metapterygoid articulation. The second derived feature of this clade, exclusive of *Agosia*, is the elongate maxillary process of the palatine. The process is short in *Agosia* (Fig. 9A) and long in other members (Fig. 9B). The elongation of the anteriorly directed maxillary process of the palatine is thus considered a further modification of the ancestral condition for the chub clade.

Above *Agosia* there are four monophyletic groups of unresolved relationships (Fig. 2, Suite A). Species of the genus *Hybognathus* (Fig. 2, Suite C) share an expanded pharyngeal process of the basioccipital not found in any other cyprinids (Fig. 13). Species of the genus *Exoglossum* (Fig. 2, Suite B) share a derived condition of the dentaries and palatines. In these two species the dentaries are very deep and twisted anteriorly such that the rami are horizontal and parallel (Fig. 14). The palatines of *Exoglossum* have a unique morphology. In these species a deep and wide supraethmoid process wraps around the preethmoids (Fig. 9B).

The clade inclusive of the genera *Nocomis*, *Campostoma*, and *Dionda* (Fig. 2, Suite D) all share the derived secondary closure of the opening in the posterior myodome (Fig. 8) and very large cephalic tubercles. The closure of the myodome is discussed above. The cephalic tubercles of these three genera are very large and erect (Lachner and Jenkins, 1971a, 1971b; Burr 1976) and are considered a synapomorphy of this group. All other cyprinids examined have small cephalic tubercles compared with these three genera.

The genera *Campostoma* and *Dionda* (Fig. 2, Suite E) share a reduced or absent ascending process condition on the premaxilla (Fig. 15), a coiled gut (Burr, 1976; Hubbs and Miller, 1978), and a derived pharyngeal pad on the basioccipital (Fig. 15). The reduced or absent ascending process on the premaxilla is apparently unique to this clade. All other cyprinids examined have an obvious ascending process. The coiled gut of these two genera is not

unique. Gut coiling also occurs in *Notropis nubilus* and *N. mekistocholas*, but the gut coiling is different in these taxa and, with reference to higher relationships (Fig. 1), gut coiling is independently evolved in these species. The pharyngeal pad of these two genera (Fig. 15) is oval and flattened and has an anteriorly directed process. Outgroups, except *Hybognathus*, typically have a triangular pad that is concave ventrally. Species of *Hybognathus* have the derived oval pharyngeal pad and anterior process (Fig. 13; Bailey and Allum, 1962), also supporting a close relationship of this genus to *Campostoma* and *Dionda*. Furthermore, the anterior margin of the pad of most outgroups is blunt, lacking any type of process. *Phoxinus erythrogaster*, *P. cumberlandensis*, and *P. oreas* have a small anterior process like that found in *Nocomis* and *Dionda*. Species of *Phoxinus*, however, lack an open posterior myodome.

The synapomorphies of *Nocomis* (Fig. 2, Suite H) and species relationships are presented by Mayden (1987). Synapomorphies for the genus *Campostoma* (Fig. 2, Suite G) include a coiled gut whose coils wrap around the gas bladder (Burr, 1976) and the loss of a supraethmoid process on the palatine (Fig. 9D). Species of the genus *Dionda* (Fig. 2, Suite F) share a tubercle pad on the subopercle that is developed only in breeding males. A similar, but convergent structure occurs in the *Phenacobius-Platygobio* lineage (see below). Because of the different locations of the pads in the two groups and morphological dissimilarities in the pads they are presently not considered homologous and are thus convergent.

The fourth lineage in the chub clade is one inclusive of the genera *Platygobio*, *Macrhybopsis*, *Extrarius*, *Erimystax*, and *Phenacobius* (Fig. 2, Suite I). These species all share: 1) a nuptial pad on the interopercle and preopercle unique to this group, 2) a short and triangular basihyal (Fig. 16H-I), 3) a single articular surface for the hyomandibular on the metapterygoid (Fig. 16E, F), and 4) enlarged sensory papillae on interradial membranes of the pectoral fin. Coburn (1983) noted the sec-

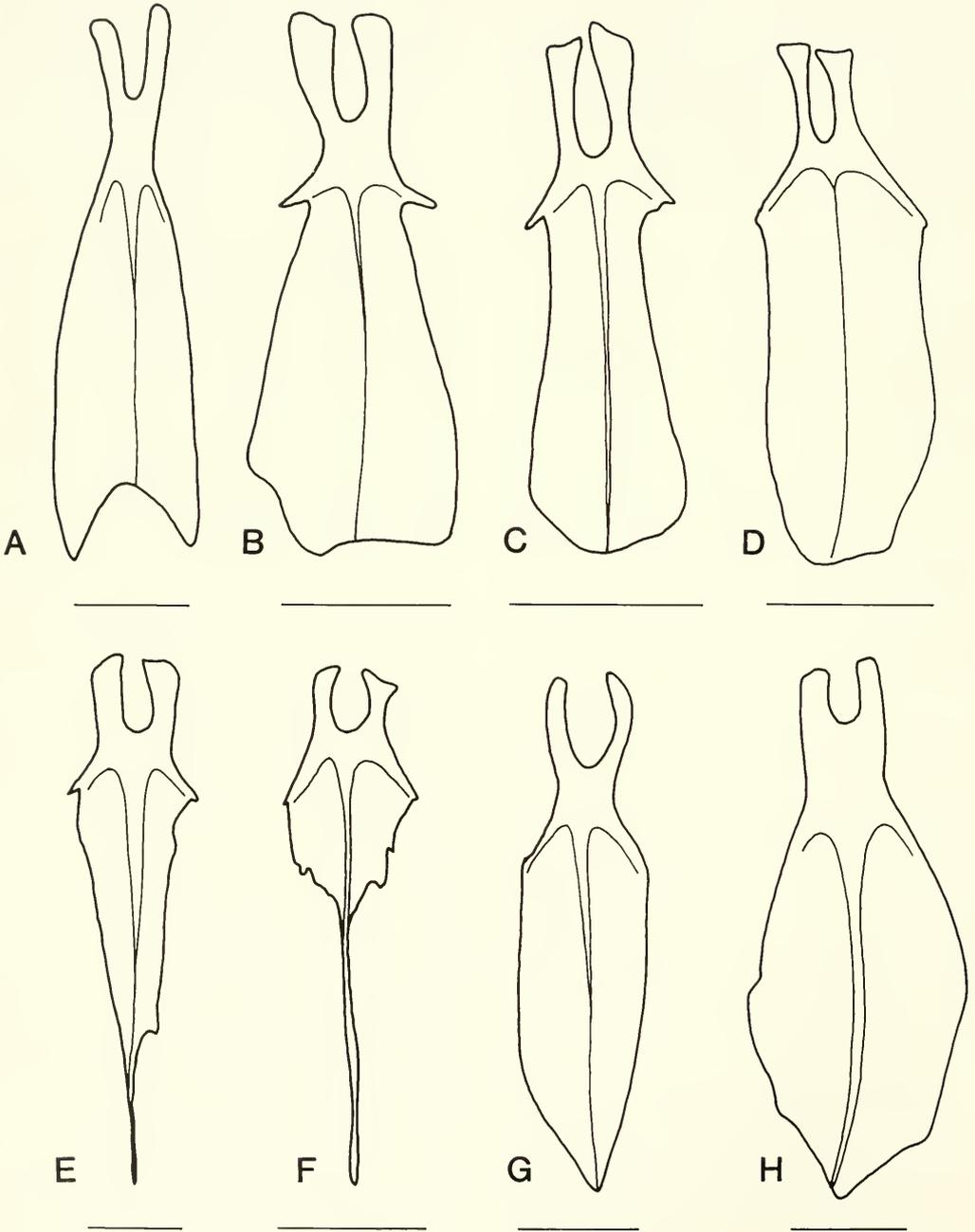


Fig. 11. Urohyals of some North American cyprinids. Up is anterior. A) *Clinostomus funduloides*, 60 mm, KU 10697. B) *Hybopsis amnis*, 52 mm, KU 18847. C) *H. winchelli*, 51 mm, TU 39705. D) *H. sabiniae*, 41 mm, KU 6237. E) *Macrhybopsis storeriana*, 94 mm, KU 12126. F) *M. meeki*, 56 mm, KU 9688. G) *Agosia chrysogaster*, 65 mm, KU 8084. H) *Campostoma oligolepis*, 85 mm, KU 12520. Horizontal bar equals 1 mm.

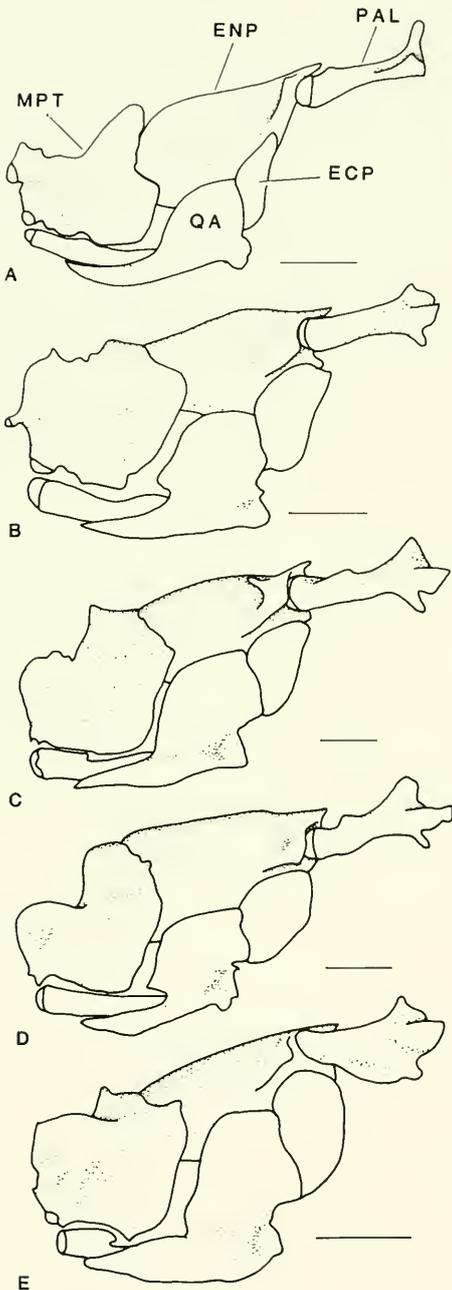


Fig. 12. Pterygoid series of some North American cyprinids illustrating concave (A) and convex (B-E) lateral surfaces of endopterygoid and metapterygoid bones. Right is anterior. A) *Notropis atherinoides*, 53 mm, KU 18935. B) *Nocomis raneyi*, 53 mm, KU 19616. C) *Erimystax insignis*, 73 mm, INHS 83108. D) *E. monacha*, 66 mm, UT 44.1031. E) *Phenacobius crassilabrum*, 53 mm, KU 19618. Horizontal bar equals 1 mm.

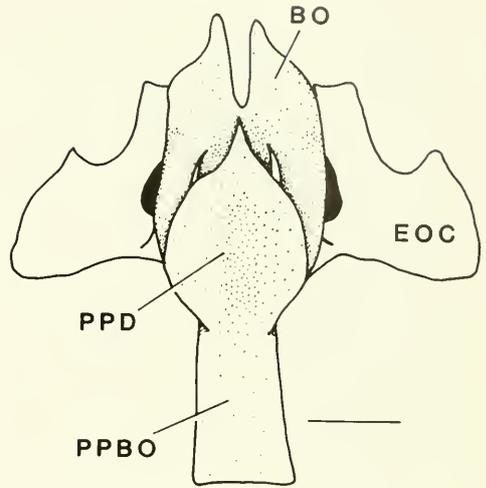


Fig. 13. Ventral view of basicranial region of *Hybognathus nuchalis* (49 mm, KU 14123) illustrating expanded pharyngeal process of basioccipital. Up is anterior. Horizontal bar equals 1 mm.

ond and third derived characters for this group and suggested other derived features in addition to these. In all outgroups the metapterygoid has a double articular surface with the hyomandibular, one posteriorly and one posteroventrally (Fig. 16A-C). The basihyal of most other cyprinids is elongate and narrow (Fig. 16G). The nuptial pad and sensory papillae in this group are unique. Interradial sensory papillae of the pectoral fins are small in outgroups.

Controversial in this group is the placement of *monacha* in the genus *Erimystax*. This species has also been closely allied to the genus *Cyprinella*. Some similarities do exist between *E. monacha* and some species of *Cyprinella* (see section below on Monophyly of *Cyprinella*). Whether or not these shared similarities are the result of common ancestry or convergence warrents further investigation. At present, I consider *monacha* to be a member of the genus *Erimystax*, based on the hypothesized synapomorphies listed above and below not only for *Erimystax*, but for the chub clade as a whole.

The *Macrhybopsis* and *Platygobio* clade (Fig. 2, Suite J) is supported by a single pigmentation character of the caudal fin and a

urohyal character. In all of these species the lower lobe of the caudal fin is darkly pigmented except for the lowermost ray which is depigmented. This color pattern is unique to these four species and is derived. In all of these species the ventral horizontal plate of the urohyal is strongly reduced to a very thin lamella (Fig. 11E, F). Primitively, this plate is well developed in cyprinids.

The genera *Extrarius*, *Phenacobius*, and *Erimystax* form a monophyletic group (Fig. 2, Suite K), all sharing the following derived features which were also noted earlier by Coburn (1983): 1) a heavy transverse process on the fourth Weberian rib, 2) a dentary with a high coronoid process and a short ventrally deflected

gnathic ramus (Fig. 17), 3) a short ascending arm on the preopercle and elongate horizontal arm, and 4) the mesial edge of pharyngobranchial 3 is notched. Outgroups and other members of the chub clade typically have a more delicate fourth Weberian rib, a short coronoid process and long gnathic ramus, subequal arms on the preopercle, and smooth mesial margin of pharyngobranchial 3.

The *Phenacobius-Erimystax* clade (Fig. 2, Suite L) is monophyletic, supported by five derived characters. Species of this clade all have 1) a narrow caudal skeleton (Fig. 18E, F), 2) a small flap of skin with taste buds, extending from beneath the anterior end of the lacrymal bone to the posterior ramus of the maxilla

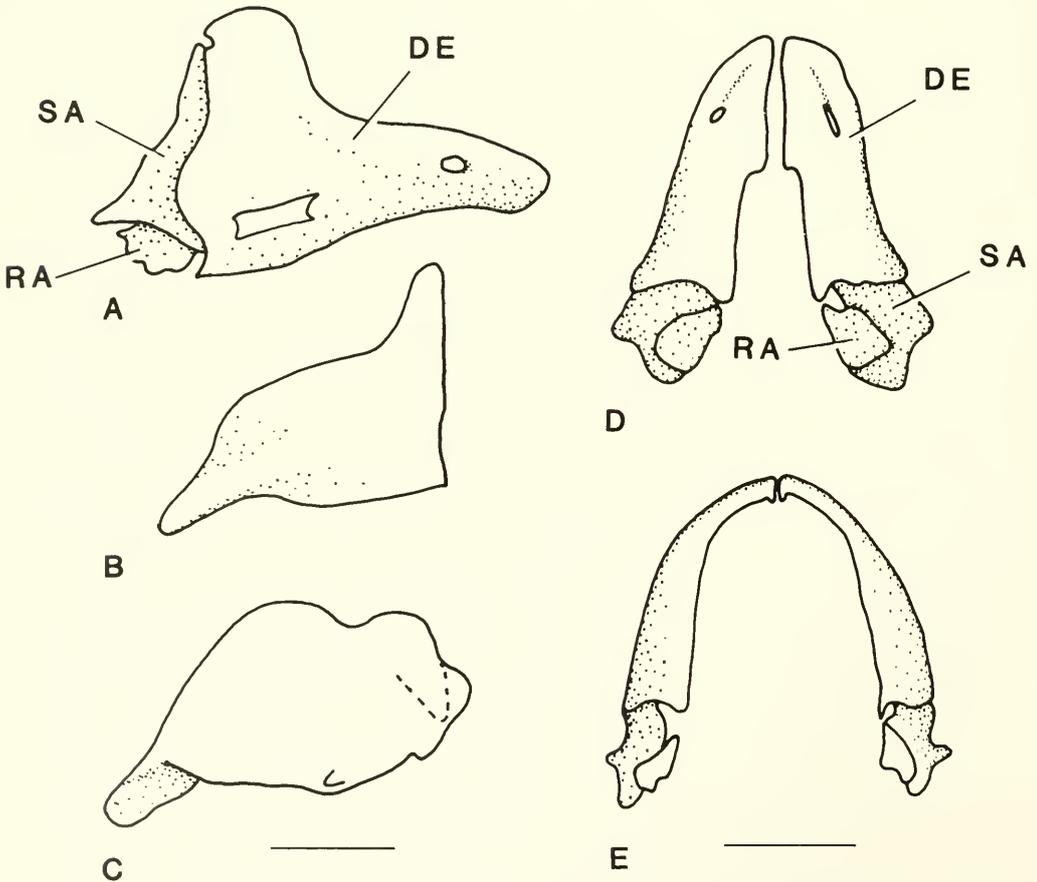


Fig. 14. Modified jaws of *Exoglossum*. A-D) *E. laurae* (47 mm, KU 18923). A) Lateral view of right lower jaw. B) Lateral view of premaxilla. C) Lateral view of maxilla. D) Ventral view of lower jaws. E) Ventral view of lower jaws of *Hemitrema flammea* (39 mm, KU 18884). Horizontal bar equals 1 mm.

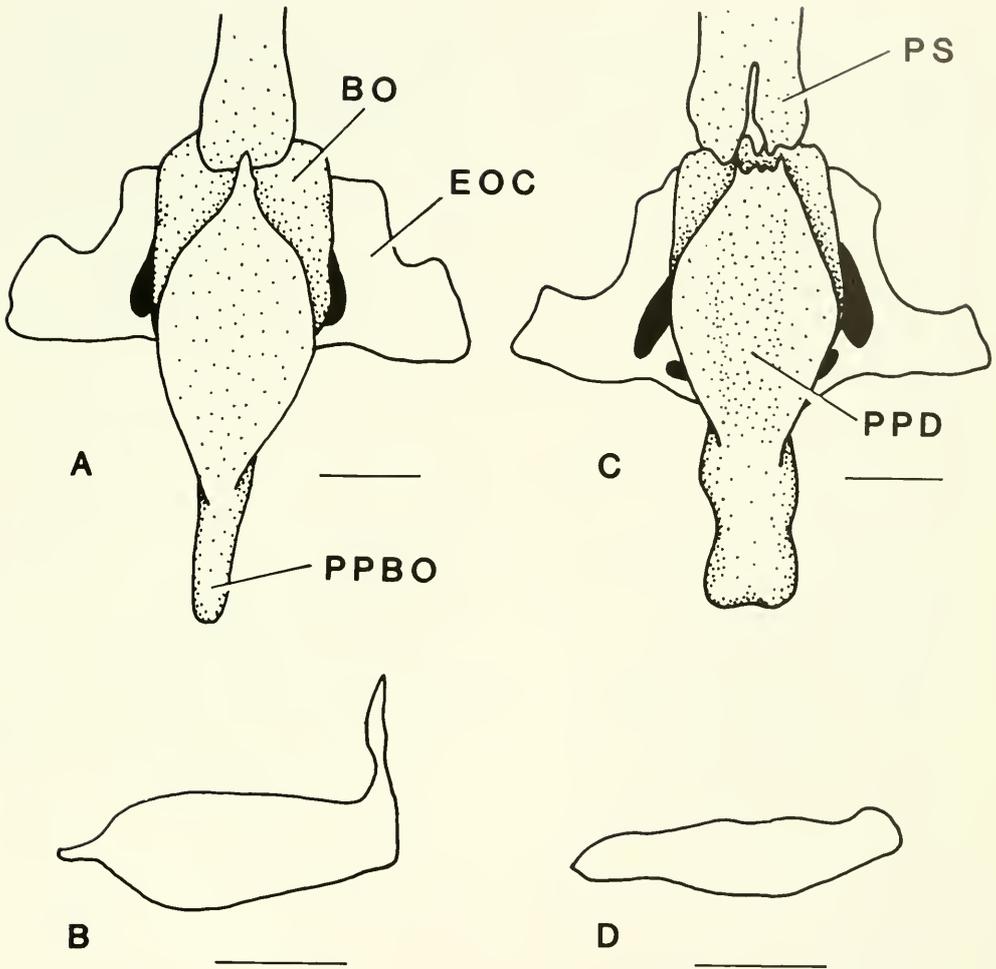


Fig. 15. Characters supporting the sister group relationship of *Campostoma* and *Dionda*. View of basicranial region and premaxilla of *Campostoma anomalum* (53 mm, KU 13200) (A and B) and *Dionda episcopa* (58 mm, KU 16891) (C and D) illustrating oval pharyngeal pad and weakly developed ascending process of premaxilla. Horizontal bar equals 1 mm.

(Jenkins and Lachner, 1971; Jenkins, pers. comm.), 3) a ventrally deflected posttemporal cephalic canal, 4) a broad platelike second infraorbital bone, and 5) reduced tuberculation on the dorsum of the head. The caudal skeleton of all outgroups examined is much broader (Fig. 18A–D). *Erimystax dissimilis*, *E. insignis*, *E. cahni*, *E. monacha*, *Phenacobius catoctomus*, *P. teretulus*, and *P. uranops* all have a much compressed caudal and precaudal skeleton, relative to any *Cyprinella* and other cyprinids surveyed. The posttemporal canal of

outgroups is straight. The maxillary flap of skin of these species is unique to this group and in most outgroups the second infraorbital is not very broad. The reduced tuberculation on the dorsum of the head is derived since other species of the chub clade and other cyprinids typically have considerable tubercle development in this area.

Monophyly of the genus *Phenacobius* (Fig. 3, Suite M) is supported by four characters: 1) loss of maxillary barbel, 2) heavy dentary, maxillary, and premaxillary bones (Fig. 17), 3)

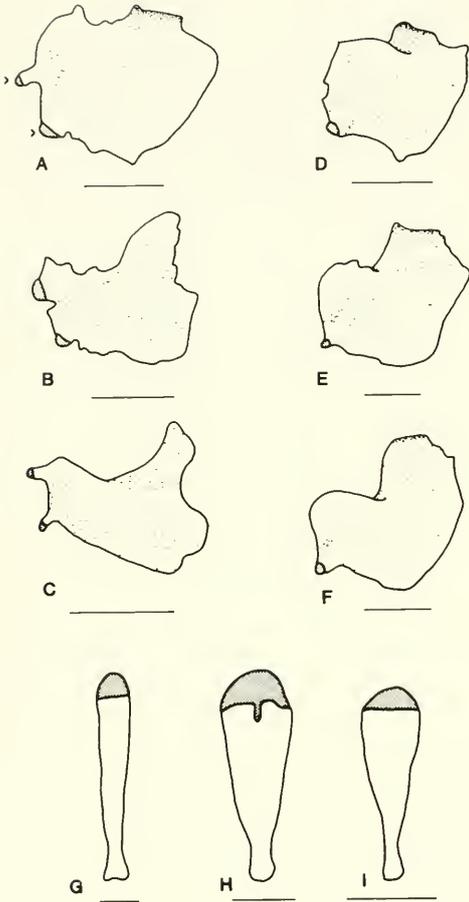


Fig. 16. Metapterygoids (A–F) and basihyals (G–I) of some North American cyprinids. Hyomandibular–metapterygoid articular processes are identified by arrows. Right is anterior for A–F. Up is anterior for G–I. A) *Nocomis raneyi*, 53 mm, KU 19616. B) *Notropis atherinoides*, 53 mm, KU 18935. C) *N. volucellus*, 40 mm, KU 17025. D) *Phenacobius crassilabrum*, 53 mm, KU 19618. E) *Erimystax insignis*, 73 mm, INHS 83108. F) *E. monacha*, 66 mm, UT 44.1031. G) *Couesius plumbeus*, 76 mm, KU 18881. H) *Erimystax insignis*, 73 mm, INHS 83108. I) *E. monacha*, 66 mm, UT 44.1031. Cartilage is represented by stippled pattern. Horizontal bar equals 1 mm.

a broad anteriorly directed maxillary process on the palatine (Fig. 9K–O), and 4) a unique tuberculation pattern on the pectoral fins of breeding males (Fig. 19A). Within the clade supported by Suite I of Fig. 2 all species except *Phenacobius* have a maxillary barbel. The absence of a barbel in this group is interpreted

as a secondary loss. The dentary, maxillary, and premaxillary of *Phenacobius* is very large and heavy, more so than most outgroups examined (Fig. 17). In most members of this chub clade the anteriorly directed maxillary process of the palatine is narrow (Fig. 9). In all *Phenacobius* the maxillary process is broader (Fig. 9K–O). This morphology is considered a further modification of the narrow ancestral condition of the chub clade. The pectoral fin tuberculation pattern in this group is different from other cyprinids examined (Fig. 19A). Species of *Phenacobius* have three rows of tubercles per ray, with the anteriormost row being the longest and extending from the base of the ray to near the distal margin. The posterior two rows are gradually shorter. In most outgroups the tubercle rows are symmetrical. Basally, a single row is formed and branches into two to four rows distally.

Within *Phenacobius*, *P. mirabilis* is the sister to other members. All species except *P. mirabilis* (Fig. 3, Suite N) have short anterior arms on the urohyal with mesially directed

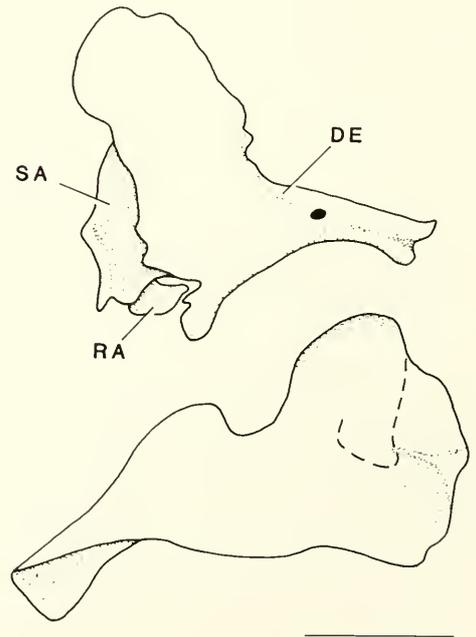


Fig. 17. Modified lower jaw (upper) and maxilla (lower) of *Phenacobius crassilabrum*, 53 mm, KU 19618. Right is anterior. Horizontal bar equals 1 mm.

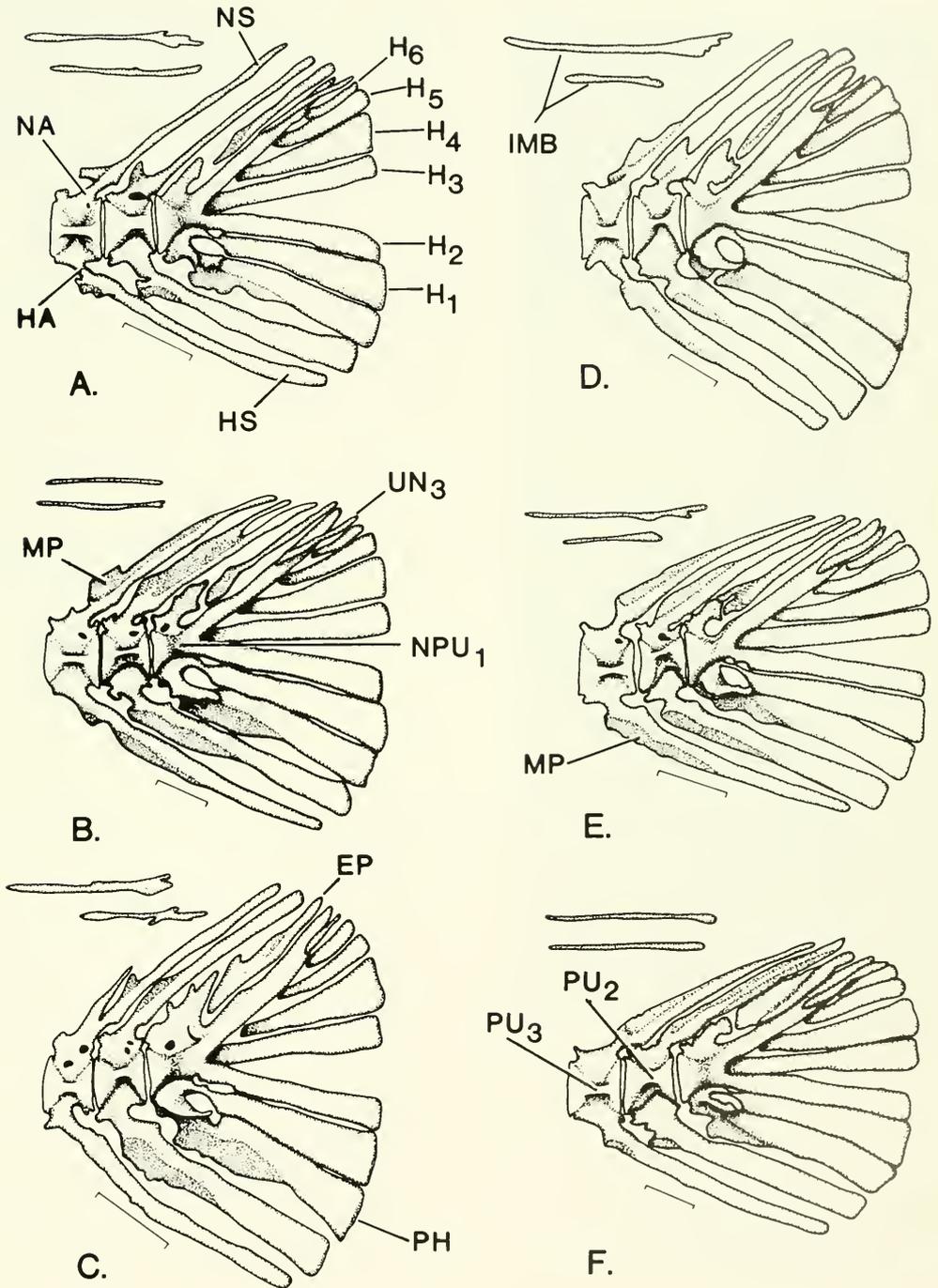


Fig. 18. Caudal skeletons of some North American cyprinids. Left is anterior. A) *Lythrurus fumeus*, 51 mm, KU 6244. B) *Luxilus coccogenis*, 72 mm, INHS 79244. C) *Cyprinella panarcys*, 43 mm, UMMZ 208212. D) *Cyprinella xaenura*, 71 mm, KU 18994. E) *Erimystax cahni*, 58 mm, KU 19614. F) *Phenacobius uranops*, 82 mm, KU 19619. Horizontal bar equals 1 mm.

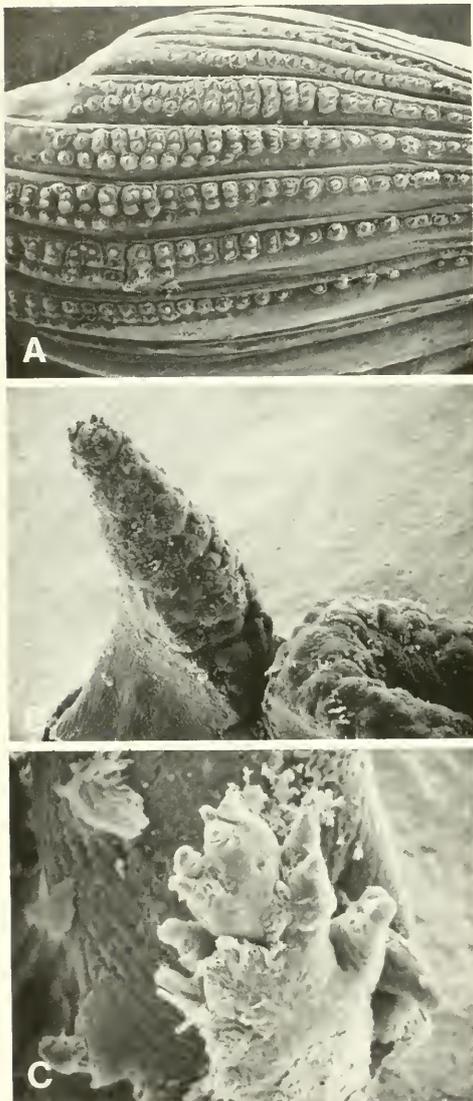


Fig. 19. Characters supporting the monophyly of the genera *Phenacobius* and *Erimystax*. A) Scanning electron micrograph of pectoral fin tuberculation in *Phenacobius mirabilis* (61 mm, KU 15151) illustrating the graduated rows of tubercles on each ray. B) SEM of barbel of *Platygobio gracilis* (79 mm, KU 8351) illustrating the simple primitive barbel morphology. C) Barbel of *Erimystax cahni* (71 mm, REJ 737) illustrating the derived "stellate" condition of the genus.

processes (Fig. 20). *Phenacobius catostomus*, *P. crassilabrum*, and *P. uranops* (Fig. 3, Suite O) have two mesially directed processes on the

palatine, one anteriorly and one posteriorly, that surrounds the preethmoids (Fig. 9). *Phenacobius crassilabrum* and *P. uranops* (Fig. 3, Suite P) share three derived features. These include: 1) a narrow pharyngeal pad on the basioccipital (Fig. 20B), 2) a broad shelf connecting the anterior and posterior mesial processes of the palatine (Fig. 9), and 3) a second osseous articular surface dorsally on the metapterygoid (Fig. 16D). The narrow pharyngeal pad is unique in the chub clade. As mentioned above, *Phenacobius* plus *Erimystax*, *Extrarius*, *Macrhybopsis*, and *Platygobio* have only a single cartilage articular surface on the metapterygoid. This condition is reversed in *P. uranops* and *P. crassilabrum*. The second process appears to be different in these two species, in that the dorsal process is ossified and a cartilage tip is not present. In all outgroups with two metapterygoid processes the dorsal process has a cartilage tip.

Monophyly of the genus *Erimystax* (Fig. 3, Suite Q) is supported by two derived characters: 1) a unique "stellate" barbel (Fig. 19C) and 2) an elongate basihyal. The barbel in *Erimystax* has large, fleshy processes extending off of the tip, producing a shape similar to a spiked mace (Fig. 19C). The barbel of *Erimystax monacha* is more intermediate between the "stellate" morphology as seen in other species of *Erimystax* and the morphology of other barbeled members of the chub clade. The processes of the barbel in *E. monacha* are smaller and fewer than are typical in other members of the genus. Other barbeled cyprinids have a relatively smooth texture to the barbel. Moore (1950) and Branson (1962) illustrated this derived barbel, but did not comment on its systematic significance. The elongate basihyal of these species (Fig. 16H, I) is hypothesized to be a reversal to the more primitive morphology from the derived triangular basihyal uniting these species with the genera *Platygobio*, *Macrhybopsis*, *Phenacobius*, and *Extrarius*.

Within *Erimystax*, a trichotomy presently exists between *E. monacha*, *E. x-punctata*, and a clade inclusive of *E. cahni*, *E. insignis*, and *E.*

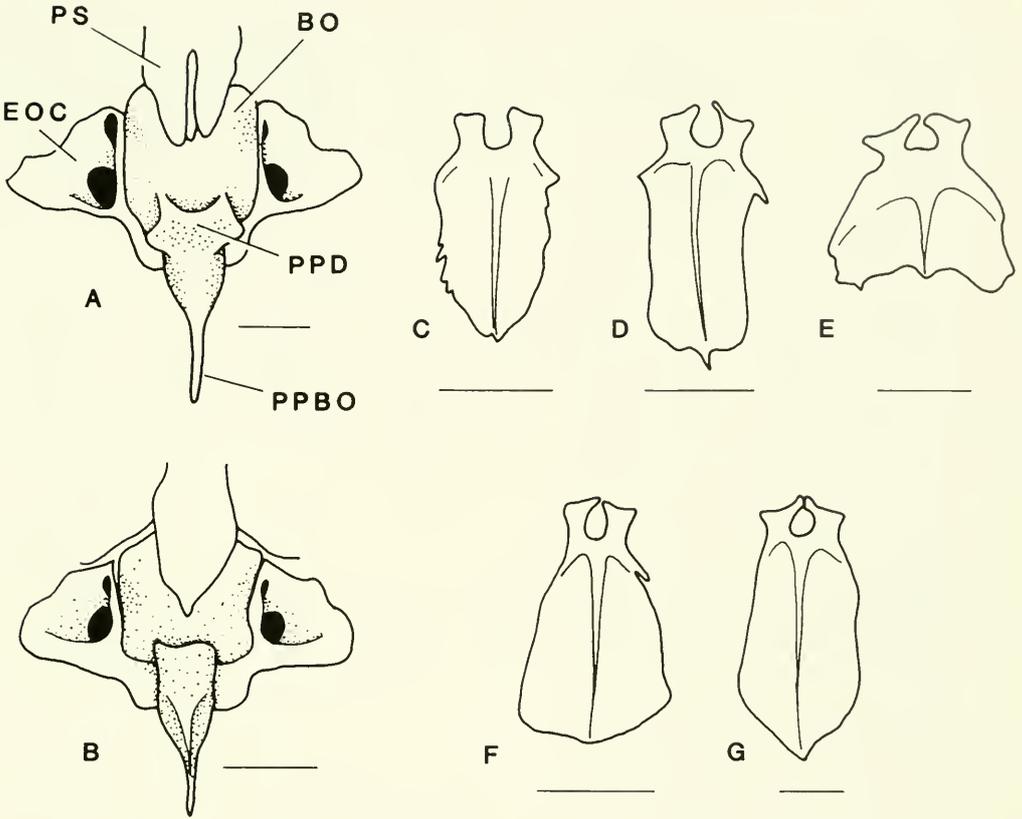


Fig. 20. Osteological characters of the genus *Phenacobius*. A) Basicranial region of *P. mirabilis* (60 mm, KU 16387) illustrating pharyngeal pad with small lateral processes. B) Basicranial region of *P. crassilabrum* (53 mm, KU 19618). C) Ventral view of urohyal of *P. mirabilis* (same data as above). D) Urohyal of *P. teretulus* (68 mm, KU 18929). E) Urohyal of *P. wanops* (84 mm, KU 19619). F) Urohyal of *P. catostomus* (55 mm, KU 18897). G) Urohyal of *P. crassilabrum* (53 mm, KU 19618). Horizontal bar equals 1 mm.

dissimilis. The latter three species (Fig. 3, Suite R) share a narrowly developed maxillary process of the palatine (Fig. 9Q, S, T). This morphology is hypothesized to be derived for this group, reduced from the broader condition typical of other members of the genus and the chub clade. *Erimystax insignis* and *E. dissimilis* (Fig. 3, Suite S) both have dark and distinct blotches along the flanks. This derived pigment pattern is unique to these species in the clade of cyprinids with an open myodome. *Erimystax monacha* may represent the sister group to other members of the genus if one considers the well-developed "stellate" barbel morphology to be a synapomorphy of all members, exclusive of *E. monacha*.

Genus *Pimephales* (Fig. 1, Suite 3). Four species are included in this group. *Pimephales notatus* and *P. promelas* form a monophyletic group, sister to a clade composed of *P. vigilax* and *P. tenellus*. Justifications for these relationships are presented by Mayden (1987).

Genus *Hybopsis* and related species (Fig. 1, Suite 4). Included in this clade (Fig. 4) are the species traditionally placed in the subgenus *Hybopsis* (Jenkins and Lachner, 1971) (except *storeriana* see above), plus *Hybopsis boucardi*, *H. calientis*, *H. dorsalis*, *H. longirostris*, *H. sabiniae*, *H. alborus*, *H. bifrenatus*, and *Eri-cymba buccata*. An alternative explanation for this group of cyprinids is convergent evolution. Many of these species are benthic dwell-

ing forms with somewhat similar habitat characteristics. Thus, it is possible that this grouping may be artificial, due to convergent evolution of morphological characteristics for a similar benthic lifestyle.

All of the species of this group share a deep premaxillary process on the maxillary (Fig. 21B,C). Outgroups typically do not have a deep premaxillary process (Fig. 21A). Some species of the genus *Cyprinella* also develop a similar, but convergent deep process. Species of the *Hybopsis* clade also share two derived conditions of the palatine. As described above, outgroups typically have a distinct perpendicular maxillary process on the palatine. In members of this clade, inclusive of *Hybopsis*, the maxillary process of the palatine is somewhat L-shaped with a long anterolaterally directed process (Fig. 22A). This process is not considered homologous with that found in the chub clade. In the chub clade the maxillary process of the palatine is directed anteriorly (Fig. 9B), but in the *Hybopsis* clade the process is directed anterolaterally. This anterolateral process is an independent modification of the perpendicular maxillary process typical of outgroups.

The second derived character from the palatine for this clade involves the palatine-preethmoid socket. As mentioned above, the primitive condition of the palatine socket is a well-developed depression anteromesially on the palatine. In members of the *Hybopsis* clade the articular surface on the palatine for the preethmoid is a deep, quasi-socket and groove, extending anteroventrally to posterodorsally, much like members of the chub clade. In the *Hybopsis* clade, however, the socket is different, being restricted posteriorly by a mesially directed shelf on the palatine (Fig. 22B). A similar palatine morphology is found in the *volucellus* species group (Fig. 1) (see below).

Within the *Hybopsis* clade, two less inclusive monophyletic groups are supported; the *dorsalis* species group and a clade inclusive of the genus *Hybopsis*, *H. boucardi*, and *H. calientis* (Fig. 4). All other members are involved in an unresolved polytomy with these two

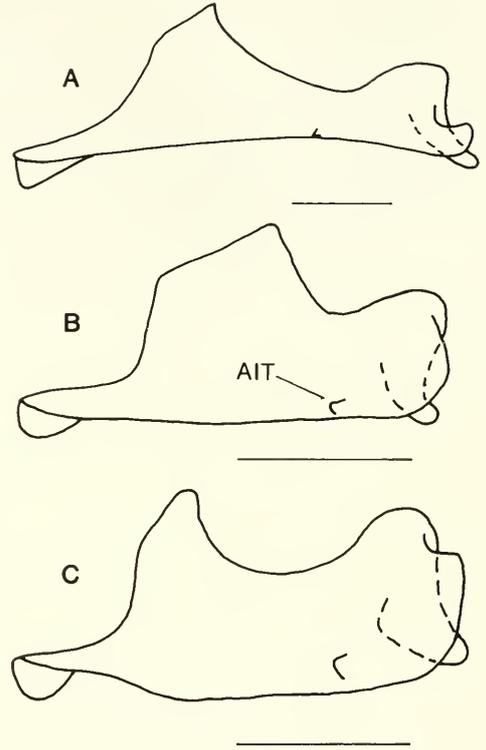


Fig. 21. Lateral view of maxilla of some North American cyprinids illustrating the deep premaxillary process of the *Hybopsis* clade. A) *Notropis bairdi*, 50 mm, KU 18474. B) *Hybopsis calientis*, 42 mm, TU 30695. C) *H. annis*, 42 mm, KU 18847. Horizontal bar equals 1 mm.

clades.

The monophyly of the *dorsalis* group (Fig. 4, Suite B) was recognized by Coburn (1982) and is supported by two derived characters: 1) a deep anterior notch in the mesethmoid-supraethmoid and 2) an elongate and straight kinethmoid. Most outgroups have only a shallow notch in the anterior mesethmoid, a condition considered primitive. Some members of the *volucellus* species group also possess a convergent deep anterior mesethmoid notch. The kinethmoid of most outgroups is short and robust, unlike that found in the *dorsalis* group.

Species united by Suite C (Fig. 4) share a derived, very deep maxilla (Fig. 23B–D). This condition is nearly unique to this group. Outgroups typically have a narrow isthmus on the maxilla separating the ascending process from

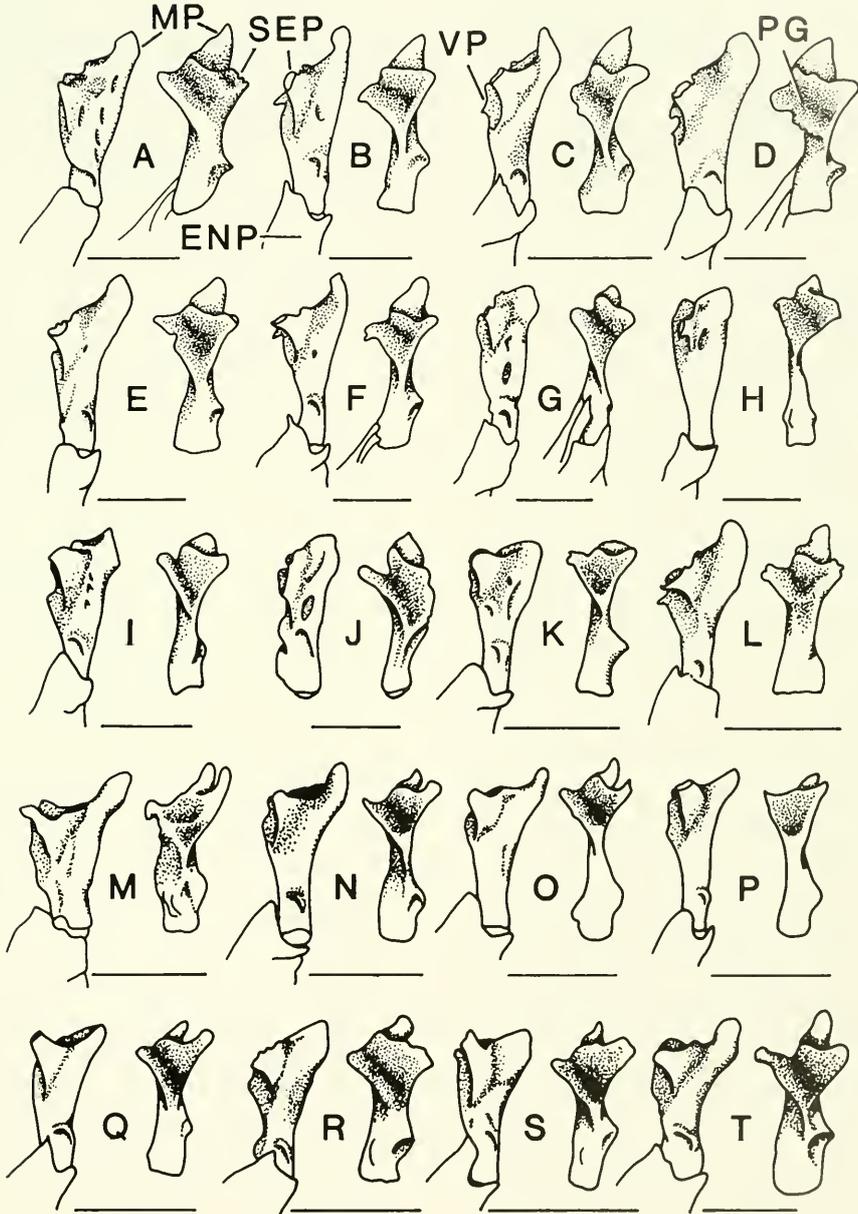


Fig. 22. Dorsal (left) and medial (right) views of palatines of some North American cyprinids with a derived anterior preethmoid articular morphology. Up is anterior. A) *Hybopsis hypsinotus*, 49 mm, KU 18968. B) *H. annis*, 57 mm, KU 18847. C) *H. amblops*, 65 mm, KU 6318. D) *H. winchelli*, 54 mm, TU 39705. E) *H. lineapunctata*, 52 mm, KU 18885. F) *Notropis heterolepis*, 51 mm, KU 11296. G) *Hybopsis labrosa*, 55 mm, INHS 88319. H) *H. zanema*, 52 mm, INHS 88320. I) *H. longirostris*, 47 mm, KU 17965. J) *H. sabinae*, 41 mm, KU 6237. K) *H. rubrifrons*, 75 mm, KU 8829. L) *Notropis maculatus*, 50 mm, KU 1551. M) *N. emiliae*, 53 mm, KU 18855. N) *N. ozarcanus*, 45 mm, KU 7664. O) *N. spectrunculus*, 41 mm, KU 5473. P) *N. volucellus*, 41 mm, KU 17025. Q) *N. aguirrepequenoi*, 41 mm, UMMZ 97399. R) *Hybopsis calientis*, 41 mm, TU 30695. S) *Notropis tropicus*, 29 mm, TU 43597. T) *Hybopsis boucardi*, 51 mm, UMMZ 191686. Horizontal bar equals 1 mm.

the premaxillary-rostral process of the maxilla. A similar, but convergent maxillary morphology is also seen in a few species of *Cyprinella*.

All species united by Suite D (Fig. 4) share six derived characters: 1) mandibular canal attached to the retroarticular (Fig. 24B–D), 2) long interhyal, 3) enlarged first pair of hypobranchials, 4) elongate first basibranchial, 5) broad posterior parasphenoid (Fig. 25C, D), and 6) an oval orbit. The presence of the mandibular canal crossing the retroarticular, also discussed by Coburn (1982), and the broad posterior parasphenoid in these nine species are unique. Most outgroups from within and outside the clade defined by an open posterior myodome have a short interhyal, short first basibranchial, and a small first pair of hypobranchials. Thus, these three conditions are hypothesized to be derived for the group. As seen in live specimens, all species of *Hybopsis*, except *H. hypsinotus*, have an oval orbit and eye. This characteristic is apparently unique to this group.

The *Hybopsis labrosa*-*H. zanema* species group (Fig. 4, Suite E) is supported by four characters. These are: 1) enlarged and antrorse tubercles on the dorsum of the head, 2) enlarged and antrorse predorsal tubercles, 3) large and slightly antrorse tubercles on the caudal peduncle, and 4) heavily pigmented membranes of the dorsal fin. These four characters are not unique to this group. Similar structures and color patterns occur in the genus *Cyprinella*, a group sometimes thought to be closely related (Jenkins and Lachner, 1971). The dorsal head tubercles and predorsal tubercles appear to be similar between these two groups, but the caudal peduncle tubercles and the dorsal fin pigment patterns are different. The caudal peduncle tubercles of the *C. pyrrhomelas* and *C. nivea* species groups of *Cyprinella* are located in the center of each scale. Those of the *H. labrosa* group may be single and centrally located, but are generally two per scale, one dorsally and one ventrally. The dorsal fin of the *H. labrosa* group also differs from *Cyprinella* in having melanin dis-

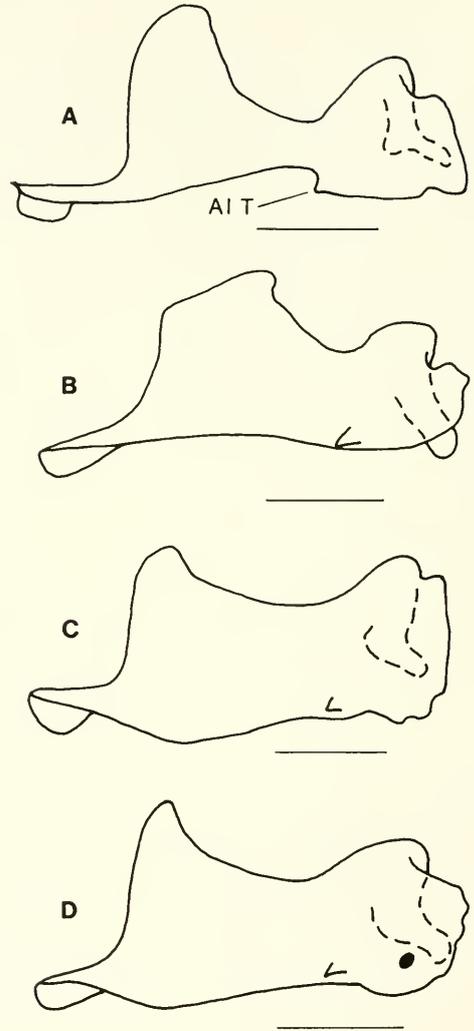


Fig. 23. Lateral view of maxilla of some North American cyprinids illustrating deep isthmus in some species of *Hybopsis*. Right is anterior. A) *H. sabinae*, 43 mm, KU 6237. B) *H. boucardi*, 57 mm, UMMZ 191686. C) *H. lineapunctata*, 54 mm, KU 18885. D) *H. hypsinotus*, 49 mm, KU 18968. Horizontal bar equals 1 mm.

tributed in all membranes and not just the posterior membranes as is typical of species of *Cyprinella* thought to be allied to the *H. labrosa* group. The sister group relationship between *H. zanema* and the undescribed "thinlip" chub (Fig. 4, Suite F) is supported by a single derived character. Both species have very elongate anterior urohyal processes. Most

outgroups, especially other *Hybopsis*, have short processes.

The monophyly of the remaining species of *Hybopsis* (Fig. 4, Suite G) is supported by 1) a truncated posterior margin of the horizontal plate of the urohyal (Fig. 11B, C) and 2) laterally directed and pointed processes on the urohyal near the neck, before the urohyal forks anteriorly (Fig. 11B, C). The truncated horizontal urohyal plate rarely occurs outside of this group, occasionally seen in some species of *Notropis*. The lateral processes seen on the neck of the urohyal are also found in *Macrhybopsis storeriana*, some specimens of *Phenacobius*, and about 40% of the specimens of *Notropis hudsonius*. Based on the distribution of other characters, the occurrence of these processes in all these groups is considered convergent.

The *Hybopsis amblops-winchelli-amnis* clade (Fig. 4, Suite H) is supported by a posteriorly directed supraethmoid process on the palatine (Fig. 22). This character is unique to this group. Outgroups have an anteriorly directed supraethmoid process. *Hybopsis linea-punctata* is a member of this group, but the supraethmoid process in this species is oriented perpendicular to the axis of the palatine. This condition is hypothesized to be a modification of the posteriorly directed process since this species, *H. amnis*, and *H. winchelli* form a monophyletic group (Fig. 4, Suite I) with unresolved relationships. These three species share the derived condition of having a well-developed depression on the palatine anteromesially, between the supraethmoid and maxillary processes (Fig. 22).

Pteronotropis-Notropis clade (Fig. 1, Suite 5). The clade of cyprinids supported by stem 5 is composed only of certain species of the previously conceived genus *Notropis*. Although variation is known to occur within some of the included groups, most of these species have a smooth and straight margin on the anterior wing of the hyomandibular (Fig. 26B–E). Almost all outgroups, below stem 5 and outside the group defined by an open myodome, have an obvious notch in the anterior margin of

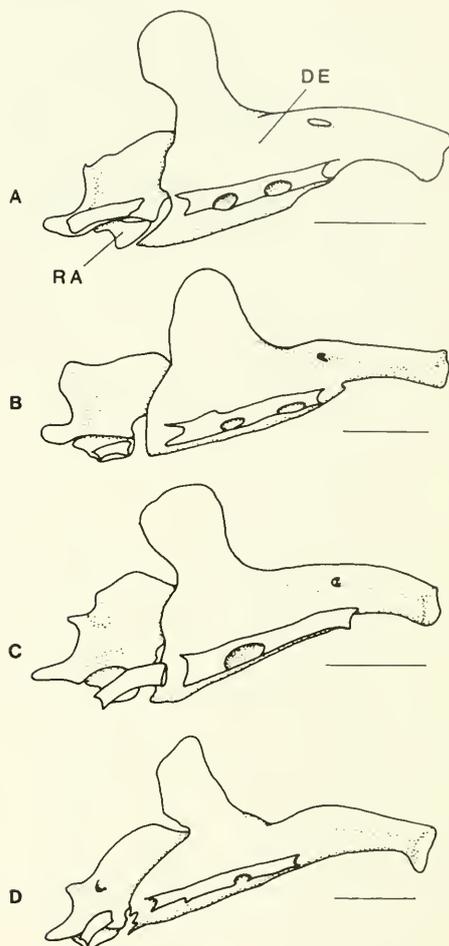


Fig. 24. Lower jaws of some species of North American cyprinids illustrating the positions of the mandibular canal relative to the retroarticular bone. Right is anterior. A) *Macrhybopsis storeriana*, 94 mm, KU 12126. B) *Hybopsis amnis*, 42 mm, KU 18847. C) *H. hypsinotus*, 49 mm, KU 18968. D) *H. zanema*, 52 mm, INHS 88320. Horizontal bar equals 1 mm.

the hyomandibular (Fig. 26A). Thus, the smooth wing condition is hypothesized to be derived within the clade defined by an open myodome. Exceptions to the smooth hyomandibular wing inside this clade include *Pteronotropis signipinnis*, some species of the genus *Cyprinella* (Fig. 26F), some members of the *Notropis volucellus* group, and some species in the subgenus *Notropis* (Coburn, 1982).

Genus *Pteronotropis* (Fig. 1, Suite 6). These four species (*P. signipinnis*, *P. hypselopterus*, *P. euryzonus*, *P. welaka*) all share a derived condition of the preethmoid socket of the palatine. In the primitive condition the socket is generally deep. In these four species the socket is shallow (Fig. 10 R–U). Other species with a convergently shallow preethmoid articular surface include *Lythrurus ardens*, *Notropis scabriceps*, *N. altipinnis*, *Cyprinella trichroistia*, and *C. gibbsi*.

Pteronotropis signipinnis, *P. hypselopterus*, and *P. euryzonus* form a monophyletic group

based on four derived characters. All three species share: 1) a very broad lateral stripe, 2) very bright orange, red, and blue colors, 3) a palatine with a long and rounded shaft (Fig. 10 R–T), and 4) mandibular tubercles with tips curled dorsally. These are the only species found in this study to have a rounded palatine shaft. *Pteronotropis welaka* and outgroups have a more compressed shaft. Within the genus, *Pteronotropis euryzonus* is the sister to *P. signipinnis*, and these two species form the sister to *P. hypselopterus*. The sister relationship of *P. euryzonus* and *P. signipinnis* is

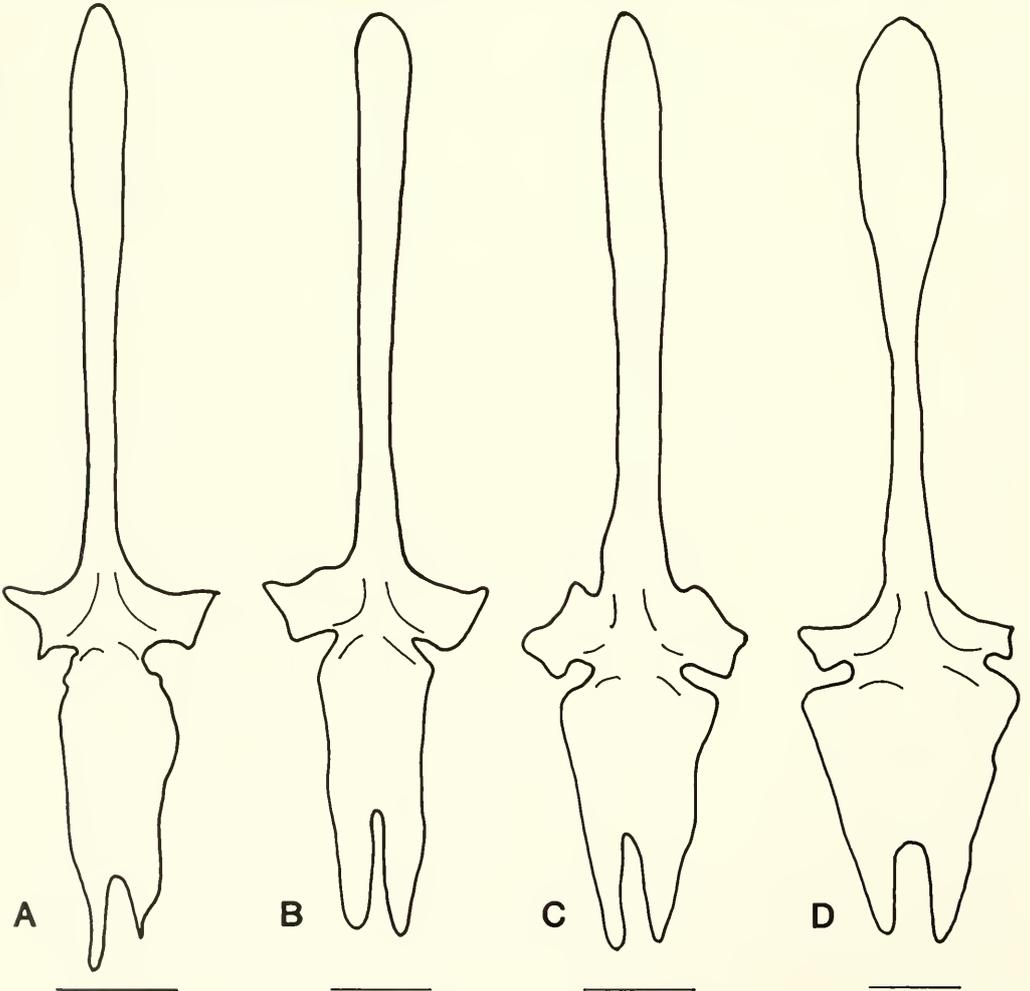


Fig. 25. Parasphenoids of some North American cyprinids. Up is anterior. A) *Notropis atherinoides*, 53 mm, KU 18935. B) *Cyprinella trichroistia*, 60 mm, KU 18853. C) *Hypbopsis zanema*, 52 mm, INHS 88320. D) *H. amnis*, 57 mm, KU 18847. Horizontal bar equals 1 mm.

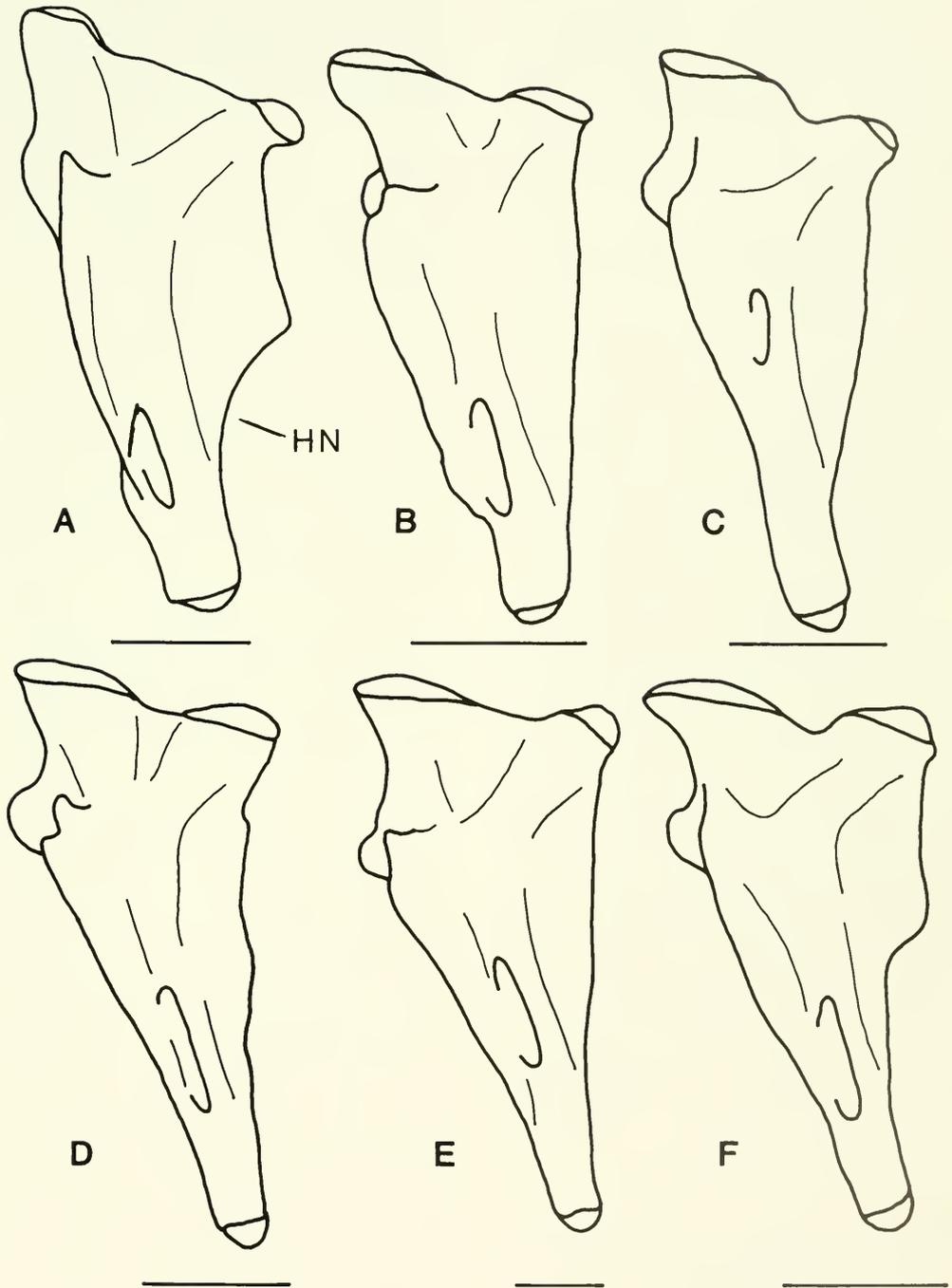


Fig. 26. Right hyomandibular of some North American cyprinids illustrating smooth and notched anterior wings. Right is anterior. A) *Nocomis raneyi*, 53 mm, KU 19616. B) *Pteronotropis euryzonus*, 43 mm, KU 19233. C) *Lythrurus bellus*, 57 mm, KU 14511. D) *Notropis atherinoides*, 55 mm, KU 18935. E) *Luxilus pilsbryi*, 86 mm, KU 13009. F) *Cyprinella gibbsi*, 57 mm, KU 18892. Horizontal bar equals 1 mm.

supported by a uniquely derived, tightly packed row of tubercles along the lateral surface of each mandible. This "comb row" of tubercles is illustrated by Bailey and Suttkus (1952, plate IIB). The monophyly of the *Pteronotropis* clade is also supported by some allozyme data (Dimmick, 1987; W. Dimmick, pers. comm.).

***Lythrurus-Notropis* clade** (Fig. 1, Suite 7). Included in this group are at least eight monophyletic groups. These include the genera *Lythrurus*, *Luxilus*, *Cyprinella*, and the subgenera *Alburnops*, *Hydrophlox*, and *Notropis* of *Notropis*, as well as the *Notropis volucellus* and *Notropis texanus* species groups (Fig. 1). These groups can be divided, based on shared derived characters, into two major monophyletic groups, one including the genera *Lythrurus*, *Luxilus*, and *Cyprinella*. The other clade includes the remaining taxa listed above.

Two derived characters are hypothesized to support the monophyly of this clade. One involves the basihyal and the other a fleshy groove anterior to the lacrymal. These eight groups share one derived feature of the basihyal not found in any other cyprinids examined. All have an ossified posteroventral process from the basihyal, directed toward and sometimes (in more derived clades) extending beneath the first basibranchial (Fig. 27). This process and the anteroventral surface of basibranchial 1 are joined by a ventral basihyal ligament. This basihyal process is not found in any other cyprinids.

This process was also noted and discussed by Coburn (1982) for many of these species, but was not found in his study to include as many taxa as noted here. In members of the *Lythrurus-Luxilus-Cyprinella* clade the basihyal projection is generally small, but in other species (discussed below) it is quite large.

A groove extending up along the anterior margin of the lacrymal, separating it from the rest of the snout (Fig. 27), is found in most species outside this clade and in cyprinids with a closed myodome. All species of the clade defined by stem 7 (Fig. 1) inclusive of

Lythrurus, *Luxilus*, *Cyprinella*, *Alburnops*, *Hydrophlox*, *Notropis*, and the *Notropis texanus* species group, except the *Notropis volucellus* species group, lack this groove. Thus, the absence of the groove in these species supports the monophyly of this clade. Based on other characters, the groove present in members of the *Notropis volucellus* species group is hypothesized to be a reversal, defining the *Notropis volucellus* species clade.

Other species included in this clade, but not sharing synapomorphies of stem 13 (Fig. 1), cannot at this time be placed in any of the monophyletic groups. These include *Notropis scabriceps*, *N. uranoscopus*, *N. asperifrons*, and *N. hypsilepis*. These species presently are involved in a polytomy at stem 7 with the clade containing the *Lythrurus-Luxilus-Cyprinella* lineage and the clade inclusive of the subgenera and species groups of *Notropis* from *Alburnops* through *Notropis* (Fig. 1). Their generic status is retained until such time that they can logically be related to other groups.

***Lythrurus-Luxilus-Cyprinella* clade** (Fig. 1, Suite 8). The monophyly of these three clades is supported by three derived characters. Species of this group share 1) large cephalic tubercles, 2) submarginal tubercles on body scales, and 3) a triangular palatine. Most outgroups within and outside the clade defined by an open myodome have very fine tubercles on the dorsal surfaces of the head. In these three genera, however, the tubercles are large, especially in the genera *Luxilus* and *Cyprinella*. Convergent enlarged tubercles occur in some species of *Hybopsis*, *Nocomis*, *Campostoma*, *Semotilus*, and *Dionda*. Based on other characters (Figs. 1, 2, 4), however, the development of large cephalic tubercles is hypothesized to be independent in these groups. In all outgroups examined, except *Notemigonus*, the tubercles on flank scales of breeding males are developed near the edge of the scale (Fig. 28A). In most species of these three genera, however, the tubercles are not at the edge of the scale, but are submarginal (Fig. 28B). These species may have edge tubercles, but they also develop marginals. The only exceptions are

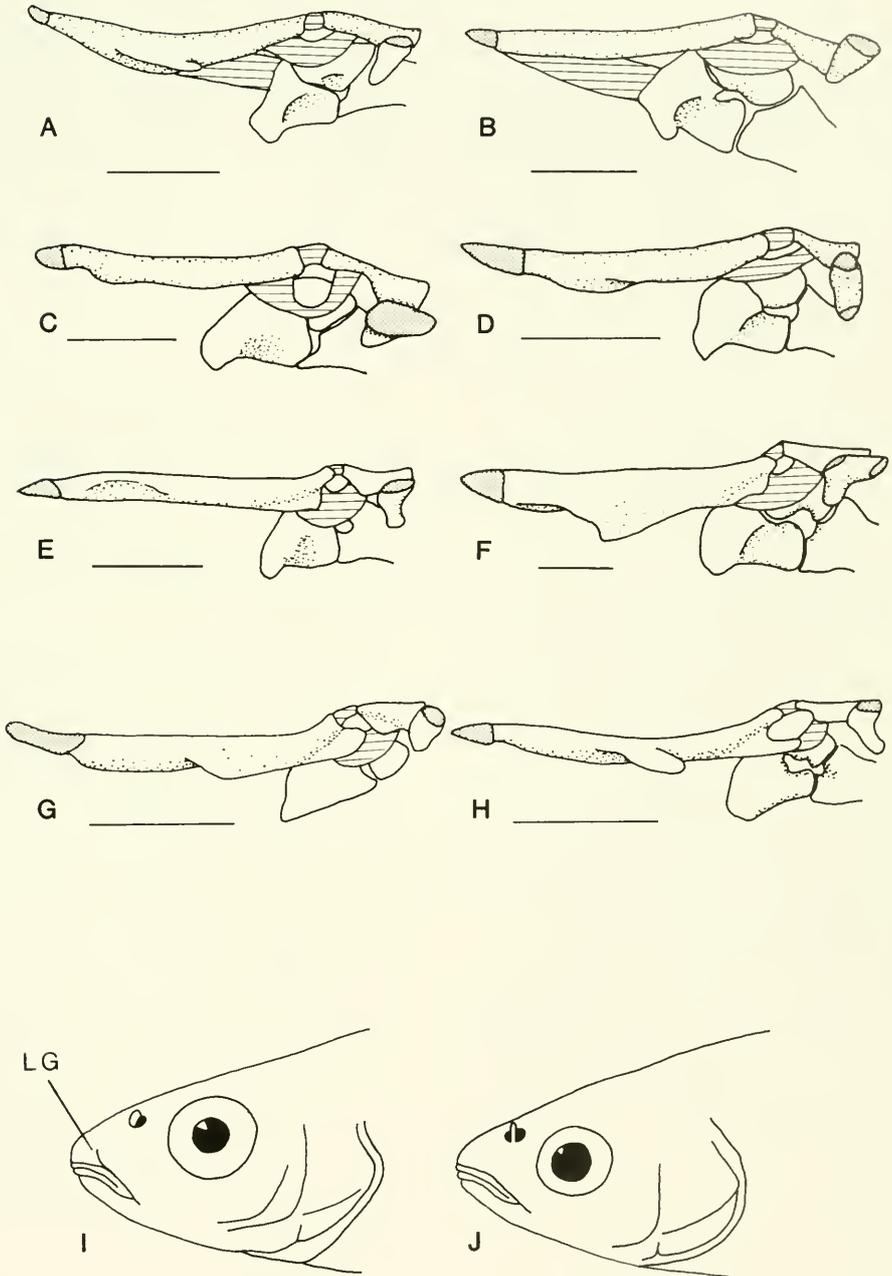


Fig. 27. Lateral view of basihyal illustrating presence or absence of posteroventral projection, and lateral view of head illustrating lacrymal groove in some eastern North American cyprinids. Left is anterior. A) *Phoxinus erythrogaster*, 52 mm, KU 13198. B) *Couesius plumbeus*, 65 mm, KU 18881. C) *Hybopsis amnis*, 57 mm, KU 18847. D) *Notropis topeka*, 50 mm, KU 19033. E) *Lythrurus fumeus*, 56 mm, KU 6244. F) *Luxilus zonatus*, 85 mm, KU 12648. G) *Notropis asperifrons*, 47 mm, KU 18886. H) *N. altipinnis*, 43 mm, KU 18974. I) Outline drawing of head of *Phenacobius mirabilis*, illustrating lacrymal groove above lips. J) Outline drawing of head of *Cyprinella spiloptera*, illustrating absence of lacrymal groove. Horizontal pattern in A–H represents ligaments and stippled regions represent cartilage. Horizontal bar equals 1 mm.

Luxilus pilsbryi, *L. cardinalis*, and *L. zonatus*. In these species the breeding males have edge tubercles only.

As mentioned earlier, several morphological aspects of the palatine are important systematically in cyprinids. Most species within and outside the clade defined by the open myodome have a maxillary process. This process is obviously perpendicular to the axis of the palatine (Fig. 10; 29A, E, I, M) in these species. Three modifications of this primitive morphology occur in the open myodome clade. The first two have been discussed above. The third derived condition of the palatine occurs in the *Lythrurus-Luxilus-Cyprinella* clade. In adults of these species the palatine is triangular when viewed dorsally (Fig. 29D, H, L, O). Juveniles of these taxa have the primitive laterally directed maxillary process (Fig. 29A, E, I, M). Species with this morphology do not have a well-developed maxillary process (Fig. 29). Thus, based on outgroup comparison, the triangular morphology is considered derived for this clade. Developmental data also support this triangular shape as being derived. Adults of species with the triangularly shaped palatines have a well-developed maxillary process as juveniles and a smooth transition from the primitive to the derived morphologies is obvious with increasing body size (Fig. 29).

Genus *Lythrurus* (Fig. 1, Suite 9). The monophyly of this genus was discussed by Snelson (1972) and is supported by three derived features. These are: 1) small scales, 2) reduced anterodorsal squamation, and 3) an enlarged urogenital papilla of breeding females (Fig. 30). All three characters are unique to this group. The papilla of other breeding shiners is never as enlarged as in species of *Lythrurus*.

Within *Lythrurus* a trichotomy exists between *L. fumeus*, *L. lirus*, and a clade composed of the sister species *L. ardens* and *L. umbratilis*, and their sister group, the *roseipinnis* complex (*L. bellus*, *L. atrapiculus*, *L. roseipinnis*.) The *L. ardens*-*L. umbratilis* sister relationship is supported by the presence in breeding males of dark vertical bars on the dorsal

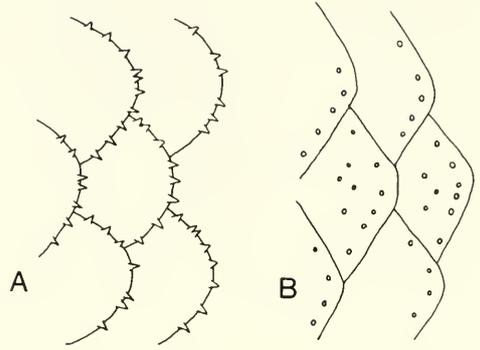


Fig. 28. Distribution of breeding tubercles on lateral body scales in some North American cyprinids. Left is anterior. A) *Notropis rubricroceus*, 55 mm, UAIC 5990.01. B) *Cyprinella camura*, 60 mm, KU 10734.

and dorsolateral surfaces. The monophyly of the *roseipinnis* complex is discussed by Stein et al. (1985).

The sister group relationship between the *roseipinnis* complex and the clade composed of *L. ardens* and *L. umbratilis* is supported by three characters. These are: 1) blue and red breeding colors along sides, 2) a dark spot at origin of dorsal fin, and 3) a very elongate scapular process against the mesial surface of the cleithrum (Fig. 31). The coloration in *L. fumeus* and *L. lirus* is pale or yellowish with no blues or reds, as is also true for most outgroups, except the genera *Luxilus*, *Cyprinella*, and the subgenus *Hydrophlox* of *Notropis*. *Lythrurus fumeus*, *L. lirus*, and outgroups lack a dark spot at the origin of the dorsal fin. The scapular process is common to all cyprinids with an open myodome, except *Cyprinella* and *Luxilus*, in which it is small or absent. In most outgroups to *Lythrurus*, however, the scapular process is shorter than that found in the *roseipinnis* complex, *L. ardens*, and *L. umbratilis* (Fig. 31).

***Luxilus-Cyprinella* clade** (Fig. 1, Suite 10). The sister group relationship of these two subgenera is supported by ten derived characters: 1) broad and flat supraethmoid, 2) flank scales taller than wide, especially near the lateral line, 3) cephalic tubercles large, 4) tubercles on dorsum of head in two rows

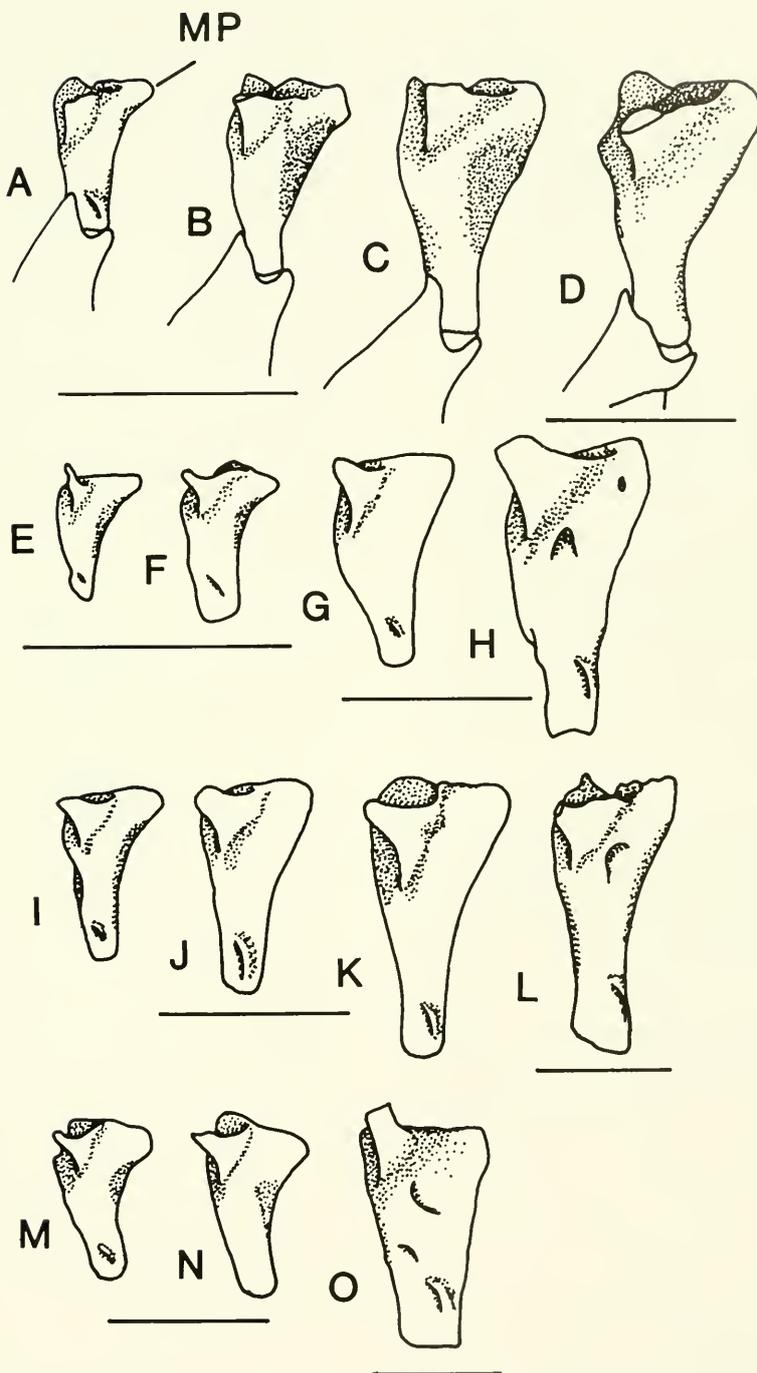


Fig. 29. Ontogenetic transformation from the primitive palatine with a well-developed lateral maxillary process to the derived palatine without a maxillary process, typical of the genera *Lythrurus*, *Luxilus*, and *Cyprinella*. Up is anterior. A-D) *Cyprinella garmani* at 24, 30, 35, and 49 mm. E-H) *C. camura* at 18, 23, 37, and 45 mm. I-L) *C. whipplei* at 36, 45, 52, and 64 mm. M-O) *Luxilus cerasinus* at 36, 40, and 57 mm. Horizontal bar equals 1 mm.

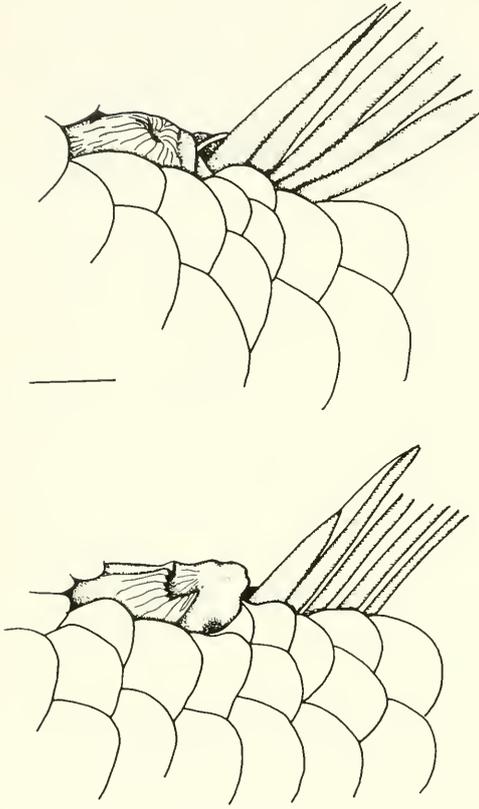


Fig. 30. Genital papillae of breeding *Cyprinella lutrensis* (above, 46 mm, KU 17297) and *Lythrurus fumeus* (below, 44 mm, INHS 87307) illustrating enlarged papilla for species of the genus *Lythrurus*. Both females were gravid and collected with tuberculate males. Left is anterior. Horizontal bar equals 1 mm.

anteriorly, 5) mandibular tubercles in rows, 6) suborbital tubercles absent, 7) supraorbital tubercles in rows, 8) posterodorsal process of scapula absent or small, 9) occipital region of cranium compressed, and 10) loss of pleomerism (the correlation between maximum body size and number of vertebrae).

The broad and flat supraethmoid is unique to this group of cyprinids with an open myodome. Outgroups have a narrow supraethmoid with concave margins and concave dorsal surface, producing a “butterfly” shape (see Harrington, 1955). As noted by Coburn (1982) scales of these two clades are taller than wide as measured from the focus of the scale. This characteristic is not unique to this clade, also

occurring in some members of the *Notropis volucellus* species group (Fig. 1). In this group, however, the elevated scales are confined to the lateral-line series.

The enlarged tubercles characteristic of *Cyprinella* and *Luxilus* are found in other, unrelated cyprinids, as well as in the closely related genus *Lythrurus*. The larger tubercles of *Cyprinella* and *Luxilus* are interpreted as derived, representing increased modification of large tubercles in the genus *Lythrurus*. In *Lythrurus* and most outgroups the supraorbital and mandible tubercles are scattered, representing the primitive conditions for cyprinids with an open posterior myodome. These same outgroups also generally have suborbital tubercles and the dorsal cephalic tubercles in a scattered pattern throughout development (Fig. 32). Thus, the linear development of dorsal head tubercles (Fig. 32 B–E), the single row of supraorbital tubercles, the linear mandibular tubercles, and the absence of suborbital tubercles are hypothesized to be derived characters for these two genera. Reversed conditions are known for the mandibular and supraorbital tubercle patterns. In the genus *Cyprinella* some species have scattered mandibular and supraorbital tubercles and *C. gibbsi* develops tubercles on several suborbital surfaces (see Phylogenetic Relationships section below).

As discussed above, the scapula in most cyprinids within and outside the clade defined by the open posterior myodome has some development of a posterodorsal process against the mesial surface of the cleithrum (Fig. 31). In *Cyprinella* and *Luxilus* the process is absent or very small (Fig. 31). In *Luxilus* and *Cyprinella* the occipital region of the cranium is compressed, reaching an extreme in the *lutrensis* clade of the genus *Cyprinella*. In lateral view the occipital region of these two clades is more nearly vertical than in outgroups, including the genus *Lythrurus* (Fig. 33). In outgroups the occipital region is more elongate (Fig. 33). Thus, the compressed condition of these two genera is considered derived.

Coburn (1982) discussed pleomerism in cyprinids and found that for all species except

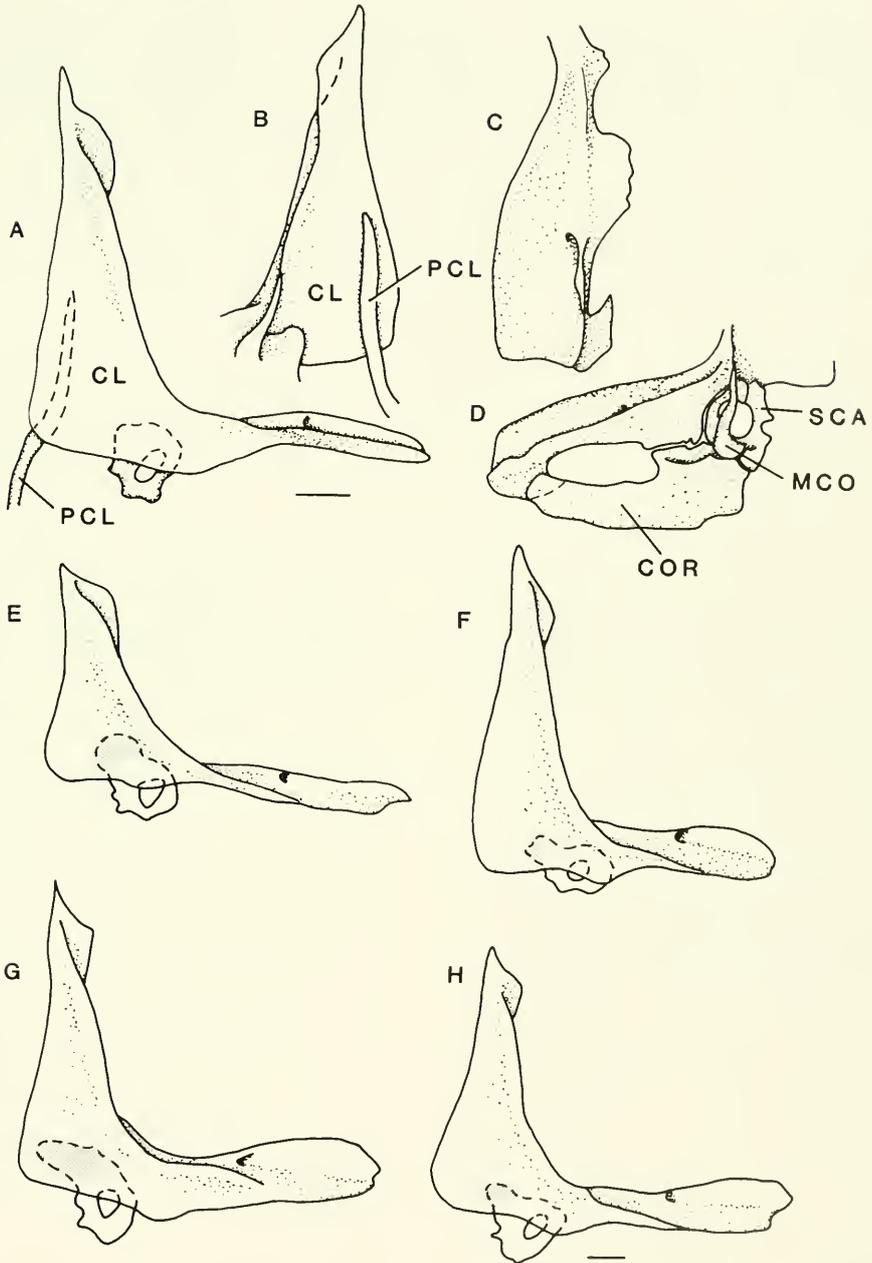


Fig. 31. Pectoral girdle of some *Cyprinella* and outgroups. A-D) *Cyprinella xanura*, 71 mm, KU 18994: A - lateral view of cleithrum with postcleithrum and scapula; B - mesial view of cleithrum, dorsal postcleithrum, and dorsal mesocoracoid; C - dorsal view of cleithrum; D - mesial view of coracoid, mesocoracoid, scapula, and cleithrum. E-H) Lateral view of cleithra and scapula illustrating relative heights of ascending arm of cleithrum and length of posterior process of scapula. E) *Notropis telescopus*, 67 mm, KU 15231. F) *Cyprinella analostana*, 58 mm, INHS 74347. G) *Lythrurus umbratilis*, 56 mm, KU 15521. H) *Luxilus cardinalis*, 79 mm, KU 15281. Stippled pattern represents extent of scapular process. Horizontal bar equals 2 mm; bar below *xanura* is for all species, except *cardinalis*.

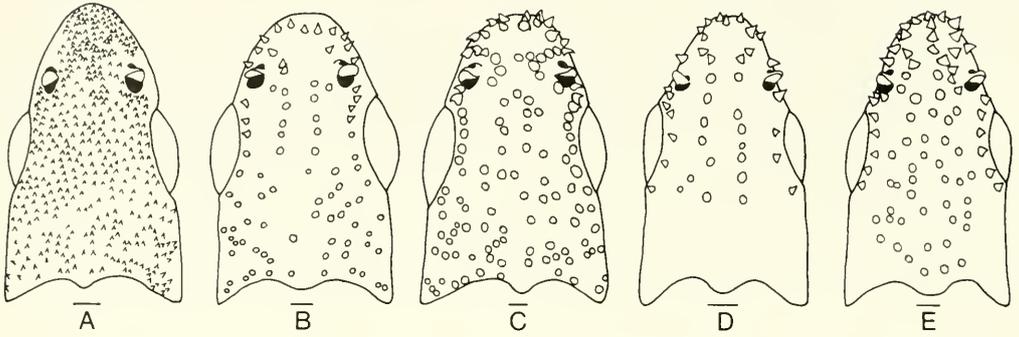


Fig. 32. Tubercle patterns of dorsum of head in the genera *Luxilus* and *Cyprinella* and outgroup, illustrating linear tubercle pattern early in development for the former two genera. A) *Notropis rubricroceus*, 56 mm, UAIC 5990.01, 10 June 1980. B) Early breeding male of *Luxilus cardinalis*, 64 mm, KU 20737, 13 April 1983. C) Peak breeding male of *L. cardinalis*, 85 mm, KU 20963, 9 May 1984. D) Early breeding male of *Cyprinella proserpina*, 41 mm, TNHC 9771, 8 May 1979. E) Peak breeding male of *C. proserpina*, 50 mm, TNHC 9771, 8 May 1979. Open circles are tubercles viewed from above. Horizontal bar equals 1 mm.

those in the genera *Luxilus* and *Cyprinella*, there is a high correlation between maximum size and number of vertebrae. Thus, the lack of correlation between maximum body size and number of vertebrae is suggested to further substantiate the sister group relationship of these two groups.

Genus *Luxilus* (Fig. 1, Suite 11). Gilbert (1964) and Buth (1978) supported the monophyly of this genus. From the present study three characters are hypothesized to support the monophyly of *Luxilus*: 1) retrorse preorbital tubercles (also see Gilbert, 1964), 2) cleithral region with intense pigmentation (Gilbert, 1964), and 3) epibranchial 3 with an elongate and curled uncinat process (Fig. 34B, C). Apparently, all three characters are unique to this genus. The preorbital tubercles of outgroups are erect, the cleithral region is never as heavily pigmented as in this clade, and the uncinat process of other cyprinids is short and straight (Fig. 34A). Coburn (1982) also noted a unique and derived scale morphology for species of *Luxilus*.

Genus *Cyprinella* (Fig. 1, Suite 12). The monophyly of *Cyprinella* is supported by 34 osteological, behavioral, coloration, and tuberculation characters. The hypothesized derived characters are listed below. Only the non-osteological characters are discussed in reference to polarity justifications. For discus-

sions and illustrations of osteological characters see the osteology section in this paper. The monophyly of *Cyprinella* is substantiated by the following derived traits: 1) anterior border of trigeminal foramen formed by pterosphenoid only, 2) preopercle wide medially and anteriorly, 3) interopercle deep posteriorly, 4) anterior hyomandibular wing with notch, 5) lateral shelf of quadrate wide, 6) symplectic broad, 7) frontals truncated anteriorly and anterolaterally, 8) frontals slightly broadened laterally, 9) supraethmoid very broad, 10) supraorbital canal on frontals with elaborate development of canaliculi in a dendritic pattern, 11) metapterygoid articulation with interhyal narrow, 12) ventral horizontal plate of urohyal narrow, 13) vomer with some neck developed, 14) interorbital septum shallow, 15) lacrymal elongate, 16) occipital region compressed, 17) ascending wings of parasphenoid broad, 18) insertion of A1 branch of *adductor mandibulae* on maxilla placed anterior to isthmus, 19) coronoid process of dentary vertical, 20) posterior margin of gnathic ramus tall, 21) fused pharyngobranchials 2 and 3 with rough dorsal surface, 22) anterior margin of epibranchial 1 with elongate process located medially, 23) ceratohyals broad, 24) neural complex and fourth neural spine tall, 25) caudal skeleton broad, 26) anterior margins of cleithra together straight and blunt, 27)

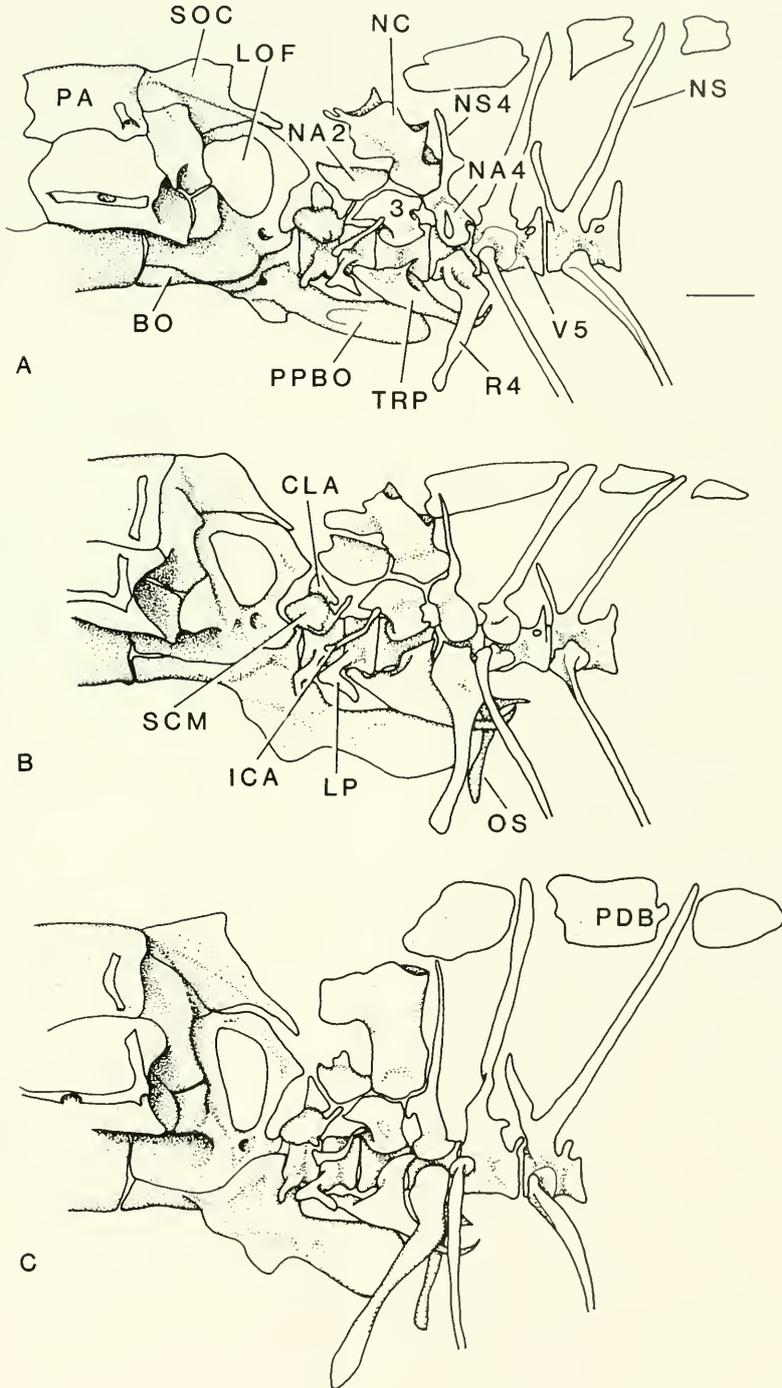


Fig. 33. Lateral view of occipital regions, Weberian apparatus, and anterior vertebrae and arches of some species of *Cyprinella* and close relatives. Left is anterior. A) *Lythrurus funeus*, 54 mm, KU 6244. B) *Cyprinella galactura*, 57 mm, KU 12029. C) *C. garmani*, 50 mm, KU 5416. Horizontal bar equals 1 mm.

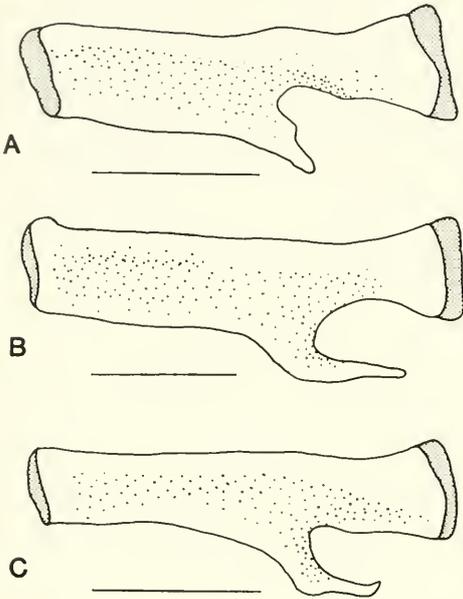


Fig. 34. Third epibranchial and elongate unciniate process of the genus *Luxilus* and outgroups, illustrating the derived elongate and curled unciniate process of the genus *Luxilus*. A) *Lythrurus ardens*, 72 mm, KU 4136. B) *Luxilus chrysocephalus*, 80 mm, KU 12654. C) *L. zonatus*, 67 mm, KU 12648. Horizontal bar equals 1 mm.

scapular bar pigment behind opercle and above pectoral fins, 28) spawning in crevices (not known for all species but hypothesized to be a synapomorphy), 29) pigmentation on scales above and below the lateral line in diamond-shaped pattern (Fig. 35), 30) gular stripe present (Fig. 36), 31) number of pharyngeal teeth in secondary tooth row 1 or 0, 32) tubercles on dorsum of head antrorse, 33) tubercle pattern discontinuous between dorsum of head and snout, and 34) caudal-peduncle scales above and below the lateral line with scattered central tubercles.

The derived scapular bar and gular stripe pigment patterns are unique to this genus. The diamond-shaped pigment pattern on scales is not unique to this group. A similar, but convergent color pattern occurs in *Erimystax monacha*, *Notropis maculatus*, *Hybopsis zanema*, and *H. labrosa*. The development of erect tubercles on the dorsum of the head is primitive for cyprinids with an open myo-

dome. Only a few species observed in this study have antrorse cephalic tubercles. These include *Lythrurus ardens*, *L. lirus*, *Cyprinella*, *Hybopsis zanema*, *H. labrosa*, and *Erimystax monacha*. The latter three species have previously been thought to be closely related to *Cyprinella*. With reference to Fig. 1, however, antrorse tubercles have evolved at least three times, once in *E. monacha* (Fig. 3), once in the ancestor of *H. labrosa* and *H. zanema* (Fig. 4), and once in the ancestor of *Cyprinella* (Fig. 1).

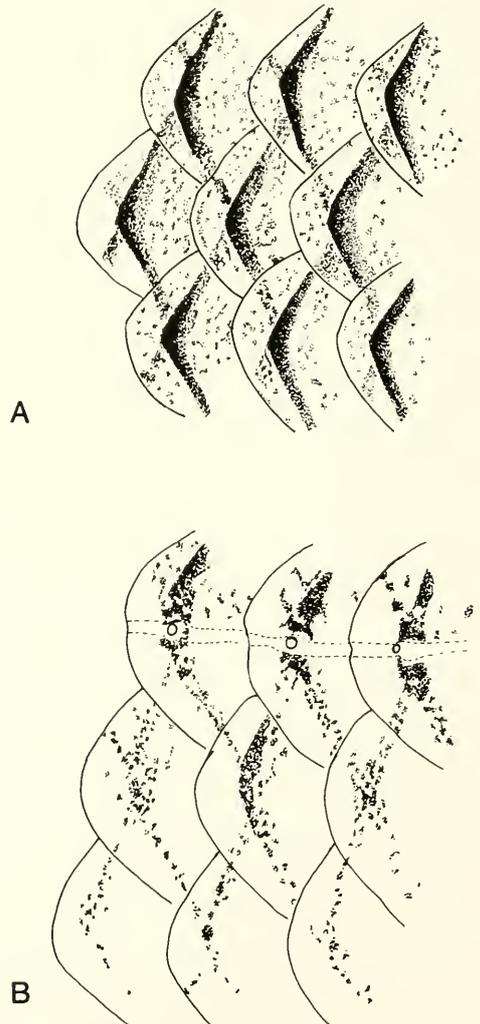


Fig. 35. Pigmentation on lateral body scales of *Cyprinella proserpina*, 42 mm, TNHC 9771. A) Scales above lateral line. B) Scales below lateral line.

A similar argument may be applied to the evolution of the diamond-shaped pigment pattern described above.

In most *Cyprinella* a hiatus exists between the snout tubercles and tubercles on the dorsum of the head. A few exceptions are known; *Cyprinella proserpina*, *C. panarcys*, *C. ornata*, *C. camura*, *C. galactura*, *C. pyrrhomelas*, and *C. xaenura* have no hiatus. In almost all outgroups the hiatus is absent between these two tuberculate regions. Thus, the hiatus is hypothesized to be a derived feature of *Cyprinella* and has apparently been reversed in some species of this group (see Phylogenetics section below). Generally, central tubercles do not exist on caudal-peduncle scales of outgroups, especially *Lythrurus* and *Luxilus*. Some members of the earlier discussed chub clade and the *Hybopsis* clade, however, develop convergent central scale tubercles on the caudal peduncle. The central tubercles of members of *Cyprinella*, are considered derived for the group.

Where known, all species of the genus *Cyprinella* have a distinctive and derived spawning behavior. All species are crevice spawners (Rabito and Heins, 1985). To date, spawning habits are known for *C. analostana*, *C. callitaenia*, *C. camura*, *C. galactura*, *C. leedsii*, *C. lutrensis*, *C. spiloptera*, *C. venusta*, and *C. whipplei*. Males of these species defend

territories around substrates where some type of crevice exists for deposition of eggs. This behavior is considered derived over the spawning behaviors typical of other species within and outside the clade with an open posterior myodome. Although not known for all species of *Cyprinella*, the behavior is predicted to be a synapomorphy for the genus. Outgroups typically deposit eggs in gravel substrates or release eggs in the open water column (Rabito and Heins, 1985).

Erimystax monacha appears to be an exception to this generalization of outgroup spawning behaviors. *Erimystax monacha* has been observed spawning in crevices like species of *Cyprinella* (R. E. Jenkins and N. M. Burkhead, pers. comm.) and a single hybrid between this species and *Cyprinella galactura* was reported by Burkhead and Bauer (1983). Because of the similar spawning habits and secondary sexual characteristics shared between *E. monacha* and species of the genus *Cyprinella*, one may hypothesize a close relationship between *E. monacha* and some species of *Cyprinella*, principally members of the *whipplei* clade. This is a reasonable hypothesis because secondary sexual characteristics and breeding behaviors shared by these species appear to be homologous. However, results from the present study indicate that it is more parsimonious to include *monacha* in the genus *Erimystax* of the chub clade than in the genus *Cyprinella*.

Pharyngeal dentition is variable in and between species groups having an open posterior myodome. However, because all species of *Lythrurus* and *Luxilus* modally have a 2, 4-4, 2 pharyngeal dentition and species of *Cyprinella* have 1, 4-4, 1 or 4-4 dentition, the reduction to a single tooth or no teeth in the secondary row is considered derived for the genus.

Genus *Notropis* (Fig. 1, Suite 13). Included in this group are the subgenera *Alburnops*, *Hydrophlox*, and *Notropis*, and the *volucellus* and *texanus* species groups. *Notropis greeniei* and *N. harperi* are also members of this clade, but are unassignable at this time to

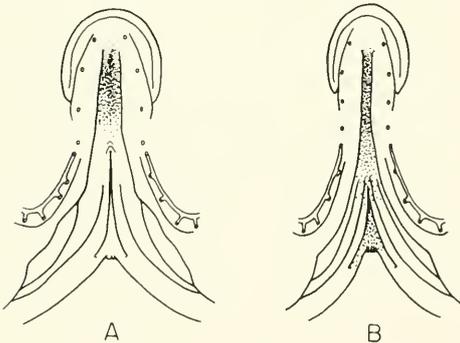


Fig. 36. Pigmentation of the gular region in the genus *Cyprinella*. A) Pattern present in all species of the *whipplei* clade and most members of the *lutrensis* clade. B) Pattern present in the *rutila* and *proserpina* species pairs.

any of the above groups. All of these groups and species are in an unresolved polytomy, except the subgenus *Notropis* and the *texanus* species group, which are sister clades (Fig. 1). All of these monophyletic species groups and subgenera share a single derived character of the basihyal projection mentioned above. In these species the posterior projection of the basihyal is well developed and rod like, sometimes extending below the first basibranchial. The basihyal projection is longer than that of the *Lythrurus-Luxilus-Cyprinella* clade and is thus considered a further modification of the presumably short ancestral condition. This conclusion is supported developmentally. Species with the elongate basihyal projection have a small process, like that observed in the *Lythrurus-Luxilus-Cyprinella* clade as juveniles. The only exception noted is that juveniles of *Lythrurus umbratilis* have a longer process than adults. As mentioned above, since no other cyprinids have this basihyal projection, the more elongate condition is considered evidence of the monophyly of this clade.

Subgenus *Alburnops* (Fig. 1, Suite 14). Seven species are presently included in this group: *Notropis edwardraneyi*, *N. blennius*, *N. simus*, *N. girardi*, *N. potteri*, *N. buccula*, and *N. bairdi* (Fig. 5). *Notropis orca* (Chemoff et al., 1982) may also belong to this clade. This species was not included in my analysis. In all seven of these species the palatine is extremely flattened medially (Fig. 10). This morphology is unquestionably derived since almost all outgroups have a thick palatine. Other taxa with a compressed palatine include *Notropis amoenus*, *N. stilbius*, *N. photogenis*, *N. scepticus*, *N. candidus*, *N. shumardi*, *N. oxyrhynchus*, and *N. jemezianus*, all of the subgenus *Notropis*, and *N. hypsilepis*. Because some members of the subgenus *Notropis* have a flattened palatine and since the *texanus* species group is the sister to *Notropis*, these morphologies are presently considered convergent in the two subgenera. This may not prove valid when additional data are available on subgeneric relationships.

Within *Alburnops*, one species group is

recognized including *N. potteri*, *N. buccula*, and *N. bairdi* (Fig. 5). This group is defined by an enlarged lacrymal and an elongate palatine (Figs. 10A,B; 37D–F). Other members of *Alburnops* and close outgroups have shorter palatines at a similar body size (Fig. 10C,D) and shorter lacrymals (Fig. 37A–C). *Notropis potteri* and *N. buccula* are sister species based on a greatly elongated lacrymal (Fig. 37E,F). Other species relationships in this subgenus are unresolved.

***Notropis volucellus* species group** (Fig. 1, Suite 15). Eight species are included in this clade. *Notropis heterolepis*, *N. emiliae*, and *N. maculatus* form one monophyletic group, sister to another composed of *N. buchanani*, *N. tropicus*, *N. volucellus*, *N. ozarcanus*, *N. spectrunculus*, and the undescribed “sawfin” shiner (Fig. 6). All of these species share two derived characteristics of the palatine. They all have a long, deep, and restricted preethmoid socket anteromesially on the palatine and an antero-laterally directed maxillary process (Fig. 22). Justification for this derived character of the palatine is presented under the discussion of the monophyly of the *Hybopsis* clade and is not repeated here. The conditions present in the *Hybopsis* clade and in the *Notropis volucellus* species group are similar but not homologous (Fig. 22).

Within the *Notropis volucellus* species group, *N. heterolepis*, *N. maculatus*, and *N. emiliae* share five derived characters (Fig. 6, Suite B): 1) pharyngeal pad of basioccipital narrow and without laterally flared edges, 2) interopercle deep, 3) operculum with deeply concave dorsal margin, 4) secondary tooth row of pharyngeal arch elevated on a pedestal, and 5) ascending arm of the pharyngeal arch flattened. These characters are discussed by Coburn (1982). In close outgroups and other members of the *volucellus* species group the pharyngeal pad is triangular with laterally directed wings, the interopercle is narrower, the dorsal margin of the opercle is only slightly concave, the ascending arm of the pharyngeal arch is rounded, and the secondary tooth row is not elevated.

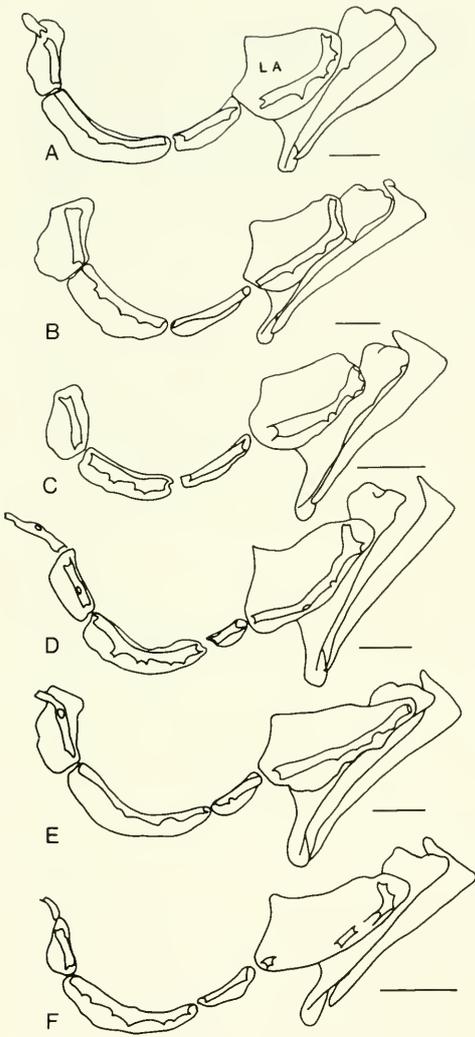


Fig. 37. Lacrymal bone and infraorbital series of species in the subgenus *Alburnops*. A) *Notropis blennioides*, 44 mm, KU 16045. B) *N. simus*, 48 mm, UMMZ 125064. C) *N. girardi*, 43 mm, KU 8039. D) *N. bairdi*, 53 mm, KU 18474. E) *N. potteri*, 49 mm, KU 14222. F) *N. buccula*, 36 mm, KU 14286. Horizontal bar equals 1 mm.

Notropis emiliae and *N. maculatus* share three characters (Fig. 6, Suite C) that were discussed by Gilbert and Bailey (1972). These include a long anterior arm of the pharyngeal arch, snout tuberculation, and crosshatched pigment pattern on lateral scales. I agree with these authors that these are derived characters suggestive of a close relationship.

Species of the second clade within the *Notropis volucellus* species group (Fig. 6, Suite D) share three derived features. These are: 1) elevated lateral-line scales, 2) supraethmoid broadened anteriorly with expanded dorso-lateral corners, and 3) very broad and posteriorly directed ascending wings of the parasphenoid. Other than the elevated flank scales in *Cyprinella* and *Luxilus*, the elevated lateral-line scale condition in these species is unique and derived. The broadened supraethmoid of these species (Fig. 38A,C) is also derived because a similar morphology is not frequently observed in outgroups. The broad and posteriorly directed ascending wings of the parasphenoid is derived for this group because close outgroups have narrow and laterally directed ascending wings of the parasphenoid.

Notropis volucellus, *N. spectrunculus*, *N. ozarcanus*, and the undescribed species (Fig. 6, Suite E) all share a ventrally deflected canal on the lacrymal bone (Fig. 38B,D). No other species of this group and close outgroups have this deflected canal. The group including *N. spectrunculus*, *N. ozarcanus*, and the undescribed species (Fig. 6, Suite F) is defined by two unique and derived features. All three species share two rows of large and erect tubercles on the leading ray of the pectoral fin of breeding males and a darkened spot on the leading 4–5 membranes and rays of the dorsal fin.

Subgenus *Hydrophlox* (Fig. 1, Suite 16). This clade was diagnosed by Swift (1970) as having the derived features of bright red and/or orange breeding colors in males, mainly concentrated on the body, lips, snout, cleithrum, and fins. Included here are *N. rubellus*; the *rubricroceus* species group which includes *N. rubricroceus*, *N. chiliticus*, *N. baileyi*, *N. chlorocephalus*, and *N. lutipinnis*; and the *leuciodus* species group including *N. leuciodus*, *N. nubilus*, and *N. chrosomus*. Monophyly and relationships in the *leuciodus* group are presented by Mayden (1987). Monophyly of the *rubricroceus* group is supported by Coburn (1982). All of these species share a derived high number of scale radii. Relationships of the three species groups of *Hydrophlox* (*rubel-*

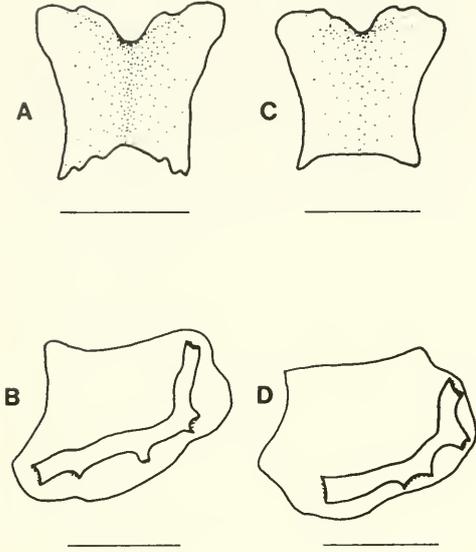


Fig. 38. Supraethmoid and lacrymal bone of *Notropis volucellus* (A and B; 40 mm, KU 17025) and *N. spectrunculus* (C and D; 41 mm, KU 5473). Horizontal bar equals 1 mm.

lus group, *rubricroceus* group, and *leuciodus* group) are unresolved.

Subgenus *Notropis*-*N. texanus* species group (Fig. 1, Suite 17). This clade of *Notropis* is diagnosed by Coburn (1982). All these species share the derived condition of having a large endopterygoid which extends beyond the vertical plate of the quadrate (Fig. 39). In most outgroups the endopterygoid terminates at or anterior to the posterior terminus of the vertical quadrate blade.

***Notropis texanus* species group** (Fig. 1, Suite 18). This group is more inclusive than that described by Swift (1970). Eight species are included: *N. petersoni*, *N. heterodon*, *N. anogenus*, *N. altipinnis*, *N. texanus*, *N. chalybaeus*, *N. boops*, and *N. xaenocephalus*. All of these species share four derived features (discussed by Coburn, 1982): 1) pharyngeal teeth with distinctly serrated edges, 2) large lapillar otolith, 3) black lateral stripe, bordered dorsally by a narrow depigmented stripe, and 4) enlarged tubercles on the snout and lower jaw. Within this group relationships are presently unresolved, except for the *N. boops*-*N. xaenocephalus* species pair. These two species

share the derived features of an enlarged eye and a large vomerine process on the palatine.

Subgenus *Notropis* (Fig. 1, Suite 19). Fourteen species are included in this clade, which was diagnosed by Coburn (1982). These include *N. candidus*, *N. shumardi*, *N. oxyrhynchus*, *N. jemezianus*, *N. atherinoides*,

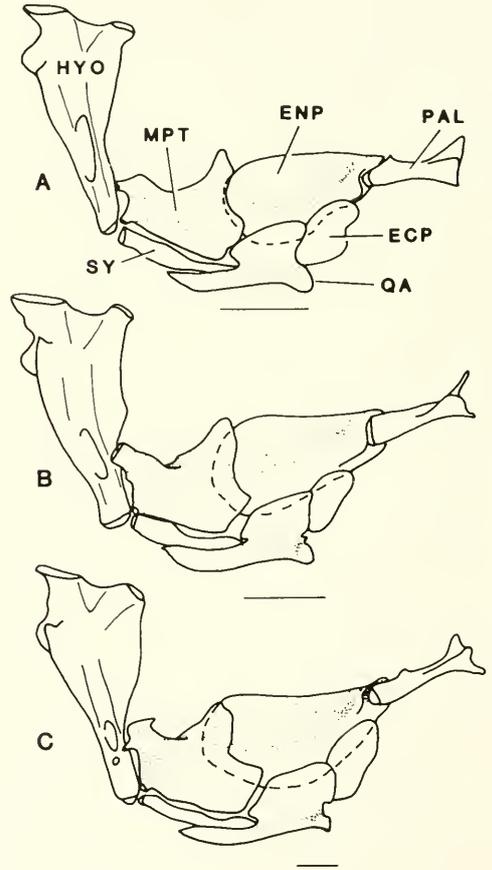


Fig. 39. Pterygoid series of some species of *Notropis* illustrating short and long endopterygoids relative to anterior fan of quadrate. A) *Notropis volucellus*, 40 mm, KU 17025. B) *N. texanus*, 44 mm, KU 19797. C) *N. amoenus*, 70 mm, INHS 77856. Horizontal bar equals 1 mm.

N. perpallidus, *N. amabilis*, *N. amoenus*, *N. stilbius*, *N. photogenis*, *N. telescopus*, *N. ariommus*, *N. scepticus*, and *N. semperasper*. For a discussion of monophyly of this group and species relationships within the subgenus see Coburn (1982).

SYSTEMATICS OF *CYPRINELLA**CYPRINELLA* GIRARD

Cyprinella Girard 1857, Proc. Acad. Nat. Sci. Philadelphia (1856) 8(5):196–197. Type: *Leuciscus bubalinus* Baird and Girard, 1853 [= *Leuciscus lutrensis* Baird and Girard 1853], by subsequent designation of Jordan and Gilbert, 1877:91.

Codoma Girard 1857, Proc. Acad. Nat. Sci. Philadelphia (1856) 8(5): 194–195. Type: *Codoma ornata* Girard, 1857, by subsequent designation of Jordan and Gilbert, 1877:91.

Moniana Girard 1857, Proc. Acad. Nat. Sci. Philadelphia (1856) 8(5): 199. Type: *Leuciscus lutrensis* Baird and Girard, 1853, by subsequent designation of Jordan and Gilbert, 1877: 91.

Photogenis Cope 1868, Proc. Acad. Nat. Sci. Philadelphia (1867) 19: 163–164. Type: *Leuciscus spilopterus* Cope, in Günther, 1868, by subsequent designation of Cope in Jordan and Copeland, 1877:154.

Erogala Jordan, in Jordan and Brayton, 1878, Bull. U. S. Nat. Mus. 12:20–21. Type: *Photogenis stigmaturus* Jordan, 1877b [= *Cyprinella venusta* Girard, 1857], by original designation.

Diagnosis. In addition to the synapomorphies listed under the previous section relating *Cyprinella* to other North American cyprinids, species of the genus *Cyprinella* may be distinguished from other cyprinids by the following derived characters: scapular bar of pigment behind opercle and above pectoral fins; spawning in crevices (not known for all species but hypothesized to be a synapomorphy); exposed margins of lateral scales taller than wide; pigmentation on scales above and below lateral line in diamond-shaped pattern; gular stripe present; fins of breeding males with milky-white deposition; number of pharyngeal teeth in secondary row 1 or 0; tubercles on dorsum of head strongly antorse; tubercle pattern discontinuous between dorsum of head and snout; caudal-peduncle scales above and below lateral line with scattered central tubercles; anterior border of trigeminal foramen formed

by pterosphenoid only; preopercle wide medially and anteriorly; interopercle deep posteriorly; anterior hyomandibular wing with notch; lateral shelf of quadrate wide; symplectic broad; frontals truncated anteriorly and anterolaterally; frontals slightly broadened laterally; supraethmoid very broad; supraorbital canal on frontals with elaborate development of canaliculi in a dendritic pattern; metapterygoid articulation with interhyal narrow; ventral horizontal plate of urohyal narrow; vomer with some neck developed; interorbital septum shallow; lacrymal elongate; occipital region compressed; ascending wings of parasphenoid broad; insertion of A1 branch of *adductor mandibulae* on maxilla placed anterior to isthmus; coronoid process of dentary vertical; posterior margin of gnathic ramus tall; fused pharyngobranchials 2 and 3 with rough dorsal surface; anterior margin of epibranchial 1 with elongate process located medially; ceratohyals broad; neural complex and fourth neural spine tall; caudal skeleton broad; and anterior margins of cleithra together form straight and blunt surface.

Composition. The following 27 species are included in the genus *Cyprinella*: *C. ornata*, *C. lutrensis*, *C. garmani*, *C. formosa*, *C. bocagrande*, *C. lepida*, *C. rutila*, *C. xanthicara*, *C. proserpina*, *C. panarcys*, *C. spiloptera*, *C. camura*, *C. whipplei*, *C. analostana*, *C. chloristia*, *C. venusta*, *C. galactura*, *C. pyrrhomelas*, *C. xaenura*, *C. caerulea*, *C. trichroistia*, *C. gibbsi*, *C. callistia*, *C. nivea*, *C. leedsi*, *C. callisema*, and *C. callitaenia*.

Distribution. Members of the genus *Cyprinella* inhabit rivers of eastern North America from the Atlantic Slope to central Mexico (Fig. 40). All species occur east of the Rocky Mountains except *C. ornata* and *C. formosa*. These species are found in parts of northwestern Mexico.

Classification of *Cyprinella*. The classification below is arranged in order of the phylogenetic relationships of the species, following the phylogenetic listing convention of Nelson

(1974) and Wiley (1979):

lutrensis clade

C. ornata (Girard)

lutrensis species group

C. lutrensis (Baird and Girard)

C. garmani (Jordan)

formosa species group

C. formosa Girard

C. bocagrande (Chernoff and Miller)

lepida species group

C. lepida Girard

rutila species pair

C. rutila (Girard)

C. xanthicara (Minckley and Lytle)

proserpina species pair

C. proserpina (Girard)

C. panarcys (Hubbs and Miller)

whipplei clade

C. piloptera (Cope)

whipplei species group

C. camura (Jordan and Meek)

C. whipplei Girard

C. analostana Girard

C. chloristia (Jordan and Brayton)

venusta species group

C. venusta Girard

C. galactura (Cope)

pyrrhomelas species group

pyrrhomelas species pair

C. pyrrhomelas (Cope)

C. xaenura (Jordan)

caerulea species complex

C. caerulea (Jordan)

C. gibbsi (Howell and Williams)

C. trichroistia (Jordan and Gilbert)

nivea species group

C. callistia (Jordan)

C. nivea (Cope)

C. leedsi (Fowler)

C. callisema (Jordan)

C. callitaenia (Bailey and Gibbs)

SPECIES ACCOUNTS

Below are accounts of the 27 species in the genus *Cyprinella*. Each account includes an abbreviated synonymy, including only genuine synonyms for each species. For a more complete synonymy of each species see Gibbs (1955; 1957a, 1957b, 1957c; 1961; 1963), Contreras-Balderas (1975), and various original descriptions. Each summary description includes meristic, coloration, and tuberculation characteristics, as well as distributional information, etymology, and an ecological summary. Data presented below are original from this study and/or summarized from Bailey and Gibbs (1965), Chernoff and Miller (1982), Contreras-Balderas (1975), Cross (1967), Denoncourt and Messersmith (1982), Forbes and Richardson (1908), Garman (1881), Gibbs (1955; 1957a, 1957b, 1957c; 1961; 1963), Girard (1857), Howell and Williams (1971), Hubbs and Miller (1978), Jordan (1877a, 1877b, 1877c; 1878a; 1878b; 1885), Jordan

and Brayton (1878), Jordan and Evermann (1896), Jordan and Meek (1884), Koehn (1965), Lytle (1972), Matthews (1987), Meek (1904), Minckley and Lytle (1969), Pflieger (1975), Smith (1979), Trautman (1957; 1981), and original descriptions of species. Patterns of breeding tubercles and melanophore distributions in dorsal fins for species of *Cyprinella* and close relatives are illustrated in Figs. 41–48. Species are illustrated in Plates 1–4. Species Accounts below are arranged in order of the phylogenetic relationships of the species, following the phylogenetic listing convention of Nelson (1974) and Wiley (1979).

CYPRINELLA ORNATA (GIRARD)

Ornate Shiner

Plate I

Codoma ornata Girard, 1857:195. [Orig. descr.; Type locality: Río Chihuahua and tribu-

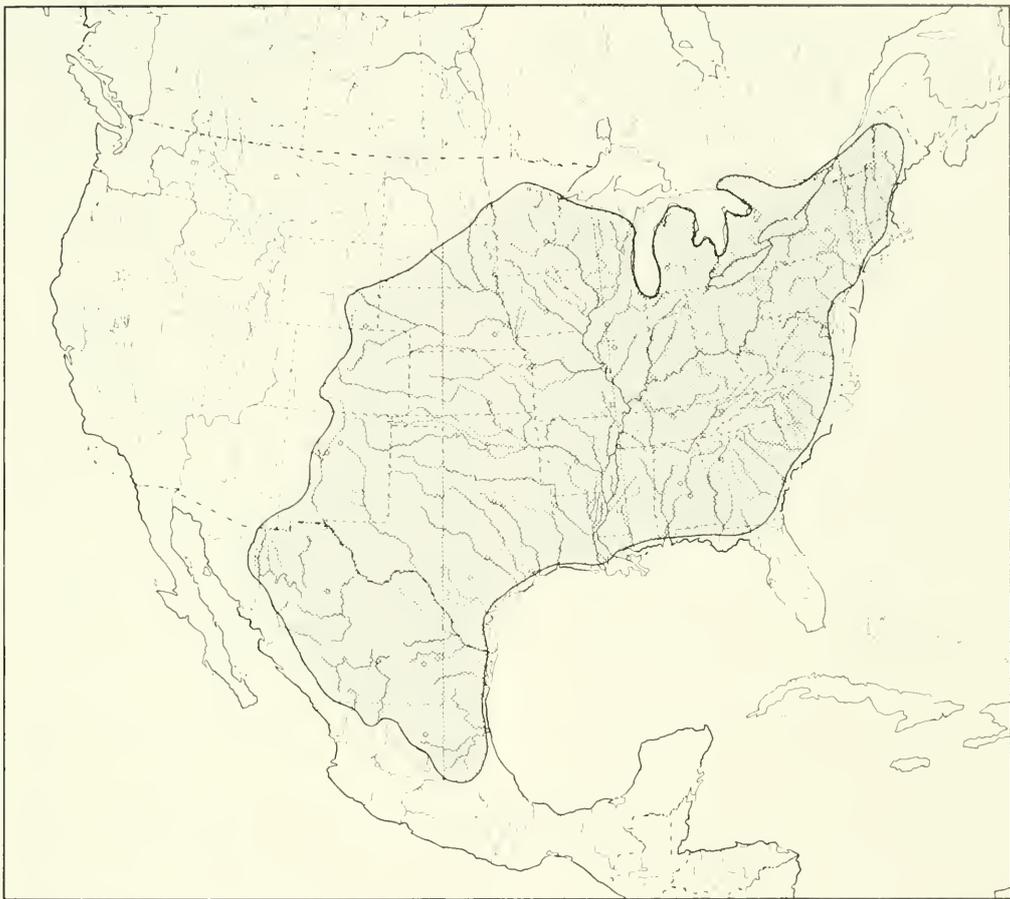


Fig. 40. Composite distribution for the ranges of species in the genus *Cyprinella*.

taries, near Chihuahua City, Chihuahua, México]

Diagnosis. Anal rays 7–8; tall and dark vertical bars along flanks; head blunt; base of caudal fin with whitish patches; hiatus between dorsal head and snout tubercles absent; pigmentation on scales above and below lateral line diffuse and scattered, not particularly diamond-shaped; supraethmoid process of palatine not strongly inflected above horizontal; anterior hyoideal foramen of ceratohyal located laterally; posterior hyoideal foramen of ceratohyal located mesially; hypohyal foramen small; sixth hypural absent; dorsal process of epibranchial four short; dorsolateral

shelf of dentary strongly developed; isthmus of maxilla deep; vomer without neck; posterior margin of horizontal urohyal plate oval and without notch; epiphyseal bar placed anteriorly without modifications to frontals.

Description. A medium-sized *Cyprinella*, attaining a maximum SL of about 60 mm. Body robust and only slightly compressed, deepest predorsally. Head rounded to subconical. Mouth terminal to subterminal, clinally variable, jaws unequal. Snout blunt. Orbit generally small. Caudal peduncle robust and deep. Dorsal fin not expanded in breeding males; origin over pelvic fin insertion.

Dorsal fin rays 6–9 (usually 8); anal rays 6–9 (7 in lower Conchos race and 8 in all others); pelvic rays 6–9 (7–8); pectoral rays 9–16 (13–14); principal caudal rays 17; dorsal procurrent rays 10 or 11, ventral procurrent rays 10–11 (10).

Exposed margins of lateral body scales higher than wide. Lateral-line scale rows 37–47 (41–43) in upper Conchos and 32–43 (36–38) in others; predorsal scales 15–24 (19–21 in Conchos and 16–18 in others); total predorsal circumferential scales 32–40 (34–37) in upper Conchos and clinal in others (25–38, generally 27–32, depending on drainage); predorsal scales above lateral line 15–19 (17) in upper Conchos and 11–16 (13–15) in others, below lateral line 15–19 (16–17) in Conchos or 12–18 (13–15) in others; total caudal-peduncle scales 16–22 (18–20) in Conchos or 12–20 (16–18) in others; scales above lateral line 5–10 (generally 7 in all but upper Conchos with 9), scales below 5–11 (7 in all except Yaqui and upper Conchos with 7–9).

Pharyngeal teeth 4–4, strongly hooked, and with well-developed grinding surfaces. Total gill rakers 6–8 (8). Total vertebrae 36–39 (37–38), precaudals 18 or 19, caudals 18–20 (19). Dorsal fin insertion above vertebrae 12–14 (12).

Lateral line complete to hypural plate. Supratemporal canal narrowly interrupted, pores 2. Supraorbital canal without interruptions and not joined with other canals, pores 7–8 (8). Infraorbital canal complete, pores 9–10 (10). Preoperculo-mandibular canal complete, total pores 11, mandibular pores 2.

Intestine simple, with single loop, Type I (Kafuku, 1958). Peritoneum silvery with speckling of melanophores.

Coloration in life.— Reproductive males darkly pigmented, nearly black in peak condition. Otherwise, dorsum dark, 9–14 lateral bars, variable in length, sometimes coalescing to form lateral stripe, darkest posteriorly. Lateral stripe obscured in peak males. Basicaudal spot present and usually separate from lateral stripe. Venter lightly pigmented, cream to white in some; other peak condition males mostly

dark bluish-black; gular region with scattered melanophores; postanal stripe absent in all but Mezquital race, in which it may be present. All fins darkly pigmented on rays and membranes, except for narrow distal white band. Base of caudal fin with whitish patches.

Females, like males, but paler. Venter unpigmented, including gular and branchiostegal regions. Intense black coloration over all of body not developed.

Tuberculation.— In prenuptial males dorsum of head mostly covered with erect tubercles located laterally in rows behind orbit and with clusters of erect organs between nares, above orbits, and between each orbit and naris. Internarial cluster of tubercles represents continuation of snout organs with dorsal tubercles. Snout tubercles erect and clustered, not necessarily in rows. Preorbital organs erect and continuous with snout tubercles and single row of 5–6 erect supraorbital tubercles. Remainder of head devoid of tubercles.

Body tuberculation weak compared to that of other species of the *lurensis* clade. Predorsal tubercles absent. Along flanks, 0–3 small, retrorse organs developed subcentrally on each scale, as in other members of this group. Broad band of organs on lower portion of caudal peduncle not developed. Each scale with 0–10 small, retrorse, subcentral tubercles; no central organs present in specimens examined. Strongest development occurs below lateral line.

All fins except pectorals with slight tubercle development on first 2 rays distally. First ray of pectoral fin with 1 row of tubercles, 1 organ per segment. Posterior rays 2–6 with 1 basal row, which continues onto posterior branch; anterior branch with 1 row. Each ray with 1 retrorse organ per segment. Ventral erect tubercles developed on paired fins.

Distribution. Contreras-Balderas (1975) recognized five races of *Cyprinella ornata*. These races are endemic to the upper Río Mezquital, Río Nazas, upper Río Conchos, lower Río Conchos, upper Río del Fuerte (not seen by Contreras-Balderas), and upper Río Yaqui of northwestern México. A distribution

map of the species, excluding Río del Fuerte populations, is provided by Contreras-Balderas.

Ecology. The biology of this species is poorly known. It inhabits clear streams with rubble or gravel substrate, where it frequents riffle or fast-water habitats. Spawning has been observed by Minckley (pers. comm.). Apparently this species spawns upside down under rocks. Such behavior is known to occur in the cyprinid genus *Pimephales* (Cross, 1967), a genus to which *C. ornata* has been thought to be related because of these reproductive characteristics and gross morphological similarities (Miller, 1976). It is not unusual, however, for species of *Cyprinella* to spawn on the undersides of objects in crevices (Pflieger, 1965), where their adhesive eggs attach to any substrate after spawned. Hendrickson et al. (1980) observed breeding *C. ornata* on 16 June over bedrock and boulder riffles, defending areas around crevices and loose rocks on the bottom. Ova were attached to the undersides of the stones. Meek (1904) believed spawning to occur in early June. In May, 1987, adult males from the Río Conchos, Río Yaqui, and Río del Fuerte were observed defending territories in riffle and raceway habitats around gravel and cobble substrate (Mayden, unpub. data). No eggs were found attached to any of the substrate materials.

Etymology. The name *ornata* is Latin from *ornare* meaning ornamented or showy, referring to coloration of breeding individuals.

Comments. Contreras-Balderas (1975) recognized five races of *C. ornata*, the Río Mezquital, Río Nazas, upper Río Conchos, lower Río Conchos, and upper Río Yaqui. Populations from the upper Río del Fuerte were not examined. These "races" were found to differ meristically, morphometrically, and in color and tuberculation patterns; and may eventually be recognized as distinct species.

The relationship of the ornate shiner to other minnows has been uncertain. Gibbs (1957a) considered the ornate shiner to be a member of *Cyprinella*. Contreras-Balderas (1975, 1978) and Miller (1976, 1978) recog-

nize the genus *Codoma* for the ornate shiner and have considered the possibility that it is related to the genus *Pimephales*. This conclusion is based on gross morphological similarities, snout tuberculation, and spawning habits of the species. Results of this analysis are in agreement with Gibbs and demonstrate that *C. ornata* represents the sister group to the remaining members of the *lutrensis* clade.

CYPRINELLA LUTRENSIS (BAIRD AND GIRARD)
Red Shiner
Plate I

Leuciscus lutrensis Baird and Girard, 1853:391. [Orig. descr.; Type locality: Otter Cr., trib. to N. Fk. Red River, either Kiowa or Tillman Co., OK]

Leuciscus bubalinus Baird and Girard, 1853:391. [Orig. descr.; Type locality: Otter Cr., trib. to N. Fk. Red River, either Kiowa or Tillman Co., OK. Hubbs and Ortenburger (1929), as first revisers, chose *lutrensis* over *bubalinus*, as both were described on the same page]

Cyprinella beckwithi Girard, 1857:197. [Orig. descr.; Type locality: Sluices of Arkansas River, near Ft. Makee, KS]

Cyprinella gunnisoni Girard, 1857:197. [Orig. descr.; Type locality: Cottonwood River, ca. 5 mi NW Durham, Marion Co., KS (after Gilbert, 1978a)]

Cyprinella suavis Girard, 1857:197. [Orig. descr.; Type locality: near San Antonio, TX]

Cyprinella umbrosa Girard, 1857:197. [Orig. descr.; Type locality: Coal Creek, trib. to South Fork Canadian River, N of McAlester, Pittsburg Co., OK]

Moniana leonina Girard, 1857:199. [Orig. descr.; Type locality: Leon River, trib. to San Antonio River, Bexar Co., TX]

Moniana frigida Girard, 1857:200. [Orig. descr.; Type locality: Salado Creek, just E San Antonio, Bexar Co., TX; Río Sabinal, at Sabinal, Uvalde Co., TX; Río Medina, at Castroville, Medina Co., TX; Río Nueces, ca. 7 mi W Uvalde, Uvalde Co., TX; Río Frío, ca. 10 mi

NE Uvalde, Uvalde Co., TX]

Moniana pulchella Girard, 1857:200. [Orig. descr.; Type locality: Sugar Loaf Creek, trib. Poteau River, about 20–25 mi S Fort Smith, AR, vicinity of Poteau, OK]

Moniana complanata Girard, 1857:200. [Orig. descr.; Type locality: Río Grande (or tributary), Brownsville, Cameron Co., TX]

Moniana laetabilis Girard, 1857:200. [Orig. descr.; Type locality: Hurrah Creek (trib. Pecos River), ca. 10 mi NE Santa Rosa (35°05' 23.7"N, 104°43'27.3"W), Guadalupe Co., NM]

Moniana couchi Girard, 1857:201. [Orig. descr.; Type locality: Río San Juan, vicinity of China, Nuevo León, México]

Moniana gibbosa Girard, 1857:201. [Orig. descr.; Type locality: trib. to Río Grande, Brownsville, Cameron Co., TX]

Cyprinella billingsiana Cope, 1871:439. [Orig. descr.; Type locality: Missouri River, St. Joseph, MO]

Moniana jugalis Cope, 1871:439–440. [Orig. descr.; Type locality: Missouri River, St. Joseph, MO]

Hypsilepis iris Cope in Cope and Yarrow, 1875:653–654. [Orig. descr.; Type locality: Río Grande, at San Ildefonso, ca. 10 mi E Los Alamos, Santa Fe Co., NM]

Cyprinella forbesi Jordan, 1878b:57–58. [Orig. descr.; Type locality: Illinois River, Union Co., IL]

Notropis forlonensis Meek, 1904:70–71. [Orig. descr.; Type locality: Río Forlon, trib. Río Pánuco, Forlon, Tamaulipas, México]

Notropis lutrensis blairi Hubbs, 1940:6–8. [Orig. descr.; Type locality: Garden Springs (=Monument Spring), trib. Peña Colorado Creek (Maravillas Creek drainage), 12–13 mi SSW Marathon, Brewster Co., TX. Elevation 3700 ft]

Diagnosis. Anal rays 9; body generally deep; fins of breeding males red; chin bar short; scapular bar well developed; flank scales above lateral line with single central tubercle; neck on ceratobranchial 1 bent mesially; posterior process of quadrate deep and heavy; anterior notch on vomer deep; hypohyal foramen small.

Description. A moderately large *Cyprinella*, reaching a maximum of about 75 mm SL. Body form geographically variable. Individuals from Mississippi River tributaries, Río Grande proper, and Río Grande tributaries (ríos San Juan, Pecos, and Conchos) have a very deep body with highly arched back, deepest at dorsal origin, and are highly compressed. Head large and deep. Snout pointed. Orbit small. Mouth and gape width moderately large, maxillary extending to middle or anterior orbit. Caudal peduncle deep and robust. Dorsal fin origin over or slightly posterior to insertion of pelvic fin. Individuals from Gulf Coastal drainages (here considered *C. l. suavis* and *C. l. forlonensis*) are much more slender and elongate with a narrower body, head, and caudal peduncle, larger orbit, and smaller mouth. Dorsal fin not expanded in breeding males and inserted over pelvic fin insertion. These trends are discussed by Matthews (1987) for populations within the United States and by Contreras-Balderas (1975) for populations in México.

Values for meristic characters generally increase from east to west and southward from upper Mississippi, through the Platte, Kansas, Arkansas, upper Río Grande, and Conchos drainages. Meristics generally decrease east and south in the Neosho, Verdigris, Canadian, upper Red, and lower Red-Mississippi drainages. Meristics of populations from Gulf Coastal drainages from the Sabine-Calcasieu system westward are also variable. In the Sabine-Calcasieu system low circumferential and lateral-line scale counts predominate in addition to the lowest means of all drainages for caudal-peduncle and predorsal scales, but overlap occurs. Variation in meristic features of populations west of the Trinity River show no significant concordant variation other than slightly higher means for circumferential and caudal-peduncle scales.

Dorsal fin rays 6–12 (8); anal rays 8–10 (9); pelvic rays 4–9 (8); pectoral rays 8–16 (12–14); principal caudal rays 17; dorsal procurrent rays 11–13 (12), ventral procurrent rays 10–11 (10).

Exposed margins of lateral and dorsolateral

body scales higher than wide. Lateral-line scale rows 28–38 (all 33–36, except *forlonensis* with 32–34); predorsal scales 13–21 (15–18 in most, except Río Conchos with 16–19); total predorsal circumferential scales 22–33 (24–29); scales above lateral line 11–17 (13–15), below lateral line 8–15 (9–12); total caudal-peduncle scales 12–20 (14–16, most with 14, except 14–18 in Río San Fernando and 16–18 in Río Conchos and upper Río Grande); caudal-peduncle scales above lateral line 5–9 (most with 7, except ríos San Fernando, Conchos, and upper Grande with 7–9), scales below lateral line 5–7 (most with 5, except Río San Fernando and upper Río Grande with 5–7 and Conchos with 6–7).

Pharyngeal teeth generally 4–4. Teeth hooked and with well-developed grinding surfaces. Total gill rakers 8–11 (10). Total vertebrae 34–36 (35), precaudals 16–18 (17), caudals 17–19 (18). Dorsal fin insertion above vertebrae 10–12 (11).

Lateral line generally complete to hypural plate. Supratemporal canal broadly interrupted, pores 2 per side. Supraorbital canal complete, pores 8. Infraorbital canal complete, pores 10–11 (11). Preoperculo-mandibular canal complete, total pores 10–12 (11), mandibular pores 3.

Intestine with two simple flexures, forming S-shaped coil, Type I. Peritoneum silvery with sparse speckling of melanophores.

Coloration in life.—Females and nonbreeding males pallid. Dorsum olive, metallic blue, or bluish-green turning to bluish-silver laterally and white or cream ventrally. Fins lightly colored; anal and caudal sometimes with light orange or red; dorsum dusky; pectorals and pelvics depigmented except for leading rays with some melanin.

Breeding males brightly colored. Dorsum bright blue, greenish, or bluish-green. Dorsum of head same, but may be bright red or rufous. Opercles, subopercles, and posterior preopercles and interopercles generally pink or light reddish orange. Flanks lighter, with powder-blue background overlain by a dark steel-blue crosshatched pattern forming heav-

ily pigmented crescents on each scale. Centers of scales powder-blue or sometimes pinkish. Crosshatched pattern obliterated just posterior to opercle by dark blue wedge-shape scapular bar and pink or reddish rectangular area posterior to bar. Venter white, silver, cream, or red. Gular bar short and dark, extending from symphysis to retroarticular-interopercle region. Side of head silver. Pectoral and pelvic fins red to reddish-orange, except for milky-white distal margins. Anal fin darkened basally by melanin, red medially, and white distally. Caudal fin reddish except for clear or whitish distal margin. Dorsal fin heavily pigmented with interradiation and radial melanophores, over a background of light reddish tint.

The above description pertains to the most frequently observed color pattern, but variations are known to exist. As an example, Hubbs (1982) suggested that at least 5–10 different forms of “*lutrensis*” could be distinguished from the Trans-Pecos Region of Texas alone. Characteristics and distributions of these forms were not given.

One variation is what Matthews (1987) refers to as the “yellow-fin form.” These individuals are geographically restricted, have a typical *lutrensis* body form, lack the red or reddish-orange fin coloration, and have been collected with the “typical” red shiner “morph.” Populations of this form are known from Kingman, Jefferson, and Cowley Cos., KS and Baron Co., MO. Coloration basically consists of bluish dorsum and sides. The head is not red dorsally and the scapular bar is not set off from remainder of flank by depigmented or lightly pigmented rectangular region posteriorly. Pectoral, pelvic, anal, and caudal fins are consistently yellow. Another variant, in some Gulf Coastal populations, has a deep red venter, unlike breeding *lutrensis* observed elsewhere.

Tuberculation.—Dorsum of head of smaller, younger males or prenuptial males with moderately sized antrorse tubercles in linear pattern. Later in development, linear pattern of 2 rows down midline obscured by development of additional tubercles on occipital region, obliterating linear pattern on

postorbital area. Two rows anterior to postorbit. Supraorbital tubercles moderately large, about same size as dorsal head tubercles, continuing beneath each nare and connected with snout tubercles. Generally, no preorbital tubercles develop close to orbit. At anterior edge of lacrymal, where supraorbital row connects with snout tubercles, 3–5 erect, moderately large tubercles are formed. Snout tubercles few and scattered, antrorse posteriorly and erect anteriorly, and separated from dorsal head tubercles by wide hiatus. Except for a few erect, moderately large tubercles restricted to dorsal one-third of opercles, no other tubercles develop on head.

Predorsal scales generally with 3 moderately large tubercles in transverse row, similar in size to dorsal head tubercles or slightly smaller. Central tubercle sometimes slightly larger than lateral tubercles. At edge of each predorsal scale several retrorse organs (some erect) present. Along flanks, scales with 1–2 centrally located antrorse organs, smaller than predorsals by half. Around these, 0–5 erect submarginals may develop per scale, but are generally absent. Flank scales also with 3–15 retrorse edge tubercles similar in size to submarginals and about one-half size of central tubercles. Below lateral line, above and anterior to pelvic fins, each scale with small edge tubercles only.

Caudal peduncle tuberculation complex, beginning above and posterior to pelvic fins and extending to hypural plate. Maximum development above anal fin. Below lateral line, 1–4 (almost always 3 in peak males) moderately large, antrorse organs in center of each scale. Marginal to these, 1–4 moderately large and slightly antrorse organs developed. Along edge of scale, 3–8 small retrorse tubercles developed in a series. Scales above lateral line similar, but organs much smaller.

Tubercle development on dorsal fin does not occur until male is in peak breeding condition. Pelvic fins tuberculate, with a single row per ray and 2 tubercles per segment. Dorsal and anal fins both with tubercle development on first ray; both with a single row per ray and

single tubercle per segment. First ray of pectoral fin with a single row of tubercles and 2–3 organs per segment. Early in development, posterior rays 2–7 with single row per ray; later single row turns to 2–4 rows on main body of each ray, with several tubercles per segment. Distal to branching, pectoral fin rays of early males with single row and 2–3 organs per segment; peak breeding males generally have 2 rows and several tubercles per segment. In extremely tuberculate males, row pattern obscured by thick mat of tubercles. Ventral sides of paired fins with erect tubercles on rays.

Distribution. Native to the upper Mississippi basin as far north as southern Wisconsin and western tributaries to the Mississippi river, including the Missouri, Arkansas, and Red rivers. Along the Gulf Slope, the red shiner inhabits rivers from near mouth of Mississippi River westward and southward to the Río Panuco, México. The red shiner also occurs in the Río Grande basin, inclusive of ríos Conchos, Salado, and San Juan. This aggressive species has been introduced into many areas in U.S., and where introduced may sometimes “swamp-out” native *Cyprinella* gene pools via hybridization (Page and Smith, 1970).

Ecology. Considering the broad range of this species and its widespread use as a baitfish, little is known of its biology. Detailed studies include those of Cavin (1971), Laser and Carlander (1971), and Farringer et al. (1979). Other studies and general comments on its biology have been published (Saksena, 1962; Koehn, 1965; Cross, 1967; Islam, 1972; Minckley, 1972, 1973; Miller and Robison, 1973; Pflieger, 1971, 1975; Matthews and Hill, 1977). Basically, the red shiner is an aggressive species, capable of inhabiting a variety of habitats and environments, but is generally atypical of highland regions of the central U.S. It does well in harsh and variable environments when other species disappear (Cross, 1967) and has a high tolerance for low oxygen levels (Cavin, 1971). It prefers creeks with moderate or intermittent flow (Paloumpis, 1958), but also frequents large rivers over a sand, silt, or gravel

substrate. It appears to be quite tolerant of turbidity and siltation.

In Illinois and Missouri most red shiners live 2+ years (Lewis and Gunning, 1959; Pflieger, 1975). Its reproductive cycle in Oklahoma and Texas spans from April to September, in Missouri from May to September, in Kansas from May to October, and in Illinois from May to August. Ovarian regression in Oklahoma and Texas occurs in midsummer with increased temperature and aridity, but some data on length frequency and ovarian recrudescence indicate two peak periods of spawning activity. Most if not all individuals breed during their second summer, with very few breeding during the first summer (Farringer et al., 1979). Some data from Illinois red shiners, however, suggests that 2-year-old individuals spawn in July and the 1-year-old fish spawn later in August and September (Lewis and Gunning, 1959).

Spawning locations vary. Males and females may congregate in pools below riffles or near brush, logs, or other debris where the eggs are fertilized, settle to the substrate, and adhere to various objects (Minckley, 1972; Smith, 1979). In some cases the red shiner may spawn over nests of sunfish (*Lepomis cyanellus*, *L. humilis*). Males defend territories near the margins of the sunfish nests where the eggs are released (Minckley, 1959; Pflieger, 1975). Spawning occurs most frequently, however, in clean gravel riffles, or on submerged objects (e.g., logs and tree roots), where the eggs are deposited in crevices (Pflieger, 1975; see also Minckley, 1972). Minckley (1972) also reported that spawning may occur in midwater while the pair swims through the water column. The demersal, adhesive, and yellowish-white fertilized eggs are then spread over the substrate.

When single territories are maintained by a male, a female swims into the area, eliciting display behavior by the male consisting of several "figure 8" movements before swimming near the female. Once the male is alongside the female, the two move side by side through or near the substrate (gravel, algae,

logs, roots) while releasing eggs and milt.

Etymology. The name *lutrensis* is Latin for Otter, in reference to Otter Creek, Arkansas, where first discovered.

CYPRINELLA GARMANI (JORDAN)

GIBBOUS SHINER

PLATE I.

Notropis garmani Jordan, 1885:813. [Substitute name for preoccupied *rubripinna* Garman, 1881]

Cyprinella rubripinna Garman, 1881:91. [Orig. descr.; Type locality: Lago del Muerto, near Parras, Coahuila, México]

Diagnosis. Anal rays typically 10; body very deep; caudal peduncle very slender; anal fin placed anteriorly such that a vertical line dropped from posterior base of dorsal fin intersects base of anal fin posterior to base of second principal ray (Chernoff and Miller, 1986); gular bar short; mandibular pores 4; preorbital tubercles distributed over entire lacrymal area; dorsal head tubercles erect; pharyngeal pad of basioccipital flat.

Description. A large *Cyprinella* for the *lutrensis* clade, reaching about 60 mm SL. Body deep and strongly compressed; dorsum convex, strongly arched, deepest at dorsal origin. Head moderately large. Snout blunt to subconical. Mouth small, terminal, oblique; maxillary extending to anterior margin of orbit. Caudal peduncle narrow and elongate. Dorsal fin not expanded in breeding males and origin in both sexes over anal fin.

Dorsal fin rays 8–9 (8); anal rays 9–13 (10–11); pelvic rays 7–9 (8); pectoral rays 11–14 (12–13); principal caudal rays 17; dorsal procurrent rays 9–12 (11–12), ventral procurrent rays 10 or 11.

Exposed margins of lateral and dorsolateral body scales higher than wide. Lateral-line scale rows 33–40 (35–37); predorsal scales 16–24 (19–21); total predorsal circumferential scales 24–35 (29–30); scales above lateral line 13–19 (15–16), below lateral line 9–16 (11–13); total caudal-peduncle scales 12–17 (14); caudal-peduncle scales above lateral line

5–9 (7), below lateral line 4–7 (5).

Pharyngeal teeth 4–4, well hooked, narrow, but with moderately well-developed grinding surfaces. Total gill rakers 9–10 (9). Total vertebrae 35–36 (36), precaudals 16–18 (17), caudals 17–20 (18–19). Dorsal fin insertion above vertebra 12 or 13 (12).

Lateral line complete to hypural plate. Supratemporal canal broadly interrupted, pores 2. Supraorbital canal complete, pores 7–9. Infraorbital canal weakly developed, partially interrupted, pores 11–12. Preoperculo-mandibular canal complete, total pores 9–12 (11–12), mandibular pores 3–4 (4).

Intestine simple, single loop with two flexures, Type I. Peritoneum silvery with speckling of melanophores.

Coloration in life.—Coloration similar to that of *C. lutrensis*. Females and nonbreeding males lightly colored. Bright colors absent except on anal and caudal fins, where light red may develop. Venter cream to white. Lateral body silver-blue. Dorsum bluish-gray, venter light cream to white. Dark lateral band weak anteriorly and strong posteriorly; caudal spot absent. Dark scapular bar present immediately behind head, offset by lighter, rectangular area posteriorly. Pigment on flank scales in diagonal rows, presenting diamond-shaped pattern. Venter immaculate. Fins with scattered melanophores, appearing dusky.

Breeding males as above except more brilliantly colored over body and fins. Rectangular region behind scapular bar red. Dorsal fin heavily pigmented with melanophores and all fins reddish. Scapular bar and gular stripe dark.

Tuberculation.—Dorsum of head covered with moderately large, erect tubercles in semi-scattered pattern. Tubercles arranged linearly in small and early season males. Postorbital region with some scattered tubercles, tending to obscure linear pattern. Snout with cluster of erect tubercles equal in size to dorsal tubercles and separate from dorsum by hiatus. Above orbits, 4–5 moderately large organs arranged in single row. Remainder of head devoid of tubercles, except for few (2–3) small, erect or-

gans on dorsal operculum.

Predorsally, 3 moderately large, erect organs in semilinear arrangement in center of each scale; periphery of each scale with series of small erect organs. Scales along flanks with 5–10 small retrorse edge-tubercles each. Scales along lower caudal peduncle and 3 scale rows above anal fin heavily coated with tubercles. Center of each scale with a cluster of moderately large, antrorse organs. Antrorse submarginal organs and a series of antrorse or retrorse edge tubercles peripheral to central row. Ventral row of caudal-peduncle scales also with this pattern. Dorsally on caudal peduncle only small, erect edge tubercles present.

All fins tuberculate. Dorsal rays 1–6 with single row per ray and single organ per segment, developed medially. All rays of anal fin with a single row per ray and 1–2 tubercles per segment. Pelvic fin rays with 2–3 tubercles per segment in a single row on rays 1–5. Leading pectoral fin ray with a single row of 2 retrorse organs per segment. Pectoral rays 2–9 tuberculate; single row basally becoming 2 rows prior to segmentation. After segmentation each segment with 4–6 organs. Distal to branching, one row anteriorly with 2 organs per segment and 2 rows posteriorly, with 4 tubercles per segment. Ventrally, pectoral and pelvic fins with several erect organs per ray.

Distribution. This species is known only from ríos Nazas and Aguanaval of north-central México. A distribution map is provided by Contreras-Balderas (1975, 1978).

Ecology. Very little information. Meek (1904) thought spawning may occur in late May and in June.

Etymology. Named after Samuel Garman.

Comments. This species was thought by Meek (1904) and Contreras-Balderas (1975, 1978) possibly to be a subspecies of *C. lutrensis*. Because of the several unique characteristics of this species, I follow Miller (1978) and Chernoff and Miller (1982) in recognizing this taxon as a distinct species.

CYPRINELLA FORMOSA (GIRARD)

BEAUTIFUL SHINER

PLATE I

Moniana formosa Girard, 1857:201. [Orig. descr.; Type locality: Río Mimbres, Chihuahua, México = Mimbres River, north of Deming, Luna Co., NM (following Gilbert, 1978a)]

Notropis santamariae Evermann and Goldsborough, 1902:147. [Orig. descr.; Type locality: small pool near Lake Santa María, Chihuahua, México]

Notropis mearnsi Snyder, 1915:582–584. [Orig. descr.; Type locality: San Bernardino River, near monument 77 of the international boundary, Sonora, México]

Diagnosis. Anal rays 8; lateral line usually incomplete; gular bar short; mandibular tubercles present; breast fully scaled; dorsal margin of anguloarticular horizontal; epibranchial 4 with short mesial to dorsal process; overlap between supraorbitals and lateral ethmoids slight; basihyal deep; mentomeckelian deep.

Description. A large shiner in the *lutrensis* clade, reaching a maximum size of about 70 mm SL. Body somewhat terete and deep; dorsal profile slightly convex. Head large and triangular. Snout pointed to slightly rounded, frequently rounded in the northern Río Yaqui. Mouth subterminal and slightly oblique, but variable; northern Río Yaqui individuals with terminal mouth, Río Santa María populations with rounded snout and oblique mouth, and those from Río Sauz and Laguna de Encinillas of northern Chihuahua with very oblique mouth and round snout. Caudal peduncle moderately deep. Dorsal fin not expanded in breeding males and origin in both sexes above pelvic fin insertion.

Dorsal fin rays 7–9 (usually 8); anal rays 7–10 (8); pelvic rays 5–9 (8); pectoral rays 10–14 (12–13); principal caudal rays 15–17 (17); dorsal procurrent rays 10–13 (12–13), ventral procurrent rays 9–12 (10–11).

Exposed margins of lateral scales slightly higher than wide and crenulate. Lateral-line scale rows 34–47 (variable between drain-

ages; Santa Clara, Yaqui, and Santa María generally 35–38, and Casas Grandes and Sauz 38–43); predorsal scales 15–26 (variable as above 17–19 and 19–24); total body circumferential scale rows 26–41 (Santa Clara, Yaqui, Santa María 28–33, Sauz 31–34, Casas Grandes 33–38); scales above lateral line 13–20 (Sauz, Yaqui, Santa María 15–17, Santa Clara 17, Casas Grandes 17–19), scales below lateral line 10–19 (all 11–15, except Casas Grandes with 14–17); total caudal-peduncle circumferential scales 14–24 (Sauz and Santa Clara 17–19, Yaqui and Santa María 15–18, Casas Grandes 18–22); above lateral line 7–11 (all 7–9, except Casas Grandes with 9–11), below lateral line 5–11 (all 6–8, except Casas Grandes with 7–9).

Pharyngeal teeth 4–4, well hooked, and with moderate grinding surfaces. Total gill rakers 7 or 8. Total vertebrae 35–37 (36), precaudals 16–18 (17), caudals 18–20 (19). Dorsal fin insertion above vertebrae 11–13 (12).

Lateral line complete or incomplete. Supratemporal canal interrupted, pores 2. Supraorbital canal without interruptions and separate, pores 8–9 (9). Infraorbital canal incomplete in some before and below orbit, pores 9–11 (10). Preoperculo-mandibular canal complete, total pores 8–11 (9–10), mandibular pores 3–4 (3).

Intestine simple S-shaped loop with two flexures, Type I. Peritoneum silver with light speckling of melanophores.

Coloration in life.—Females and nonbreeding males with less intense coloration than breeding males. Dorsum olivaceous to brown; remainder of body light yellow to cream. Lateral stripe present, but lighter than in breeding males. Fins clear to light orange.

Breeding males dark and brilliantly colored. Coloration of dorsum variable within and between drainages (Chernoff and Miller, 1982). Some breeding males with blue to greenish-blue dorsum and others yellow. Remainder of body yellowish, except for reddish-orange caudal peduncle. Lateral stripe bluish and best developed posteriorly, diffuse anteriorly.

orly. Scales with pigmented edges, producing diamond-shaped pattern laterally and dorso-laterally. Belly and breast cream. Gular stripe short and dark. Fins dark reddish-orange.

Tuberculation.— In nuptial males dorsum of head covered with moderately sized, erect tubercles in scattered pattern. Smaller males from same collections or males from earlier in season with linear pattern as in young *C. lutrensis*. Linear pattern of these males later obscured with further tubercle development to form scattered pattern, at least posteriorly. Snout with several small, erect organs scattered and separated from dorsal tubercles by small hiatus. Preorbital region with 2–3 erect organs equal in size to dorsal head tubercles. Mandibular rami with 2–3 moderately large, erect tubercles at posterior edge. Small, erect organs present on upper one-third of opercle. Remainder of head devoid of tubercles.

Body tuberculation extensive. Predorsal region with 7–10 small, retrorse edge tubercles per scale; no central or subcentral tubercles present. Along flanks, 9–15 retrorse, small edge tubercles above and below lateral line; no central organs present. Tubercles of caudal peduncle organized into patch, more elaborate than in any other member of *lutrensis* group. Lower caudal peduncle and area above anal fin with similarly sized, retrorse tubercles (smaller than those on *lutrensis*) densely packed on each scale. Dorsally, most scales with a series of up to 30 small retrorse edge tubercles. Early in development, lower caudal-peduncle scales with only retrorse edge organs and a vertical row of central tubercles. Later, another row adjacent and medial to edge tubercles develops; still later, with further development of central tubercles this is obliterated and the dense pattern develops.

All fins tuberculate. Dorsal and anal fins with single row of 1–3 tubercles per segment on all rays basally and medially. Pelvic fins with same pattern, but restricted to rays 1–3. First ray of pectoral fin with single row of retrorse tubercles arranged with 2–3 per segment. Posterior rays 2–6 with fine retrorse organs in shagreen pattern, best developed an-

teriorly. Basally, pattern begins as 1 row of tightly compressed organs and increases to 4 rows before segmentation. Between segmentation and branching, 4 rows arranged in parallel with 2–3 organs per row or 8–12 per segment, with no breaks in pattern at segment margins. Beyond branching, two rows developed per branch and 2–3 organs per row or 4–6 per segment. Tubercles extend almost to edge of fin. Paired fins with well-developed rows of ventral tubercles.

Distribution. Known only from ríos Casas Grandes, Santa María, del Carmen, and Mimbres of the endorheic Guzmán basin, and ríos Yaqui, Sauz, and Bavícora of northwestern México and southern Arizona, U.S.A. Distribution maps appear in Matthews (1980) and Chernoff and Miller (1982).

Ecology. Little known other than gross habitat characteristics and associated species. Habitat described by Miller and Simon (1943) as small, turbid pools over sand, gravel, or boulder substrate. In Río Yaqui drainage Hendrickson et al. (1980) found the beautiful shiner to be rare. Where present, most common in riffles of small streams and pools of intermittent creeks. Uncommon in large rivers.

Etymology. The name *formosa* is the latin word meaning beautiful or pretty, in reference to the breeding coloration of this species.

Comments. The beautiful shiner has had a complex taxonomic history. Until recently, confusion existed as to the number of taxonomic units involved in the complex (Chernoff and Miller, 1982). Besides several races of *C. formosa* sensu stricto recognized by Contreras-Balderas (1975), two forms were formally described in this complex, *C. santamariae* and *C. mearnsi*. It appears that these may all represent a single form with a mosaic of variable morphological characters. Characteristics considered diagnostic of *C. santamariae* and *C. mearnsi* were investigated by Chernoff and Miller (1982) and found to vary inconsistently between and within populations. Thus, I follow these authors in considering the two forms as junior synonyms of *C. formosa*.

Some have considered the beautiful shiner

to be a subspecies of *C. lutrensis* (Contreras-Balderas, 1975, 1978a; Gilbert, 1978a). However, Chernoff and Miller (1982) demonstrated its distinctiveness, and my analysis of *Cyprinella* indicates that *C. formosa* is more closely related to *C. bocagrande* than to *C. lutrensis*.

CYPRINELLA BOCAGRANDE (CHERNOFF
AND MILLER)

Largemouth Shiner

Plate I

Notropis bocagrande Chernoff and Miller, 1982:514–519, Figs. 2, 3. [Orig. descr.; Type locality: Ojo Solo, ca. 39 km W Villa Ahumada, Chihuahua, México]

Diagnosis. Anal rays 8; mouth extremely large; mandibular pores 4; tubercle hiatus between dorsum of head and snout absent; scapular bar weak; gular bar short; ceratohyals elongate; isthmus of maxilla very narrow; posterior ramus of premaxilla straight; pharyngeal pad of basioccipital triangular in shape.

Description. A large *Cyprinella*, adults reaching over 70 mm SL. Body robust. Predorsal region and head of breeding adults deep and gibbous. Head large and robust. Snout short, but mouth large and terminal to slightly subterminal. Upper jaw extending under orbit, comprising more than 9.4% body length (Chernoff and Miller, 1982). Caudal peduncle thick and short. Dorsal fin not expanded in breeding males; origin in both sexes over or slightly posterior to pelvic fin insertion.

Dorsal fin rays 8–9 (8); anal rays 7–9 (8); pelvic rays 8–9 (8); pectoral rays 11–14 (13); principal caudal rays 19; dorsal procurrent rays 10–11 (11), ventral procurrent rays 9.

Exposed margins of lateral scales deeper than long. Lateral-line scale rows 32–40 (usually 36–37); predorsal scales 15–19 (18); body circumferential scales 29–36 (31–33); caudal-peduncle scales 15–20 (18).

Pharyngeal teeth 4–4; grinding surface of anterior tooth not well developed and tip not hooked; others hooked and with grinding surfaces. Total gill rakers 8–10 (9). Total verte-

brae 35–36 (36), precaudals 17–18 (17), caudals 18 or 19. Dorsal fin insertion above vertebra 12.

Lateral line complete. Supratemporal canal not interrupted at dorsal midline, pores 5–6 (5). Supraorbital canal without interruptions and not joining other canals, pores 6–9 (7–8). Infraorbital canal complete, pores 11–17 (15). Preoperculo-mandibular canal complete, total pores 9–12 (10), mandibular pores 4–5 (4).

Intestine simple S-shaped loop and with two flexures, Type I. Peritoneum silvery with light speckling of melanophores.

Coloration in life.—Females and nonbreeding males less intensely colored than breeding males. Dorsum silver-blue to olivaceous. Venter white to yellow. Lateral stripe as in males but extending onto operculum. Dorsolateral stripe light yellow. Anal fin yellow. Bases of pectoral and pelvic fins yellow, remainder clear.

Males brilliantly colored. Violet dorsally from head to caudal base, turning to iridescent light yellow dorsolaterally. Head rufescent. Plum-colored lateral stripe deeper and more diffuse anteriorly and intensely developed on caudal peduncle. Scapular bar absent or weakly developed. Caudal spot absent. Belly, breast, and ventrolateral body cream to yellow. Axil of anal, pectoral, and pelvic fins typically orange. Ventral caudal peduncle red. Gular region cream; gular stripe extending under orbit, but not to isthmus. Dorsal fin clear. Remaining fins yellow-orange.

Tuberculation.—In nuptial males top of head covered with several erect, moderately large tubercles in scattered pattern. Early season and younger males not available to determine if linear pattern exists in early development. Dorsal organs extending laterally to, but separate from, supraorbital cluster of erect, slightly smaller organs. Supraorbital tubercles continuous with preorbital tubercles by 1–2 rows; preorbitals numbering 8–10 and located on dorsal half of lacrymal. Snout covered with small, erect organs separate from dorsum by hiatus, connected in some males to preorbital organs by narrow band. Mandibles of some males with 1–5 semi-clustered, erect, small

tubercles located centrally or laterally on rami. Remainder of head devoid of organs, except for occasional erect tubercle on dorsal operculum.

Each predorsal scale scale with tubercles, best developed within 5–6 scale rows of occiput. Generally, 1–3 small, erect tubercles located centrally in semitransverse row; margins of scales armed with up to 18 erect submarginals. Flank scales with many erect to retrorse edge organs per scale, both above and below lateral line. No central or subcentral tubercles developed, except on some lateral-line scales, where 1–2 may form. Above anal fin base scales like lateral body scales. Caudal peduncle pattern begins at posterior margin of anal fin base. Lower caudal peduncle like *C. formosa* in having each scale with mat of crowded antrorse and erect organs, more complex than in other members of this species group. Scales of dorsal caudal peduncle like those of sides of body.

Dorsal and anal fins with small erect organs on all rays. Anal fin with single row on first ray. Anal rays 2–7 with 1–2 rows of tubercles basally, becoming shagreen before branching. After branching, often 2 rows per branch with 2–5 tubercles per segment. Rays 1–5 of pelvics with 1–2 rows of tubercles and 1–5 tubercles per segment, best developed on rays 2–3. Pectoral fin heavily tuberculate. Leading ray with single row of tightly packed organs. Tubercles on rays 2–5 (8) uniserial basally to 2 rows (2 per segment) before branching, continuous with shagreen to edge.

Distribution. Endemic to Ojo Solo, an isolated spring near Ejido Rancho Nuevo in the Bolsón de los Muertos of the Guzmán Basin, Chihuahua, México. See Chernoff and Miller (1982) for a distribution map of this species and *C. formosa*.

Ecology. Little known. Probably the rarest member of the subgenus. Restricted to a single spring (diameter less than 50 m), its future seems uncertain. Most specimens have been collected from deepest portions of the spring over a substrate of clay, sand, and/or mud (Chernoff and Miller, 1982).

Etymology. The name *bocagrande* is taken from the Spanish *boca* for mouth and *grande* for large, in reference to the diagnostically large mouth of this species.

CYPRINELLA LEPIDA GIRARD

Edwards Plateau Shiner

Plate I

Cyprinella lepida Girard, 1857:197–198. [Orig. descr.; Type locality: Río Frío (trib. Río Nueces), either Real or Uvalde Co., TX]

Diagnosis. Anal fin rays 9; pectoral fin rays 14; caudal-peduncle scales below lateral line 6–7; scapular bar strongly pigmented; gular bar short; supraethmoid process of palatine not strongly inflected above horizontal; posterior ramus of premaxilla straight; basihyal deep; posterior process of quadrate joins vertical plate at edge; mentomeckelian long.

Description. A small member of the subgenus, reaching a maximum of about 60 mm SL. Body terete, only slightly compressed; dorsum slightly convex. Head large, subconical, and convex above; horizontal below. Mouth small and inferior, posterior margin of maxilla to or slightly before orbit margin. Snout blunt and protruding. Caudal peduncle short and moderately deep. Dorsal fin of breeding males straight posteriorly, not expanded; dorsal origin over to slightly posterior pelvic fin insertion.

Dorsal fin rays 7–8; anal rays 9–10 (9); pelvic rays 8; pectoral rays 12–14 (13–14); principal caudal rays 17; dorsal procurrent rays 10–13 (11–12), ventral procurrent rays 8–11 (10).

Exposed margins of lateral body scales higher than wide. Lateral-line scale rows 32–34 (33–34); predorsal scales 14–16 (15–16); total circumferential scales 20–25 (21–23); circumferential scale rows above lateral line 11–13 (12–13), below lateral line 9–12 (10–11); total caudal-peduncle scales 12–14 (13–14); caudal-peduncle scales above lateral line 7, below lateral line 5–7 (6–7).

Pharyngeal teeth 4–4, hooked, with moderate grinding surface. Total gill rakers 7–8 (8).

Total vertebrae 35–37 (36), precaudals 16–18 (17), caudals 18–20 (19). Dorsal fin insertion above vertebra 11 or 12 (12).

Lateral line complete to hypural plate. Supratemporal canal narrowly interrupted, pores 2–3 (2). Supraorbital canal complete, pores 7–8 (8). Infraorbital canal complete, pores 8–11. Preoperculo-mandibular canal complete, total pores 9 or 10, mandibular pores 3.

Intestine simple S-shaped loop, Type I. Peritoneum brownish and/or silvery with speckled melanophores.

Coloration in life.— Males brilliantly colored when in breeding condition. Dorsum greenish, lighter over head. Dorsolateral scales above dark lateral stripe yellowish-purple or yellowish-blue from yellowish scales with purple margins; below lateral stripe body much lighter. Lateral body scales distinctly marked with pigment arranged in diamond-shaped pattern. Side of head with golden-orange wash and purple vertical bar at anterior margin of preopercle; black gular stripe present, but short, extending to posterior margin of mandible. All fins yellow to yellowish-orange; dorsal fin heavily pigmented, yellow primarily restricted to distal edge.

Females and nonbreeding males also brightly colored, but much less intense than breeding males; fins typically clear to slight yellow with melanophores on rays and membranes only. Lateral stripe present but more diffuse anteriorly.

Tuberculation.— Dorsum of head of nuptial males with scattered, erect tubercles posteriorly and in 2 rows anteriorly, extending to the posterior margin of orbit. Early males and younger males with smaller, erect tubercles arranged in a linear pattern as in red shiner. Post- and supraorbital row of antrorse tubercles extending to anterior margin of nares. Above orbit, organs number 5–6. Snout with a sparse clump of erect tubercles separated from dorsal tubercles by hiatus. Remainder of head devoid of tubercles.

Edge tubercles line most scales above and below the lateral line on flanks. Above lateral

line, tubercles number 5–7 per scale; below only 3–6 develop in peak males. Predorsal scales with a few erect, subcentral, and central located tubercles scattered like those in *C. lutrensis*.

Dorsal fin without tubercles. Anal fin rays 1–5 tuberculate, with 1 row per ray and 1 tubercle per segment. Pelvic ray 1 naked, rays 2–3 with 1 row and 2–3 tubercles per segment. First ray of pectoral fin with 1 row of fine, retrorse tubercles arranged with 2–3 per segment. Pectoral rays 2–7 with 1 row of fine tubercles basally, grading to 2 rows before segmentation. Between segmentation and branching, tubercles arranged in 2 rows with 2–3 tubercles per row and segment, generally 2. After branching only 1 row per branch and 2–3 per segment.

Distribution. The Edwards Plateau shiner is endemic to this physiographic region of southwestern Texas. It is found in and is characteristic of clear springs and streams in the upper tributaries of the Guadalupe River and most of the upper Nueces River System.

Ecology. Inhabits clear, cool, spring-fed headwater creeks. Hubbs (1954) reported natural hybrids between this species and *C. venusta*, and later (Hubbs, 1956) performed hybrid crosses between *C. lepida* and the closely related, but allopatric, *C. proserpina*, resulting in increased variability of meristic characters in offspring.

Etymology. The name *lepida* is derived from the Greek *lepido*, meaning having scales.

Comments. This species has had a troublesome taxonomic history. After its description by Girard in 1857 as a distinct species, Jordan and Evermann (1896) synonymized this species with *N. bubalinus*. The species remained in synonymy until 1954 when C. Hubbs resurrected *C. lepida* and determined *bubalinus* to be a junior synonym of *C. lutrensis*, as earlier noted by Hubbs and Ortenburger (1929). Although considered valid by C. Hubbs (1956, 1958), Lytle (1972), Minckley and Lytle (1969), and Bailey et al. (1960, 1970), Hubbs (1972) rejected it as a distinct species and synonymized it with *N. lutrensis*. This decision was based

primarily on its observed hybridization with *N. lutrensis* in the upper Guadalupe River, and because in west Texas numerous forms as distinct as *C. lepidac* could be recognized. Based on these observations, Hubbs (1972), Robins et al. (1980) and Matthews (1980) followed in considering this form a junior synonym of the red shiner.

Data from this analysis indicate that the Edwards Plateau shiner is in fact a distinct species based both on its close relationship to the *rutila* clade and other morphological and pigmentary characteristics. Further, since hybridization may be a shared primitive trait among organisms (Rosen, 1979), and because hybridization in the Guadalupe River occurred only after dredging operations had started (Hubbs and Strawn, 1956), I do not consider the evidence of hybridization in this case to be indicative of relatedness. It does, in fact, represent hybridization and not intergradation.

CYPRINELLA RUTILA (GIRARD)

Mexican Shiner

Plate II

Moniana rutila Girard, 1857:201. [Orig. descr.; Type locality: Río Monterrey (trib. Río San Juan), Cadereita (=Cadereyta), Nuevo León, México]

Moniana gracilis Girard, 1857:201. [Orig. descr.; Type locality: Acapulco, near Monterrey, Nuevo León, México]

Cliola montiregis Cope, 1885:168. [Orig. desc.; Type locality: Monterrey, Nuevo León, México]

Diagnosis. Anal rays 8; gular bar elongate; scapular bar weak; breeding males with purple and gold body coloration; lateral body scales above and below lateral line without tubercles; interoperculum short; coronoid process of dentary broad; lateral slope of dermopterotics steep; anterior margin of ceratobranchial 1 expanded; symplectic narrow; anterior notch of vomer shallow; mentomeckelian long; neck on epibranchial 2 straight; frontals and dermopterotics not in contact.

Description. A moderately sized *Cyprinella*, reaching about 60 mm SL. Body ter-

ete, moderately deep. Depth greatest at or near dorsal origin. Head small. Snout blunt. Orbit small. Mouth small, terminal, and oblique; lower jaw included in upper and both extending to anterior margin of orbit. Caudal peduncle short and moderately deep. Dorsal fin not expanded in breeding males; origin in both sexes slightly posterior to pelvic fin insertion.

Dorsal fin rays 8 or 9; anal rays 7–9 (8); pelvic rays 7–8 (8); pectoral rays 12–14 (13); principal caudal rays 17; dorsal procurrent rays 10–12 (11), ventral procurrent rays 9–10 (10).

Exposed areas of lateral body scales taller than wide. Lateral-line scale rows 32–36 (33–34); predorsal scales 14–15 (15); total predorsal circumferential scales 21–24 (22); scales above lateral line 12–15 (13–15), below lateral line 9; total caudal-peduncle scale rows 12–13 (12); caudal-peduncle scales above lateral line 7, below lateral line 5–6 (5).

Pharyngeal teeth 4–4, hooked, and with moderately developed grinding surfaces. Gill rakers very reduced, total on first arch 4–7 (5–6). Total vertebrae 35–36 (35), precaudal 16–17 (16), caudal 18–20 (19). Dorsal fin insertion above vertebra 11.

Lateral line complete to hypural plate. Supratemporal canal narrowly interrupted or occasionally complete, pores 2–3 (2). Supraorbital canal complete and separate from other canals, pores 7–8 (7). Infraorbital canal complete, pores 9–11 (10). Preoperculum mandibular canal complete, total pores 9–11 (9–10), mandibular pores 3–4 (3).

Intestine simple with single S-shaped loop and two flexures, Type I. Peritoneum dusky to speckled silver and brown.

Coloration in life.—Dorsum of females and nonbreeding males dark, olive to brown, due to dark crosshatched pattern on scales and darkened centers. Venter white to cream; lips with scattered melanophores. Gular stripe long, extending from symphysis to isthmus. Laterally, a variably developed blue-black stripe from caudal rays to snout, sometimes diffuse from dorsal origin anteriorly. On head, preorbital and postorbital portions of stripe may be

obscured by darker pigmentation. Stripe broken at hypural plate by vertical light stripe, creating caudal spot. Pre- and postdorsal stripes well developed. Fin pigmentation like that of *N. xanthicara*, but slightly more intense.

Breeding males as above, but with dark greenish-yellow dorsum and dorsolateral surfaces. Dorsum of head and snout green. Lateral stripe less obvious because of intense pigmentation, but visible as deep blue band. Head bright yellow laterally. Gular stripe dark blue-black. Venter bright yellow. Fins bright yellow, mixed with milky-white deposits. Dorsal fin sometimes very dark from high concentration of melanin.

Tuberculation.—Dorsum of head of mature breeding males with moderately large, slightly antrorse tubercles in scattered pattern. In smaller and early season males tubercles erect and linear. Linear pattern consists of 2 rows extending from occiput to anterior margin of nares, with some variation. Snout tubercles few, same size as head tubercles, and erect. Scattered snout tubercles separated from remainder of head tubercles by hiatus. Preorbital areas with sparse, erect tubercles. Supraorbital tubercles in single row, generally 5–6 moderately large, erect to slightly antrorse organs. Remainder of head devoid of tubercles.

Body tubercles restricted to caudal-peduncle scales, scales above anal fin, and predorsal scales. Predorsal tubercles erect when small and slightly antrorse when larger. Each scale generally with 2–3 organs located centrally in transverse row. Peripheral to these, a string of submarginal tubercles only one-half size of central organs develop around margin of scale. Caudal-peduncle tubercles restricted to 2–3 scale rows on lower half, including ventral row and 2–3 scale rows above anal fin. Each scale also with 1–6 semi-central organs and a series of submarginals. No organs present above lateral line. Young males and males early in breeding season with pattern like that of most species of *Cyprinella* (except species of the *pyrrhomelas* and *nivea* species groups) with a single large tubercle per scale.

Fin tuberculation restricted to anal, pelvic,

and pectoral fins. Anal fin with small, erect organs on medial and basal portions of all rays except first. First 4 pelvic rays with single row of tubercles (2–3 organs per segment) medially. Leading pectoral fin ray with single row of retrorse tubercles (2–3 tubercles per segment). Rays 2–6 with single row basally, turning into double row before segmentation, and triple row before branching. Each row with 2–3 organs per segment. After branching, anterior branch with single row of 2–3 organs per segment; posterior branch with 2 rows proximally and single row distally. No ventral tubercles observed on paired fins.

Distribution. Endemic to ríos San Juan and Salado of northeastern México. Distribution map provided by Lytle (1972).

Ecology. Observations by Minckley and Lytle (1969) indicate that *N. rutilus* occurs above and below riffles, in current, over gravel substrate. Concentrations of tuberculate males are typically found in fastest riffles, while females occur in adjacent eddies or pools with slower current.

Etymology. The name *rutila* is derived from Latin and means red.

Comments. Gilbert (1978a) listed *Cliola montiregis* (Cope, 1885) and *Moniana gracilis* (Girard, 1857) as junior synonyms of *C. lutrensis*. Recent examination of types of *Cliola montiregis* (ANSP 19344; 37.5 mm) and *Moniana gracilis* (MNHN 432; 39 mm) indicates that they are actually *C. rutila* and are included here in the synonymy of this species. Both specimens have 8 anal rays and a dark gular bar extending from symphysis to the isthmus, typical of *C. rutila*.

CYPRINELLA XANTHICARA (MINCKLEY
AND LYTLE)

Cuatro Ciénegas Shiner
Plate II

Notropis xanthicara Minckley and Lytle, 1969:491–502. [Orig. descr.; Type locality: Río Puente Colorado, 8.5 km S and 0.7 km W Cuatro Ciénegas, Coahuila, México]

Diagnosis. Anal rays 8; discrete blue-black

lateral band, 2 scales wide, extending from caudal fin to snout, excluding orbit; diamond-shaped pigment pattern on scales above lateral line only; gular bar elongate; scapular bar weak; supraorbital tubercles antrorse; mandibular tubercles present; caudal-peduncle tubercles present on dorsalmost scale row; uroneural 3 long; position of epiphyseal bar posteriorly placed; neck on anterior ceratohyal narrow; junction of sphenotic and frontals posteriorly placed; posterior process of quadrate joins vertical plate at edge; ectopterygoid short and broad; posteroventral and ventral edges of preopercle entire; ceratohyals moderately deep; branchiostegals narrow.

Description. A moderately sized *Cyprinella*, reaching about 60 mm SL. Body slender, elongate, not obviously compressed; more delicate than other *Cyprinella*. Head slender and pointed. Snout elongate. Mouth small, terminal, and oblique; lower jaw included in upper. Caudal peduncle slender and elongate. Dorsal fin not expanded in breeding males; origin above pelvic fin insertion.

Dorsal fin rays 8; anal rays 7–9 (8); pelvic rays 7–8 (8); pectoral rays 12–14 (13–14); principal caudal rays 17–18 (17); dorsal procurrent rays 9–11 (10), ventral procurrent rays 8–10 (10).

Exposed margins of lateral body scales higher than wide. Lateral-line scale rows 33–36 (33–34); predorsal scales 14–16; total body circumferential scales 19–23 (21–22); dorsal circumferential scales 9–13 (13), ventral 9–10 (9); total caudal-peduncle scales 10–12 (12); dorsal caudal-peduncle scales 5 or 7, ventral 5.

Pharyngeal teeth 4–4, slender, well hooked, and with serrated grinding surfaces. Gill rakers reduced, total on first arch 4–6 (5). Total vertebrae 35–36 (36), precaudals 16–18 (17), caudals 18–19 (19). Dorsal fin insertion above vertebra 11 or 12 (11).

Lateral line complete; supratemporal canal generally narrowly interrupted, but occasionally complete or broadly interrupted, pores 2–5 (2). Supraorbital canal complete and separate from other canals, pores 7 or 8. Infraorbital canal generally complete, but occasionally

interrupted below eye, pores 9 or 10. Preoperculo-mandibular canal complete, total pores 8–10 (9), mandibular pores 3.

Intestine simple with two flexures forming S-shaped loop, Type I. Peritoneum generally black, may be heavily speckled with melanin over silver background color.

Coloration in life.— Breeding and nonbreeding females and younger males similar in coloration. Dorsum olive to brownish. Remainder of body pallid, except for darkly pigmented lateral stripe and pigmented margins of lateral and dorsolateral scales, presenting crosshatched or diamond-shaped pattern. Lateral stripe 1–2 scale rows wide, extending from center of caudal fin, through a slightly enlarged caudal spot, to the posterior margin of orbit; stripe continued anteriorly to orbit by preorbital bar on both sides of head. Lateral stripe diffuse anteriorly on head. Venter light, belly immaculate. Fins clear, except for few melanophores along rays. Procurrent caudal rays and leading rays of dorsal, pectoral, and pelvic fins darkly pigmented.

Breeding males intensely colored. Minckley and Lytle (1969:498) described breeding males: “head brassy-gold over dorsum and onto snout, color interrupted on sides of snout and on opercles by dark melanophores, but continuing ventrally on opercle; yellow continuing on dorsum to caudal fin, overlying gray or brown ground color that is distinctly cross-hatched. Lateral band intensely prominent; sides below lateral band pinkish-orange; belly white, slightly suffused with yellow; pectoral fins lemon-yellow in center, color more intense anteriorly and with a dark black, leading edge; pelvic fins with a dark leading edge margined posteriorly by an iridescent, bluish line (milky-white in some), then [than] the remainder of the fin yellow; anal fin transparent distally and proximally, yellow centrally; caudal fin intense yellow in belly of lobes, light yellow proximally, with procurrent rays and central rays black; dorsal fin yellow-orange, opaque, with milky-white pigments proximally, edge with black; comea yellow, reflecting blue dorsally; pupil jet black.”

Tuberculation.—Dorsum of head in nuptial males with moderately large antrorse organs in scattered pattern from orbit to occiput; 2 rows anteriorly from orbits to nares. Smaller males and prenuptial males with slight tubercle development and linear pattern down midline of head. Snout with scattered erect tubercles, about one-half size of those on top of head and separated from head tubercles by hiatus. Preorbital area naked except for 1–3 tubercles on anterior lacrymal, connected to supraorbital tubercles by single row. Supraorbital tubercles and those below nares smaller than dorsal head tubercles and arranged in single row. Mandibles with single row of small, erect tubercles. Remainder of head devoid of tubercles.

Minckley and Lytle (1969) briefly described tuberculation: their observations are similar to mine, except they noted granular development on cheek and gular regions and noted no development on the nape.

Predorsal scales tuberculate with a pattern similar to *C. rutila*. Generally 2–3 antrorse organs, about $\frac{1}{2}$ size of dorsal head tubercles, centrally in a semitransverse row. Peripheral to these there are submarginal and edge antrorse organs in decreasing size. Along flanks, each scale above lateral line with 6–10 small, erect organs; below lateral line organs retrorse. Caudal peduncle tuberculation similar to *C. rutila*, except 5–8 retrorse, edge organs found on each scale both above and below lateral line.

All fins tuberculate. Dorsal fin with first two rays tuberculate; other rays with single row of tubercles medially and a single organ per segment. All anal fin rays with a single row and 1 tubercle per segment along entire length. Pelvic fin with first 4 rays tuberculate; each with a single row of tubercles and 1 tubercle per segment (occasionally 2). First ray of pectoral fin with a single row of tubercles and 2 organs per segment; posterior rays 2–7 with single file basally to segmentation where 2 rows begin. After segmentation, 2 rows formed with 4 organs per segment. Single row maintained on each branch; 2 tubercles per seg-

ment. Ventral tubercles well developed on pectoral fins; none observed on pelvics.

Distribution. Endemic to the Cuatro Ciénegas basin of central Coahuila, north-central México. See Minckley and Lytle (1969) for a distribution map of this species.

Ecology. The Cuatro Ciénegas shiner inhabits the upper reaches of clear, cool streams of this region. It frequents areas between current and backwater pools. Presumably it is a sight feeder. Minckley and Lytle (1969) observed surface feeding, and it is known to inspect passing items frequently. During the day it is very active in midwater or near the bottom in current, but at night it rests on the substrate (Minckley and Lytle, 1969).

Etymology. The epithet *xanthicara* is in reference to the breeding coloration developed in males of this species; from Greek *xanthos*, for yellow and *kara*, for head.

CYPRINELLA PROSERPINA (GIRARD)

Proserpine Shiner

Plate II

Moniana proserpina Girard, 1857:200. [Orig. descr.; Type locality: Devils River, just above mouth into Río Grande, Val Verde Co., TX]

Moniana aurata Girard, 1857:200. [Orig. descr.; Type locality: Pinto Creek, "Piedra Pinta," 15–20 mi SE Del Rio, Kinney Co., TX]

Diagnosis. Anal rays 8; mouth inferior; scapular bar well-developed; gular bar elongate; breeding males with yellow-orange and purple body coloration; premaxillary process of maxilla tall; isthmus of maxilla moderately shallow; insertion of *adductor mandibulae* A1 on maxilla below isthmus; posterior process of quadrate deep and heavy; supracleithrum broad.

Description. Small for a *Cyprinella*, but size average among members of the *lutrensis* clade, reaching a maximum body size of 55–60 mm SL. Body robust, not strongly compressed. Body relatively slender, maximum depth equally developed from occiput to dorsal fin origin. Head large and highly arched dorsally,

horizontal ventrally. Snout blunt and protruding over jaws. Mouth strongly inferior, well below orbit; lower jaw included in upper. Caudal peduncle relatively short and stout. Dorsal fin not expanded in breeding males and over or slightly posterior to pelvic fin insertion.

Dorsal fin rays 7–9 (8); anal rays 7–9 (8); pelvic rays 7–8 (8); pectoral rays 12–14 (13–14); principal caudal rays 15–17 (17); dorsal procurrent rays 11–14 (11–12), ventral procurrent rays 9–12 (10–11).

Exposed margins of lateral scales slightly higher than wide. Lateral-line scale rows 34–36 (35); predorsal scales 15–18 (16–17); total predorsal circumferential scales 22–27 (24–25); scales above lateral line 11–13 (11–12), below lateral line 9–12 (10–11); total caudal-peduncle circumferential scales 14; above lateral line 7, below lateral line 5.

Pharyngeal teeth 4–4, strongly hooked, with well developed grinding surfaces. Total gill rakers 5–10 (7–8). Total vertebrae 35–37 (36), precaudal 16–18 (17 in Devils R. and Independence Cr.; 18 in Pecos R.), caudals 17–20 (19 in Devils R. and 18 in Independence Cr. and Pecos R.). Dorsal insertion above vertebra 11 or 12 (11).

Lateral line complete. Supratemporal canal interrupted narrowly, pores 2–3 (3). Supraorbital canal separate and complete, pores 7–10 (7). Infraorbital canal complete, occasionally separate from trunk canal, pores 10–12 (11–12). Preoperculo-mandibular canal complete, total pores 8–10 (9), mandibular pores 2–3 (3).

Intestine simple, with single S-shaped loop, Type I. Peritoneum heavily colored with melanophores over silvery background.

Coloration in life.—Females and nonbreeding males like breeding males but less intensely colored. Olive dorsally, white or cream ventrally, and bluish-gray laterally. Cross-hatched pattern present, as well as lateral and gular stripes, but not as brightly developed as in breeding males.

Breeding males brilliantly colored (Hubbs and Miller, 1978; pers. obs.). Dorsum and dorsolateral areas bright brassy green; bluish-

purple along midline laterally. Lateral scales marked along edges with dark crescentic lines, creating a crosshatched pattern. Purplish-blue lateral stripe developed from caudal base to opercle, best developed posteriorly, diffuse anteriorly. Ventrally, postcephalic regions white to cream, except predominantly bright yellow or yellow-orange above anal fin. Dorsum of head dark greenish; laterally brassy-rose, turning to light purple ventrally. Gular stripe dark, extending from symphysis to branchiostegals at isthmus. Dorsal fin bluish anteriorly, reddish-pink posteriorly; leading rays whitish. Caudal, anal, and pelvics yellowish to yellowish-orange basally and centrally, white distally. Pectorals greenish dorsally and orange ventrally.

Tuberculation.—Early males with linear pattern of erect tubercles on dorsum of head. Top of head of nuptial males covered with moderately large, erect organs. Anteriorly some tubercles slightly antrorse. No hiatus between tubercles on snout and top of head, complete from occiput to lips. Supraorbital row (6–7 erect organs) connected to preorbital tubercles by single row. Preorbital organs few (2–3) and erect. Mandibular rami and other areas of head devoid of tubercles.

Predorsal scales with 2–3 antrorse edge tubercles one-half size of dorsal head organs; no submarginal or central organs developed. Along flanks, 5–11 small, erect edge tubercles developed per scale both above and below lateral line; no central or submarginal organs. Caudal peduncle tuberculation like that of *C. rutila*, except for several (2–8) small, retrorse edge organs per scale, below lateral line; none above.

All fins tuberculate. Dorsal rays all with single row of tubercles and single tubercle per segment, except first rudimentary ray devoid of tubercles. First 3 rays (branched and unbranched) of pelvic fins tuberculate, with single row of tubercles and 2–3 organs per segment. First pectoral ray with single row of tubercles and single tubercle per segment; tubercles closely set basally and more widely separated distally. Rays 2–7 with 1 row basally and 3 (4)

before branching, where there may be 4–9 organs per segment. After branching 1 row on anterior branch (2 tubercles per segment) and 2 rows on posterior branch (4 tubercles per segment). Venter of paired fins with several erect tubercles per ray.

Distribution. The proserpine shiner is restricted to tributaries of the lower Río Grande (including Pecos and Devils rivers) and San Felipi, Pinto, and Las Moras creeks in Texas, and Río San Carlos, Coahuila, México. Koster's (1957) report of this species from New Mexico is apparently in error (Hubbs and Miller, 1978). It seems reasonable, however, that it probably did occur in the upper Pecos at some time before increased aridity.

Ecology. Little is known of this species' biology. It prefers clear and cool streams with a sand-gravel substrate. Harrell (1978) observed benthic sight feeding and noted reproduction after a period of severe flooding. Hubbs (1956) experimented with hybridization between this species and *C. lepida*, two allopatric but closely related forms in the *lutrensis* clade, and noted increased variability in meristic characters of the offspring.

Etymology. This species was apparently named after Persephone, daughter of Zeus and Demeter, wife of Pluto and queen of the infernal regions. The name *proserpina* is the latinized form of her name.

CYPRINELLA PANARCYS (HUBBS AND MILLER)

Conchos Shiner
Plate II

Notropis panarcys Hubbs and Miller, 1978:582–589. [Orig. descr.; Type locality: Río San Pedro at Meoqui, Chihuahua, along Hwy 45 at elevation 1115 m]

Diagnosis. Anal rays 8; black subrescencic markings on flank scale pockets; scapular bar well developed; gular bar elongate; maximum body depth from occiput to dorsal origin; mouth inferior; breeding males with bluish-purple and golden body coloration; fins orange-white; neck of epibranchial 3 straight;

isthmus of maxilla very narrow; supraethmoid narrow and with emarginate lateral edges; infraorbital 4 extremely narrow; autoperotic spine small; dorsal margin of anguloarticular horizontal; dorsal supraethmoid process of palatine not strongly elevated above horizontal.

Description. A small *Cyprinella*, reaching a maximum of about 55 mm SL. Body robust, not extremely compressed. Head large. Mouth small, inferior, terminal, and oblique; lower jaw included in upper, both extending posterior to or slightly before orbit. Snout distinctly rounded and protruding. Back highly arched from occiput to dorsal origin. Caudal peduncle thickened and moderately long. Dorsal fin not expanded in breeding males; origin over to slightly posterior insertion of pelvic fin.

Dorsal fin rays 8–9 (8); anal rays 8–9 (8); pelvic rays 7–8 (8); pectoral rays 11–14 (12–13); principal caudal rays 18–19 (19); dorsal procurent rays 10–11 (11), ventral procurent rays 9–10 (9).

Exposed areas of lateral body scales elongate, higher than wide. Lateral-line scale rows 32–35 (33–34); total predorsal circumferential scales 25–29 (26–27); circumferential scales above lateral line 12–16 (13–14), below lateral line 10–13 (10–11); total caudal-peduncle scales 14–15 (14); scales above lateral line 7, scales below 5–6 (5).

Pharyngeal teeth 4–4, each usually strongly to weakly hooked, with well-developed grinding surfaces; anteriormost tooth of each arch sometimes smaller, weakly hooked, and may lack grinding surface. Total gill rakers 6–9 (8). Total vertebrae 34–36 (35), precaudals 16–17 (17), caudals 17–19 (17–18). Dorsal insertion above vertebra 11 or 12 (11).

Lateral line complete to hypural plate. Supratemporal canal narrowly to widely interrupted in most specimens with minor segments on either side of midline, pores 2 per side. Supraorbital canal complete, pores 8. Infraorbital canal complete, frequently forked posterior to orbit with branch above eye, pores 9 or 10. Preoperculo-mandibular canal generally complete, but may be reduced on ascend-

ing arm of preopercle, total pores 10, mandibular pores 3.

Intestine single S-shaped loop with two flexures, Type I. Peritoneum dark, covered with heavy concentration of melanophores.

Coloration in life.—Dorsum of females and nonbreeding males dark olive to brownish-green, fading to light cream or white on venter. Lateral stripe bluish, best developed posteriorly, diffuse or absent anteriorly. Scapular bar rectangular, not offset posteriorly by lighter, rectangular depigmented area. Dorsum of head dark olive, extending down sides to and including lips and dorsum of operculum. Venter unpigmented, except for darkly pigmented gular stripe or bar extending from symphysis to isthmus.

Body of breeding males greenish-blue or purple dorsally. Center of each flank scale blue or purple, margin golden to greenish. Elevated scales intensely marked with blackish crescents, creating a crescentic, crosshatched pattern extending down to belly. Head dorsally colored as described above, dusky laterally. Postorbital area, opercle, subopercle, interopercle, and preopercle orange, most intense on former two. Fins orange to brownish orange. Pectoral, anal, and dorsal darkened along bases and leading rays by melanophores. Pectoral, anal, and pelvic fins with conspicuous milky-white margins, less intense in dorsal and caudal fins.

Tuberculation.—In nuptial males dorsum of head from occiput to tip of snout, lateral to dorsal margins of orbit, covered with scattered, moderately large, erect organs. Supraorbital tubercles 4–6, connected to preorbitals by single row of erect organs. Snout covered with small, erect organs continuous with preorbital tubercles. Remainder of head devoid of tubercles.

Body tuberculation as in *C. proserpina*. Tubercles on predorsal scales, lower 1–2 scale rows of caudal peduncle, above anal fin, and on scales above lateral line anterior to dorsal fin origin.

Fins apparently devoid of tubercles, except for pectorals. Anterior rays with a single row

of retrorse organs per ray (Hubbs and Miller, 1978).

Distribution. Known only from the upper Río Conchos system, a major tributary of the Río Grande in northern México. See Hubbs and Miller (1978) for distribution map of this species.

Ecology. Hubbs and Miller (1978) reported collecting this species from shallow, generally clear pools over a rocky, sandy, or mud substrate. Collections of fully tuberculate males in March were from shallow and broad portions of Río San Pedro over gravel substrate. These authors also list associated species.

Etymology. The name *panarcys* derived from Greek *pan*, meaning all, and *arcys* meaning a net, describing the crescentic pattern on lateral body scales suggestive of a net.

CYPRINELLA SPILOPTERA (COPE)

Spotfin Shiner

Plate II

Leuciscus spilopterus Cope, in Günther 1868:254. [Orig. descr.; Type locality: St. Joseph R., MI (southwest part of state)]

Hypopsis fretensis Cope, 1869:382. [Orig. desc.; Type locality: near Detroit, MI]

Notropis spilopterus hypsisomata Gibbs, 1957b:195–198. [Orig. descr.; Type locality: Wonder Lake, bay in north end, McHenry Co., IL]

Diagnosis. Anal rays 8; gular bar short; fins of breeding males yellow; posterior hyoideal foramen of ceratohyal located mesially; dermopterotics invade parietals; posterior process of vomer narrow; ceratobranchial 1 with restricted neck; frontals widely broadened laterally.

Description. A relatively large *Cyprinella*, reaching a maximum of about 100 mm SL. Body depth variable between subspecies: *hypsisomata* deep-bodied and *spiloptera* elongate. Body terete, although deeper bodied individuals somewhat compressed. Head relatively small. Snout conical and protruding, especially in breeding males. Orbit relatively small. Mouth terminal or subterminal, oblique and

moderately large. Lower jaw barely contained in upper, both extending posteriorly to anterior margin of orbit. Caudal peduncle relatively short and heavy. Dorsal fin not greatly expanded in breeding males; origin in both sexes slightly posterior to pelvic fin insertion.

Dorsal fin rays generally 8; anal rays 7–9 (8); pelvic rays 8; pectoral rays 10–17 (13–14); principal caudal rays 17; dorsal procurrent rays 10–12 (11), ventral procurrent rays 10–11 (10).

Lateral body scales higher than wide, appearing elevated, especially anteriorly near lateral line. Lateral-line scale rows usually 35–39 (*spiloptera* 37–39, *hypsiosomata* 36 or 37); total circumferential scales 26–28; scales above lateral line 13–15 (13 in most, but some populations of *spiloptera* with high frequency of 14 or 15), below lateral line usually 11; total caudal-peduncle scales generally 14; scales above lateral line 7, scales below lateral line 5.

Pharyngeal teeth 1, 4–4, 1, hooked, and with or without serrated grinding surfaces. Total gillrakers 8–11 (9). Total vertebrae 35–38 (37), precaudals 17–18 (18), caudals 18–20 (19). Dorsal fin insertion above vertebra 12.

Supratemporal canal broadly interrupted, pores 2 per side. Supraorbital canal complete, pores 8–10 (8). Infraorbital canal complete or narrowly interrupted between lacrymal and infraorbital 2, pores 11–13. Preoperculo-mandibular canal complete, total pores 12, mandibular pores 4.

Intestine arranged in simple S-shaped loop, Type I. Peritoneum silvery and speckled with melanophores.

Coloration in life.—Females and nonbreeding males olive or light bluish dorsally and dorsolaterally. Dorsolateral and lateral scales outlined with dark crescents, presenting diamond-shaped pattern. Lateral stripe best developed posteriorly, diffuse and broad anteriorly from dorsal origin to head; may be dark in some. Scapular bar dark. Venter immaculate. Gular bar short and dark. Dorsal fin lightly pigmented with melanophores, increasing in darkness with increasing body size and onset of breeding season. Pelvic and anal fins clear.

Pectoral fin immaculate, except for first ray which may be lined with melanophores.

Breeding males darker and more colorful. Dorsum and flanks deep steel-blue. Snout yellow. Lateral stripe and scapular bar dark blue, broadening posteriorly. Lateral stripe expanded midlaterally between dorsal origin and operculum into a large, round darkened spot. All fins with milky-white deposits, especially distally; dorsal fin very dark with high concentrations of melanophores on membranes, especially posteriorly. Pelvic, anal, and caudal fins yellow.

Tuberculation.—Dorsum of head of nuptial males covered with scattered, moderately large, antrorse organs. Tubercles arranged in semilinear pattern in early season males, but obliterated later in season with increased tubercle development. Supraorbital region with scattered antrorse organs equal in size to dorsal tubercles. Preorbital tubercles moderately large, scattered, antrorse, and connected to supraorbital tubercles by 1–2 rows and to snout tubercles by narrow band. Snout organs scattered and clustered, antrorse posteriorly and erect anteriorly, and separated from dorsal head tubercles by wide hiatus. Mandibles with 2 rows of moderately small, antrorse organs. Preopercles with few, scattered, erect organs. Remainder of head naked.

Each scale of predorsal region with 2–3 antrorse organs, equal in size to dorsal head tubercles, arranged in transverse row arched across center of scale. Some predorsal scales with 1–4 subcentral organs; no edge tubercles present. Scales along flanks with 0–6 erect, subcentral organs above and below lateral line; some antrorse near nape. No central tubercles present except near lateral line, nape, or caudal peduncle. One to 5 antrorse, subcentral tubercles and 2–3 central, antrorse tubercles on scales on ventral half of caudal peduncle and around anal fin base. Similar pattern above lateral line on caudal peduncle, but organs smaller and equal in size.

All rays of dorsal and anal fins tuberculate. Each ray with 1 row and 1 tubercle per segment medially. One row and 2–3 tubercles per

segment on pelvic fin. First ray of pectoral fins with 1 row and 1 tubercle per segment. Posterior rays 2–8 with 1 row basally and 2–3 tubercles per segment continuous with single row on posterior branch. Anterior branch with one row and 2–3 organs per segment. No organs observed on ventral surfaces of paired fins.

Distribution. The spotfin shiner is widely distributed in eastern North America and has a distribution similar to the suggested extent of a preglacial highland fauna (Mayden, 1985). Two subspecies of the spotfin shiner were recognized by Gibbs (1957b), *C. s. spiloptera* and *C. s. hypsisomata*. The validity of these taxa, however, has been challenged recently by Schaefer and Cavender (1986). These authors proposed that the forms recognized by Gibbs represent one taxon with clinal variation in meristics and body proportions. I follow these authors, but present the ranges of the forms as presented by Gibbs (1957b). The eastern spotfin shiner, *C. s. spiloptera*, ranges throughout the Ohio River drainage northward to the Great Lakes basin, including Lakes Huron, Erie, and Ontario, and the St. Lawrence River drainage in Quebec. This form also occurs along the Atlantic Slope from the Potomac to the Hudson rivers. The western subspecies, *C. s. hypsisomata*, occurs in the upper Mississippi River Basin of northern Missouri, Illinois, Wisconsin, and Minnesota. Southern populations are found in the Ozark Plateaus in the Meramec, Gasconade, and Arkansas rivers. Intergrades, based on intermediate lateral scale counts, are known only from eastern and western drainages of Lake Michigan. A detailed distribution map is provided by Gibbs (1957b) and Lee et al. (1980).

Ecology. The biology of this species is fairly well documented. Studies include those of Hankinson (1930), Stone (1940), Starrett (1950, 1951), and Pflieger (1965), as well as comments by Trautman (1957), Cross (1967), Pflieger (1975), Gale and Gale (1977), and Smith (1979).

Cyprinella spiloptera most frequently occurs in large creeks and small rivers with clear,

permanent flow; not typical of larger turbid rivers or intermittent creeks. Usually found in or near riffles or raceways over gravel substrate in moderate to fast current.

Spawning occurs from May or early June to mid-August, with peak activity in June and early July (Pflieger, 1965, 1975). Males congregate and maintain territorial regions around submerged logs and exposed tree roots near riffles in swift current. When ready to spawn, a female moves into one of these areas from downstream, pairs with a male, and attaches eggs to undersides of logs or branches in crevices (e.g., under loose bark) (Hankinson, 1930; Pflieger, 1965). Spawning activity and species recognition are enhanced by sounds produced by this species (Winn and Stout, 1960).

Most individuals live only 2+ years, but some are known to live as long as 5 years (Stone, 1940). Maturity is apparently reached during the first year, but some do not spawn until the second year (Pflieger, 1965).

Diet of this species commonly includes terrestrial insects, such as ants, adult and immature aquatic insects, plant materials, and small fishes (Forbes and Richardson, 1908; Starrett, 1950; White and Wallace, 1973). Most feeding occurs shortly before dusk (White and Wallace, 1973) and probably shortly after dawn.

Hybridization of this species with the red shiner in Illinois was discussed by Page and Smith (1970). The gene pool of the spotfin shiner in this region was rapidly diluted with morphological characteristics, and presumably the genome, of *C. lutrensis*.

Etymology. The name *spiloptera* is from Greek *spilos*, for spot, and *pteron*, meaning wing or fin, describing the heavily pigmented last 2 interradial membranes of the dorsal fin of breeding males.

CYPRINELLA CAMURA (JORDAN AND MEEK)

Bluntnose Shiner
Plate II

Cliola camura Jordan and Meek, 1884:474–475. [Orig. descr.; Type locality:

probably Neosho River drainage in Lyons Co., Kansas (Gilbert, 1978a)]

Diagnosis. Anal rays 9; snout blunt; depigmented vertical bar at base of caudal fin; snout and dorsal fin of breeding males red; hiatus between dorsal head and snout tubercles absent; tubercle connection between supraorbital and preorbital regions narrow; mandibles of breeding males with 2 rows of tubercles; anterior neck of parasphenoid short; ascending wings of parasphenoid very broad; basibranchial one with no median constriction; neck of ceratobranchial two long and thin; neck on ceratobranchial one bent mesially; supraethmoid extremely short; frontals extremely broad; posterior wing of hyomandibular narrow; preopercle very wide over entire length; ceratohyals very deep.

Description. A moderately large and stout member of the *whipplei* clade, reaching about 90 mm SL. Body deep and compressed, greatest depth at dorsal origin. Head large and subconical. Snout blunt. Orbit small, diameter less than snout length. Mouth slightly subterminal, oblique. Lower jaw contained in upper, both extending to or slightly beyond anterior margin of orbit. Caudal peduncle deep and relatively short. Dorsal fin expanded and rounded posteriorly in breeding males; origin over to slightly posterior to pelvic fin insertion.

Dorsal fin rays 8; anal rays 8–10 (9); pelvic rays 8; pectoral rays 13–17 (15 or 16); principal caudal rays 16–17 (17); dorsal procurrent rays 10–12 (11), ventral procurrent rays 9–11 (10).

Exposed margins of lateral and dorsolateral scales taller than wide. Lateral-line scales 35–39 (36–37); total circumferential scales 24–28 (26); scales above lateral line 11–15 (13 in eastern populations, but frequently 14 or 15 in Arkansas R. specimens), scales below lateral line generally 11 (some 12 or 13); total caudal-peduncle scales 14; scales above lateral line 7, below lateral line 5.

Pharyngeal teeth 1, 4-4, 1, hooked, and with or without grinding surfaces. Total gill rakers 8–9 (9). Total vertebrae 35–39 (37–38),

precaudals 17–20 (18–19), caudals 18–21 (19–20). Dorsal fin insertion above vertebra 12.

Lateral line complete. Supratemporal canal broadly interrupted, pores 2 per side. Supraorbital canal complete, pores 9–10 (9). Infraorbital canal complete, pores 11. Preoperculo-mandibular canal complete, total pores 12–13 (12), mandibular pores 4.

Intestine arranged in simple S-shaped loop. Peritoneum silvery with heavy speckling of melanophores.

Coloration in life.—Females and nonbreeding males primarily silver-blue. Dorsum olive to steel-blue, lighter laterally to primarily silver. Belly immaculate. Weak lateral stripe from near caudal base to opercle. Anterior to dorsal fin, lateral stripe weakly developed. Lateral stripe terminates posteriorly at light, unpigmented bar at caudal base, extending full length of hypural plate and onto dorsal and ventral procurrent rays. Lateral scales narrowly outlined by melanophores, presenting crosshatched pattern. Dorsum of head plumbeous, extending ventrally to include dorsum of opercle and preopercle, lips, and lacrymal. Remainder of head white to silver, except for darkly pigmented and short gular stripe. Pelvic and anal fins clear. Dorsal fin dusky anteriorly, darkly pigmented on last 2 membranes. Leading pectoral rays sometimes outlined with melanophores. Caudal fin dusky, except for basal unpigmented region.

Breeding males bright steel-blue dorsally and dorsolaterally, each scale outlined with blue crescents. Laterally, dark, blue-black scapular bar well developed and separate from darkened lateral stripe by broad, lightly colored region. Posterior to light region, lateral stripe expanded into large dark spot. Head yellowish, except for reddish snout and plumbeous dorsum. Dorsal fin bluish basally and centrally; pink distally. Interradial membranes darkened, especially posteriorly. Pectoral, pelvic, and anal fins salmon-pink with milky-white distal margins. Caudal fin white basally and bluish distally, but pinkish over most of fin.

Tuberculation.—Dorsum of head covered with moderately large scattered, antrorse tubercles. Early in development, however, tubercles arranged linearly. Snout, preorbital, and supraorbital areas covered with moderately large, antrorse organs, all interconnected. Mandibular tubercles smaller than dorsal head organs, erect, and arranged in 2 irregular rows. Interpercle, preopercle, branchiostegals, and gular area with few small and erect organs arranged in linear pattern. Suborbital region, operculum, suboperculum, and opercular membrane naked.

Body tuberculation extensive. Predorsal scales with 2–3 central, erect, and moderately large organs, generally arranged in a slight arc perpendicular to body axis. Peripheral to these are several erect, subcentral tubercles; no edge organs present. Caudal-peduncle scales similar to predorsal scales, but central organs scattered and number 2–5. Submarginals range up to 20. Caudal-peduncle tubercles small and erect. Along flanks, tubercles small and erect and arranged subcentrally (6–12) and centrally (2–10) on a scale, both above and below lateral line.

All fins tuberculate. Dorsal and anal fins rays all bearing 1 row and 1 organ per segment. Pelvic fins with first 4 rays tuberculate, each with 1 row and 1–3 tubercles per segment. First ray of pectoral fin with single row of small, retrorse organs, 1 per segment. Rays 2–9 with single row of tubercles to branching of ray and 2–3 per segment. After branching, anterior and posterior branches with single row. Anterior branch with 1 tubercle per segment and posterior with 2 tubercles per segment. Paired fins with small, erect organs arranged in rows on ventral side of anterior rays.

Distribution. There are two disjunct populations of the bluntface shiner, one east and one west of the Mississippi River. Eastern populations occur in direct, west-flowing tributaries of the Mississippi River and eastern tributaries of the lower Tennessee River, all within the Coastal Plain province. Western populations occur in the middle Arkansas River drainage

(Illinois, Neosho, and Arkansas rivers) in Arkansas, Missouri, Kansas, and Oklahoma. Gibbs (1961) provided a distribution map of this species. This map also included an eastern Colorado locality, originally thought to be the type locality, and a population in the Osage River System (Missouri R. Drainage) and the White River. The type locality is suspect (see **Comments**) and Cross (1967) doubted the validity of the latter two localities, suggesting erroneous locality information. This seems logical since both the Osage and White rivers have been thoroughly sampled for years and no additional records of this species are known to exist.

Ecology. Bailey and Taylor (1950), Cook (1959), and Burr and Mayden (1978) described the habitat of eastern populations, and Moore (1952), Cross (1967), Cavin (1971), Miller and Robison (1973), and Pflieger (1975) noted habitat associations for western populations. Both populations occur in high-gradient, fast to moderately-fast clear water, and not low-gradient habitats typical of much of the Coastal Plain province. Adults generally prefer fast riffle and raceway habitats. Younger individuals are typically in or close to these habitats, but also frequent shallow pools. In eastern populations this species may be found over a sandy substrate, whereas in the west they typically occur over gravel or rubble, not over sand or mud. Cavin (1971) noted that this species has a low tolerance for oxygen stress.

Little is known about this species' life history, except for notes by Cook (1959), Cross (1967), Pflieger (1975), and a study by Cavin (1971). In Kansas most individuals live only 2 years, but some may live 3 years. Age classes 0 and I comprise a large proportion of populations. Young of the year have a high growth rate, reaching about 18 mm, with a maximum of 45 mm by the end of their first summer. By the end of the second summer most average about 50 mm, with a maximum of about 75 mm.

In Kansas and Missouri, the spawning season spans late May to late July (Cross, 1967; Pflieger, 1975). Ovary weight begins to

increase in late June and reaches a peak in middle to late July, with a maximum GSI (Gonadosomatic Index) of 16.4. Ovaries decreased in size in August and September (Cavin, 1971). As noted by Gale and Buynak (1978) for *C. analostana*, mature oocyte diameter of *C. camura* decreased with progression of breeding season from 0.88 in middle to late June to 0.82 in late July. Spawning has been observed and consists of crevice spawning similar to that of other *Cyprinella* species (Rabito and Heins, 1985).

Etymology. The name *camura*, is derived from the Latin *camur*, meaning turned inward, referring to the blunt snout (Gibbs, 1961).

Comments. The type locality of this species is in question. Jordan and Meek (1884) in the original description designated Fort Lyon, Colorado, as the type locality. This locality is west of the present range of *C. camura* by several hundred miles. As a possible explanation for this disjunction, Gibbs (1961) suggested that the species range has become constricted in recent years and the Ozark localities are the only remaining populations. Gilbert (1978a), however, suggested two alternatives. Perhaps Jordan and Meek meant Lyons, Kansas, or Lyon County, Kansas. The latter is the more likely of the two. Today this species is abundant in the Cottonwood River system, Lyon Co., Kansas, but is not found within several miles of the former locality. The Lyon Co., Kansas, locality is supported by the absence of the bluntface shiner in collections by Gilbert and Cragin (see Cross, 1967) from Garden City, Kansas, where other cool and clear-water species were collected. Further, Jordan (1891) did not report this species from collections in the Arkansas River system in Colorado, but listed the species from the "Arkansas River at Witchita." It is possible, however, that Gibbs is correct and the Colorado locality is the type locality, especially since *Etheostoma cragini*, a species with a distribution like western *C. camura*, is known from eastern Colorado. Further, other fishes reported from clear, spring-fed streams along the Arkansas valley in the late 19th century

(e.g., *Notropis heterolepis*, *N. topeka*, *Phoxinus*) have subsequently disappeared. Thus, more extensive western range of *C. camura* is conceivable.

Because of the disjunct nature of this species, Gibbs (1961) examined differentiation between the two populations. These populations were found to differ at the "racial" level in meristic and morphometric characteristics. Perhaps further studies may warrant subspecific or even species recognition of these forms.

CYPRINELLA WHIPPLEI GIRARD

Steelcolor Shiner

Plate III

Cyprinella whipplei Girard, 1857:198. [Orig. descr.; Type locality: Sugarloaf Creek, trib. Poteau River, ca. 20–25 mi S Fort Smith, AR, vicinity of Poteau, OK (following Gilbert, 1978a)]

Diagnosis. Anal rays 9; pectoral rays usually 15; dorsal fin of breeding males without bright coloration, other fins yellow; breeding males with a single row of mandibular tubercles; dorsal margin of anguloarticular horizontal; isthmus of maxilla very narrow; horizontal plate of urohyal broad; basihyal deep; operculum narrow and deep; symplectic narrow; interoperculum narrow; mentomeckelian long.

Description. A large *Cyprinella*, reaching a maximum length of about 130 mm SL. Body slightly compressed and moderately deep, deepest in breeding males. Head small and subconical. Snout short, pointed, and protruding, especially in breeding males. Orbit moderately small. Mouth terminal to subterminal; jaws nearly equal and extending posterior to anterior margin of orbit. Caudal peduncle deep and elongate. Dorsal fin greatly expanded in breeding males; origin slightly posterior to pelvic fin insertion.

Dorsal fin rays 8; anal rays 8–10 (9); pectoral rays 14–16 (15); pelvic rays 8; principal caudal rays 17; dorsal procurrent rays 10–12 (11), ventral procurrent rays 9–11 (10).

Lateral scales with exposed margins deeper

than wide, especially anteriorly near lateral line. Lateral-line scales 36–40 (37–38); total predorsal circumferential scales generally 26; scales above lateral line 11–15 (13), below lateral line usually 11; total caudal-peduncle scales 14; caudal-peduncle scales above and below lateral line 7 and 5, respectively.

Pharyngeal teeth 1, 4-4, 1, hooked, with narrow serrated grinding surfaces. Total gill rakers 8–10 (8). Total vertebrae 38–40 (39), precaudals 19–20 (19), caudals 19–20 (20). Dorsal fin insertion above vertebra 12 or 13.

Lateral line complete. Supratemporal canal broadly to narrowly interrupted, pores 2 per side. Supraorbital canal complete, pores 8. Infraorbital canal occasionally interrupted below orbit, but generally complete, pores 10–11 (11). Preoperculum mandibular canal complete, total pores 11, mandibular pores 4.

Intestine with simple S-shaped loop and two flexures, Type I. Peritoneum with silver background color and heavily speckled with melanophores.

Coloration in life.—Females and nonbreeding males olive to steel-blue dorsally and dorsolaterally, becoming lighter ventrally. Body silver-blue laterally, except for dark lateral stripe. Stripe best developed posteriorly, continued anteriorly to opercular margin from dorsal fin origin by broad, diffuse band and dark dorsal margin. Venter cream to white. Head olive to blue dorsally and light ventrally. Lacrymal, dorsal preopercle, and opercle and subopercle colored like dorsum, but lighter. Lips and gular stripe pigmented. Fins lightly pigmented on membranes, except dorsal, which is dusky anteriorly and darkly pigmented posteriorly, forming dark spot on last 2 membranes.

Dorsum of breeding males bright steel-blue. Laterally and ventrally body iridescent bluish-purple. Snout red. All fins lemon-yellow and milky-white. Dorsal fin heavily pigmented posteriorly, presenting large dark spot. Caudal and base of anal more dusky. Leading rays of paired fins pigmented.

Tuberculation.—Dorsum of head in peak males as in *C. analostana*, with clusters of

moderately large and antrorse organs formed on either side of midline from occiput to nares. Snout tubercles equal in size and antrorse posteriorly, grading to erect anteriorly and separate from dorsal head organs by a distinct hiatus. Preorbital organs moderately large and crowded, as in *C. galactura*, and connected to supraorbitals by 2–3 rows of antrorse organs. Supraorbital tubercles moderately large and antrorse. Tubercles on preopercles, interopercles, branchiostegals, and gular region small, scattered, and erect. Remainder of head naked.

Predorsal tubercles numerous and erect, each scale generally containing central, subcentral, and edge organs. Central tubercles largest. Caudal-peduncle tubercles present continuously around body, but best developed ventrally. Generally 10–15 scattered subcentral and 2–6 central organs per scale. Along flanks, both above and below lateral line, each scale with 7–12 erect, subcentral, and 3–4 central organs.

Dorsal fin rays with 1 row and 1 organ per segment. Anal fin rays with a single row and 2–3 tubercles per segment. First four rays of pelvic fin with single row and 2–3 per segment. Leading ray of pectoral fin with single row and one organ per segment, extending most of length of ray. Posterior rays 2–7 with single row of retrorse and crowded organs, continuing onto posterior branch. Each segment, after branching, with 2–3 organs. Before branching and on anterior branch, 1 row and single organ per segment. Pectoral and pelvic fins with erect organs on ventral surfaces.

Distribution. The steelcolor shiner, apparently widespread in the pre-glacial highland regions of eastern North America, is found today only in the Interior and Eastern Highlands, with a few northern disjunct populations. Its present distribution is typical of many species whose ranges indicate northern glacial alterations of this once widespread range (Mayden, 1985; Wiley and Mayden, 1985). In the west it is found in the unglaciated Ouachita, Kiamichi, Little, middle-lower Arkansas tributaries, White, and Meramec rivers. East of the Mississippi, it is found in the

Tennessee and Cumberland rivers, and unglaciated portions of the Ohio. Some populations are known from the once glaciated Wabash, Illinois, and Allegheny river systems. For summary maps of the distribution, see Gibbs (1963) and Lee et al. (1980).

Ecology. Typically the steelcolor shiner inhabits unmodified and treelined, moderate to high gradient streams and rivers. Generally, it is not found in small creeks or large rivers. Most frequently it occurs over a gravel substrate in riffles and raceways (Gibbs, 1963; Pflieger, 1975; Smith, 1979).

The steelcolor shiner is a sight-feeding species that schools near the top or middle of the water column. Its diet typically consists of drifting aquatic or terrestrial insects, but it also feeds on small crustaceans, mites, and earthworms, some of which are picked from the substrate (Forbes and Richardson, 1908; Pflieger, 1975).

Most individuals live only 3 years. Some females may live up to 4 years (Pflieger, 1965). Males attain a larger size than females by the end of their second summer. Maturity is reached by the second summer, but most individuals do not spawn until the third. The smallest mature males are about 49 mm; smallest females are about 38 mm (Pflieger, 1965).

The spawning season in Missouri and Ohio is from late May to mid-August (Pflieger, 1965, 1975). Trautman (1957) and Pflieger (1965, 1975) noted spawning in fast and shallow water, above the substrate, on the undersides, upper surfaces, or lower lateral surfaces of submerged logs. Eggs are deposited beneath loose bark and/or in crevices between roots and logs. Several males (20–30) may be congregated, fighting and/or spawning, around the log, with as many or more females found downstream below the log. Males maintain nonstationary territories around the spawning surface and defend these areas from other males with threatening displays and occasional battering with their tuberculate heads. Females, when ready to spawn, swim in or near the spawning area and are approached by one to several males. After a male succeeds in fighting

off others, he and the female approach the spawning area side by side, with the male slightly above the female. During the spawning act(s) the male presses the female against the log and the two vibrate while traveling along the log, releasing eggs and milt simultaneously. Males frequently eat eggs from the nest areas. The same behavior has been observed in aquaria when eggs do not remain attached. Over 100 eggs were found in stomachs of some males.

The spotfin shiner is frequently observed spawning near the steelcolor shiner, but the two species have never been observed intermingling. Typically, the spawning peak of *C. spiloptera* occurs earlier than *C. whipplei* (Trautman, 1957; Pflieger, 1965). Further, these species have species-specific vocalizations (Winn and Stout, 1960).

Etymology. This species is named after Lt. A. W. Whipple, commander of the expedition that collected the type series.

CYPRINELLA ANALOSTANA GIRARD
Satinfin Shiner
Plate III

Cyprinella analostana Girard, 1859:58–59.
[Orig. descr.; Type locality: Rock Creek, trib. of Potomac River, Washington, DC]

Diagnosis. Anal rays 9; pectoral rays usually 13 or 14; pharyngeal process of basioccipital spatulate and deep; dermopterotics extend over dialator fossa; supraorbitals narrow anteriorly and posteriorly; posterior process of vomer narrow; posterior subopercle greatly elevated; supraethmoid elongate; anterior margin of frontals smooth; ceratohyals very deep.

Description. A moderately large *Cyprinella*, adults reaching about 90 mm SL. Body deep, especially in breeding males, and moderately compressed. Head triangular. Snout pointed, protruding slightly. Mouth terminal to subterminal and oblique, extending posteriorly to anterior margin of orbit; lower jaw contained in upper jaw. Caudal peduncle thick and relatively long. Dorsal fin expanded in

breeding males; origin in both sexes slightly posterior to pelvic fin insertion.

Dorsal fin rays 8; anal rays 7–10 (9); pelvic rays 8; pectoral rays 11–16 (13–14); principal caudal rays 16–17 (17); dorsal procurrent rays 9–12 (10), ventral procurrent rays 8–10 (9–10).

Lateral scales higher than wide, appearing elevated. Lateral-line scales 33–38 (clinal, generally 36–37 in north to 35–36 in south); total predorsal circumferential scales generally 24; scales above lateral line 11–15 (13), below lateral line 11; total caudal-peduncle scales 14; scales above and below lateral line 7 and 5, respectively.

Pharyngeal teeth 1, 4–4, 1, hooked, with narrow, sometimes serrated, grinding surfaces. Total gill rakers 7–8 (7). Total vertebrae 35–36 (36), precaudals 18, caudals 17–18 (18). Dorsal insertion above vertebra 11 or 12.

Lateral line complete. Supratemporal canal broadly interrupted, pores 8–9. Supraorbital canal complete, pores 2 per side. Infraorbital canal complete, pores 11. Preoperculum-mandibular canal complete, total pores 11, mandibular pores 4.

Intestine arranged in simple S-shaped loop, Type I. Peritoneum silvery and speckled with melanophores.

Coloration in life.—Females and nonbreeding males like *C. whipplei*. Dorsum and dorso-lateral surfaces olive to silvery-blue, becoming lighter ventrally. Dorsum of head plumbeous down to lacrymal, upper opercle, and preopercle. Venter cream to white, except for pigmented lips and short, darkly pigmented gular stripe. Lateral scales above and below lateral line outlined with dark pigment, creating diamond-shaped pattern. Lateral stripe not well developed, but strongest posterior to dorsal origin. Stripe diffuse anteriorly, broad, and best developed dorsally as a narrow stripe to opercle. Dorsal fin lightly pigmented; melanophores strongest on posterior membranes. Caudal fin dusky with membrane pigment. Anal fin with some pigment basally. Pelvic fins immaculate.

Breeding males with more intense diamond-shaped lateral scale pattern and milky-white

pigments in all fins. Dorsal fin darkly pigmented, melanophores heavily concentrated in last 2–3 membranes. Anal base, caudal fin, and pectoral fin more dusky. All fins with faint yellow or gold color, more pronounced on pelvics, anal, and lower caudal. Body deep steel-blue dorsally and iridescent bluish-violet laterally and ventrally, lighter in latter region. Lateral stripe darker, especially on posterior half of body (Denoncourt and Messersmith, 1982). Lateral stripe expanded into large spot between dorsal fin and opercular membrane.

Tuberculation.—Gibbs (1963) and Denoncourt and Messersmith (1982) described tuberculation of this species. Dorsally, head pattern of young males semilinear; tubercles erect. Peak nuptial males, however, with 2 distinct areas of tubercle concentration lateral to midline and anterior to posterior margin of orbit. Dorsal tubercles of these males large and antrorse. Between orbit and occiput tubercles scattered, but generally in 2 lateral, concentrated patches. Preorbital and supraorbital regions with moderately large, antrorse organs, sparsely distributed as in *C. camura*. These regions connected by single row of equal-sized tubercles between orbit and naris on either side. Erect and scattered snout organs separate from dorsal head tubercles by small hiatus. Except for the 2 rows of antrorse, moderately large organs on each mandible, remainder of head naked.

Body tuberculation extensive. Predorsal tubercle pattern similar to that of *C. camura* and *C. galactura*, except each scale generally with fewer and larger tubercles. Predorsal organs antrorse and moderately large and range from 2–6. Generally, central organs best developed, subcentral organs only occasionally formed. Up to 8 subcentral, erect organs formed per scale above and up to 6 scale rows below lateral line along flanks. Occasionally small, erect central tubercle developed on each scale on or near lateral line. Caudal peduncle tuberculation well developed. Pattern similar to that of Mississippi River drainage relatives, except for a reduction of centrally located organs to 1 or 2. Each scale with up to 8 subcentral and 1–2

antrorse, central tubercles. Central organs sometimes slightly larger. This pattern continuous around caudal peduncle, but not well developed above lateral line.

Dorsal fin without tubercles. All anal fin rays with single row and 1 organ per segment. Pelvic rays with 1 row and 1 retrorse tubercle per segment. Leading pectoral ray with a single row and tubercle per segment; rays 2–6 with 1 row and 1 retrorse organ per segment before branching; occasionally 2 per segment. Beyond branching, single row continuous with posterior branch, 1 organ per segment; anterior branch with single row and tubercle per segment. No ventral organs observed on paired fins.

Distribution. The satinfin shiner is, with the exception of some populations in the southern Lake Ontario drainages, an Atlantic Slope endemic. This species is found in streams from the Peedee River System in North Carolina north to the Hudson River. Gibbs (1963) and Lee et al. (1980) presented distribution maps of this species.

Ecology. Considerable data exist on the biology of this species. The habitat of the satinfin shiner is similar to that of *C. whipplei*, generally in moderately small to large streams over a substrate of gravel, rubble, and/or sand. This species can occasionally be found in or near tidal areas of some rivers.

Denoncourt and Messersmith (1982) detailed many aspects of the life history of this species in Pennsylvania. Most individuals have a normal life span of 3 years, some reach 4. A mean fork length (snout to caudal fork) for age group 1+ was 58.6 mm, 67 mm for 2+, and 84 mm for 3+. Growth rates are similar for age classes, with no significant sexual dimorphism. About 70% of adult body size was attained by the end of the first year. Breeding in Maryland spans from May to late August (Stout and Winn, 1958). In Pennsylvania, spawning lasts from late May to early July, as evidenced from GSI (Gonadosomatic Index), condition factors, and breeding tuberculation and colors (Denoncourt and Messersmith, 1982). Condition factors are greatest in females, reach a

high in May–July (2.12–2.66) and are lowest from September to December (2–2.22). Age group 2 females have their highest values in May and June, while group 1 are later in July, indicating an earlier spawn by older age groups. This pattern was similarly noted by Stone (1940), but Gale and Buynak (1978) found no data to support this hypothesis. GSI values are greatest for both sexes in May and June, dropping sharply and maintaining a low level from July to December, indicating the end of spawning activities in July.

Ovary weights are greatest in June and decrease considerably, along with mean size of ova, by the end of July. During most of the year four distinct size classes of ova are apparent in ovaries, except in late July when only three are present. Mean diameter of ova ranged from 0.027 to 0.91 mm. Fecundity ranged from 545 to 3344 eggs, with a mean potential fecundity of 1598 per female. The actual fecundity was, however, estimated to be closer to 877 eggs per female. Gale and Buynak (1978) and Stone (1940) suggested a slightly lower fecundity, 6–634 or 409–864 eggs per female, respectively.

Cyprinella analostana is a fractional crevice spawner, spawning several times in a season and depositing its eggs in crevices under loose submerged bark, between exposed tree roots, in crevices in rocks and wood, or under flat rocks (Stone, 1940; Gale and Buynak, 1978). This species, like others of the genus, is known to produce vocalizations used in species and sex recognition (Stout and Winn, 1958; Stout, 1959; Winn and Stout, 1960). Males guard the nest area, protecting it from other males by rapidly swimming around the site and towards the intruding male with fins erect. Defending males also produce a knocking sound. When approached by a receptive female a purring sound is produced by males and spawning occurs (Stout, 1959; Winn and Stout, 1960). The spawning and prespawning behaviors of this species are similar to those of the spotfin shiner, *C. spiloptera* (Gale and Gale, 1977; Gale and Buynak, 1978). Under controlled conditions a given pair may spawn

3–11 times in a season with 6–634 eggs released each time. Time between spawnings ranged from 3 to 31 days, being bimodal for 5 and 8 days. Apparently most eggs are released during these spawning peaks and only a few are spawned between, unlike the behavior of *C. spiloptera*, which displays no peak in activity (Gale and Gale, 1977). Freshly spawned eggs average about 1.5 mm in diameter, but as the season progresses the mean diameter decreases (Gale and Buynak, 1978).

Eggs hatch in 6–8 days at 20–25°C (Gale and Buynak, 1978) or within 11 days at 20–20.5°C (Stone, 1940). After hatching larvae are inactive until 6 days posthatching, when they are about 6 mm long. At this time they begin to feed.

Etymology. The name *analostana* derives from Analostan Island in the Potomac River, Washington, D. C., the location where Girard originally collected this species.

Comments. Populations of this species from the Peedee River System are considered intergrades by Gibbs (1963) with the Santee River endemic, *C. chloristia*. With the exception of 6 individuals, however, all specimens from this drainage are typical for *C. analostana*. On this basis, Gibbs (1963) relegated *C. chloristia* to a subspecies of *C. analostana*. Based on diagnostic meristic differences presented by Gibbs (1963) and osteology (presented herein), I prefer not to follow this treatment and follow Bailey et al. (1970) and Robins et al. (1980) in considering *C. chloristia* distinct at the species level.

CYPRINELLA CHLORISTIA (JORDAN AND
BRAYTON)
Greenfin Shiner
Plate III

Codoma chloristia Jordan and Brayton, 1878:21–23. [Orig. descr.; Type locality: Saluda River, Farr's Mills, W of Greenville, Greenville Co., SC]

Diagnosis. Anal rays 8; mandibular pores 3; neck of epibranchial I bent posteriorly; premaxillary process of maxilla short; supraor-

bital tubercles in single row.

Description. One of the smallest members of the genus, reaching a maximum length of about 60 mm SL. Body deep, especially in breeding males and females, and compressed; maximum depth at dorsal origin. Head moderately small and triangular. Orbit small. Snout relatively short and pointed, especially in peak males where it protrudes over lips. Mouth terminal and oblique, extending posteriorly to orbit margin. Lower jaw contained in upper jaw. Caudal peduncle deep and relatively short. Dorsal fin of breeding males expanded slightly.

Dorsal fin rays 8; anal rays 7–9 (8); pelvic rays 8; pectoral rays 11–17 (14); principal caudal rays 16–17 (17); dorsal procurrent rays 9–12 (11), ventral procurrent rays 8–10 (9–10).

Lateral body scales elevated, margins taller than wide. Lateral-line scale rows 32–36 (35); total predorsal circumferential scales generally 24; scales above lateral line 11–13 (11), below lateral line 11; total caudal-peduncle scales 14; scales above and below lateral line 7 and 5, respectively.

Pharyngeal teeth 1, 4-4, 1, hooked, with narrow, sometimes serrated, grinding surfaces. Total gill rakers 7–9 (8). Total vertebrae 35–37 (36), precaudals 17–19 (18), caudals 17–19 (18). Dorsal fin insertion above vertebra 11 or 12.

Lateral line complete. Supratemporal canal broadly interrupted, pores 2 per side. Supraorbital canal complete, pores 8–9 (8). Infraorbital canal complete, pores 9–12 (11). Preoperculo-mandibular canal complete, total pores 10, mandibular pores 3.

Intestine arranged in single S-shaped loop, Type I. Peritoneum silvery with scattered melanophores.

Coloration in life.— Nonbreeding and breeding individuals essentially like the northern sister species *C. analostana*. Gibbs (1963) noted that the lateral stripe of the greenfin shiner was more narrow and better developed. He associated this difference with the observation that *C. chloristia* typically inhabits clearer streams than *C. analostana*.

Tuberculation.— Dorsum of head with

moderately large, antrorse tubercles in a semi-scattered pattern from orbit to occiput. Tubercles arranged into 2 clusters, following areas where rows are normally developed on either side of midline of head. Anterior to posterior margin of orbits, arrangement linear like *C. analostana* and *C. whipplei*. Preorbital organs few, antrorse, and connected to supraorbital organs by single row. Supraorbital tubercles 5–6, antrorse, moderately large, and arranged in single row. Snout tubercles separate from dorsal head organs by a distinct hiatus; posterior organs antrorse and change to erect anteriorly. Mandibular tubercles erect and somewhat scattered, but occasionally in 2 rows. Remainder of head devoid of tubercles.

Predorsal region with a tubercle pattern as in *C. whipplei*, *C. analostana*, *C. venusta*, and *C. galactura*. Caudal peduncle pattern like *C. analostana*; central tubercles larger than subcentrals and reduced to 1–3. Along flanks, above lateral line, scales lined with 2–8 erect, small organs; below lateral line each scale lined with 2–8 antrorse small organs. No central tubercles developed, except occasionally on lateral-line scales and near caudal peduncle region.

All rays of dorsal and anal fins tuberculate. First rudimentary ray tuberculate along full length. Posterior rays with varying degrees of tubercle development; anterior rays generally have greatest development, with 1 row along ray medially and 1 organ per segment. Only first 3 rays of pelvic fins tuberculate; each ray with 1 row extending entire length and 1 organ per segment. First ray of pectoral fin with single row and 1 retrorse organ per segment. Rays 2–6 with single row per ray and usually single retrorse tubercle per segment; occasionally 2 tubercles per segment. No ventral organs observed on either paired fins.

Distribution. Endemic to the Santee River drainage of North and South Carolina, above the Fall Line. Gibbs (1963) and Lee et al. (1980) provide distribution maps of this species.

Ecology. Limited information exists. Except for habitat preference, the biology of this

species is probably similar to *C. whipplei* and *C. analostana*. *Cyprinella chloristia* appears to inhabit small rivers and streams of Montane and upper Piedmont provinces, differing from its closest relative *C. analostana*, which is typically associated with large riverine habitats.

Etymology. The name *chloristia* is from the Greek *chloros*, for green, and *histon* for sail, in reference to the greenish color of the dorsal fin observed by Jordan and Brayton.

Comments. This species was considered a subspecies of *C. analostana* by Gibbs (1963) and later elevated to species status by Bailey et al. (1970) and Robins et al. (1980). Gibbs (1963) united these species on the basis of an hypothesized area of intergradation between the two taxa in the Peedee River drainage. Data supporting intergradation were from 6 of 189 specimens examined, all of which appeared intermediate. Other collections were typical of “normal” *C. analostana* in meristic data, although some clinal variation was observed. Here I follow Bailey et al. (1970), Gilbert and Burgess (1980), and Robins et al. (1980) in considering this form a distinct species and suggest that additional populational-level studies be conducted to determine if gene flow has contributed to the intermediate conditions of some Peedee River specimens, as suggested by Gibbs (1963). Even if headwater capture transfer introduced some *C. chloristia* into the Peedee, it is doubtful that the limited extent of this possible “hybridization” event, not intergradation, should warrant uniting these two forms as a single evolutionary unit.

CYPRINELLA VENUSTA GIRARD

Blacktail Shiner

Plate III

Cyprinella venusta Girard, 1857:198. [Orig. descr.; Type locality: Río Sabinal at Sabinal, Uvalde Co., TX]

Cyprinella notata Girard, 1857:198. [Orig. descr.; Type locality: Río Seco (=Seco Creek) at D'Hanis, Medina Co., TX]

Cyprinella cercostigma Cope, 1868:157. [Orig. descr.; Type locality: Pearl River,

Monticello, Lawrence Co., MS]

Photogenis eurystomus Jordan, 1877b:356. [Orig. descr.; Type locality: Nancys Creek, trib. Chattahoochee River, Atlanta, Fulton Co., GA]

Photogenis stigmaturus Jordan, 1877b:337. [Orig. descr.; Type locality: trib. Etowah River (probably Silver Creek), near Rome, Floyd Co., GA]

Cyprinella calliura Jordan, 1877c:61–62. [Orig. descr.; Type locality: Alabama River system, Selma, Dallas Co., AL. Originally given as Black Warrior River, but this river is not near Selma (after Gilbert, 1978a)]

Photogenis leucopus Jordan and Brayton, 1878:41–42. [Orig. descr.; Type locality: Chattahoochee River at Shallow Ford, NW of Gainesville, Hall Co., GA]

Luxilus chickasavensis Hay, 1881:506. [Orig. descr.; Type locality: Chickasavensis River, Enterprise, Clark Co., MS]

Cliola urostigma Jordan and Meek, 1884:474–477. [Orig. descr.; Type locality: San Saba River (trib. Colorado River), at Fort McKavit (McKavett), ca. 45 air mi SE San Angelo, Menard Co., TX]

Notropis cooglei Hildebrand and Towers, 1928:18. [Orig. descr.; Type locality: Pelucia Creek, S of Greenwood, Leflore Co., MS]

Diagnosis. Anal rays 8; caudal spot large and dark; scales below lateral line along flanks without central tubercles; mesial neck of epibranchial 1 bent posteriorly; retroarticular long and L-shaped; insertion of *adductor mandibulae* A1 on maxilla below isthmus; hypohyal foramen restricted to anterior ceratohyal; overlap between supraorbitals and lateral ethmoids slight; ligament connection between epibranchial 1 and 2 mesial to uncinat process of epibranchial 2.

Description. One of the largest members of the genus, reaching about 150 mm SL. Body slender and elongate to moderately deep, but varies between subspecies; *venusta* generally deepest and *stigmatura* most slender form. Head moderately large, but variable, *stigmatura* with shortest head. Orbit moderately small, smallest in *venusta*. Snout subconical, acute in

peak males. Mouth terminal or subterminal, oblique, large; jaws equal and extend to anterior margin of orbit. Caudal-peduncle depth and length variable between subspecies, *venusta* deepest and *stigmatura* more slender. Dorsal fin origin posterior to pelvic fin insertion; fin somewhat expanded in breeding males.

Dorsal fin rays generally 8; anal rays 8 (except some *stigmatura* with high frequency of 9); pelvic rays 8; pectoral rays 14–15 (high frequency of *venusta* with 13); principal caudal rays 17; dorsal procurrent rays 11, ventral procurrent rays 9–11 (10).

Exposed margins of lateral scales taller than wide. Lateral-line scale rows 34–48 (usually 36–43, but variable between subspecies: *venusta* 37 or less, *stigmatura* 40–43, *cercostigma* 38–40); total predorsal circumferential scales generally 24–26; scales above lateral line 13–17 (15, although generally 13 in *venusta*), below lateral line 11; total caudal-peduncle scales generally 14; above lateral line 7, below lateral line 5.

Pharyngeal teeth 1, 4-4, 1, hooked, and with or without serrations on narrow grinding surfaces. Total gill rakers 7–9 (7). Total vertebrae 37–39 (38), precaudals 19–20 (19), caudals 18–20 (19). Dorsal fin insertion above vertebra 12 or 13 (13).

Lateral line complete. Supratemporal canal complete or broadly to narrowly interrupted, pores 2 per side when interrupted or 5 when complete. Supraorbital canal complete, pores 8. Infraorbital canal complete, pores 10 or 11. Preoperculo-mandibular canal complete, total pores 10, mandibular pores 4.

Intestine simple S-shaped loop, Type I. Peritoneum silvery with thick speckling of melanophores.

Coloration in life.— Females and non-breeding males similarly colored. Dorsum dark bluish to olive, extending down sides to near lateral band, becoming lighter. Lateral band dark and narrow posteriorly, fading and broadened anteriorly where the most obvious development is a narrow line continuing forward from dorsal margin. Posteriorly on caudal peduncle, lateral band very distinct, with well-

developed caudal spot which may be rounded or squarish, depending on race. Venter unpigmented, except for short, dark gular bar, and pigmented lips, anal fin base, and lower caudal peduncle. Scapular bar weakly developed. Lateral and dorsolateral scales with pigmented edges, forming diamond-shaped pattern on sides. Lateral line pores more heavily pigmented anteriorly, producing dotted pattern along path of canal. Fins clear, except base of anal and caudal and leading ray of pectoral. Dorsal fin dusky with melanophores on all membranes, increasing in intensity posteriorly.

Breeding males brilliant steel-blue dorsally, less laterally. Lateral band very dark and expanded into large spot between dorsal fin and opercle, immediately posterior to a large lightly pigmented region. Fins with milky-white coating. Anal and caudal fins yellow and dorsal darkly pigmented.

Tuberculation.—Dorsum of head covered with many moderately large, antrorse organs in scattered pattern. Preorbital, suborbital, and snout regions with similar sized organs. Preorbital tubercles thickly concentrated and connected to supraorbitals by wide band, 2–3 organs wide. Snout organs concentrated in clump, separate from dorsal tubercles by hiatus; erect anteriorly and antrorse posteriorly. Mandibular region with 2 semilinear rows of tubercles medially. Except for small semiantrorse organs scattered on preopercle, remainder of head naked.

Tubercles on body scales well developed. Predorsal scales each with 2–3 centrally located, antrorse organs in transverse pattern and 2–4 subcentral organs around perimeter. Predorsal tubercles similar in size to those on top of head. Along flanks, each scale with 0–5 (generally 3–4) erect, subcentral organs; close to nape some begin to appear antrorse. Lateral-line scales sometimes with single, centrally located, erect organ. Caudal-peduncle scales with 4–7 small and erect subcentral and 1–4 central tubercles per scale, best developed ventrally.

Dorsal and anal fins tuberculate on all rays

in peak males; first ray with erect tubercles over full length. Posterior rays with single row and 1 per segment, best developed medially. Pelvic fin rays 2–6 tuberculate medially, consisting of single row and 1 organ per segment. Pectoral fin with retrorse tubercles; first ray with single row and 1 tubercle per segment. Rays 2–8 each with single row basally of small, crowded organs, continuing onto posterior branch (generally 2–3 per segment). Anterior branch with single organ per segment. No ventral organs noted on paired fins.

Distribution. The blacktail shiner is a North American Coastal Plain endemic, ranging from the Río Grande, Texas, east along Gulf of Mexico to Suwannee River, Florida, and north in the Mississippi Embayment to southern Illinois. The western subspecies, *C. v. venusta*, is distributed west of the Mississippi River and smaller, direct eastern tributaries. *Cyprinella v. cercostigma* is distributed along the Gulf Coast east of the Mississippi River from Lake Ponchartrain, Louisiana, drainage to the Suwannee River. *Cyprinella v. stigmatura* is found in the upper Mobile Bay System in the Alabama and Tombigbee rivers, primarily above the Fall Line. Intergrades between the latter two subspecies have been proposed from the Cahaba, Alabama, and Tallapoosa rivers.

Ecology. Very little is known for such a wide ranging, common, and evolutionarily interesting species. Typically it inhabits streams or moderately sized rivers with sparse vegetation, strong current, and sand or gravel substrate. In Missouri, spawning occurs from June to August. Eggs are deposited in crevices, as in other species of *Cyprinella*, and territories are defended by males (Pflieger, 1975; Rabito and Heins, 1985). Males and females produce sounds which females use to attract males (Delco, 1960); both use these sounds for species recognition.

Hybrid swarms have been commonly reported between this species and *C. lutrensis*, even though the two species apparently have the ability to discriminate each other through species specific sounds (Delco, 1960). Hubbs et al. (1953) and Hubbs and Strawn (1956) dis-

cussed introgressive hybridization with *C. lutrensis* and related the frequency to ecological disturbances. Smith (1979) reported hybrids of these species from Illinois.

Etymology. The epithet *venusta* is named after the Roman goddess of love, Venus. The name for the eastern subspecies *cercostigma* is derived from the Greek, *kertos* for tail, and *stigma* for spot, referring to the spot at the base of caudal fin. The slender subspecies, *stigmatura* is named also for the caudal spot after the Greek *stigma* and *oura* for tail.

Comments. Until rather recently, the black-tail shiner has had a complex taxonomic history, as evidenced by the synonymy. At least 10 names have been used to describe this species, mainly because of poor communications in the 1800s and early 1900s, and poor collections from the southeast. Bailey et al. (1954) first doubted the validity of the four names in use at that time, recognizing only one, *Cyprinella venusta*. As first reviser, Hubbs (1954) chose *venusta* over *notata*, both described in the same publication. Since that time, the taxonomy has remained stable with the recognition of three subspecies, *venusta* Girard, *cercostigma* Cope, and *stigmatura* (Jordan). Further work in this species seems warranted since only a small area of intergradation was noted by Gibbs (1957c) between *cercostigma* and *stigmatura*. All three forms may eventually warrant species status.

CYPRINELLA GALACTURA (COPE)

Whitetail Shiner

Plate III

Hypsilepis galacturus Cope, 1868:160. [Orig. descr.; Type locality: Holston River system, Virginia (following Gibbs, 1961:339 and Gilbert, 1978a)]

Diagnosis. Anal rays 9; snout pointed; large depigmented spots on upper and lower caudal peduncle at base of caudal fin; snout of breeding males red; hiatus in tubercles between snout and dorsum of head absent; mandibular tubercles scattered; operculum very broad; hypohyal foramen very small; premaxillary

process of maxilla short; frontal-sphenotic connection placed posteriorly.

Description. One of the largest and more elongate members of the genus, reaching about 100 mm SL. Body terete and elongate, only slightly compressed. Head subconical, large, and elongate. Orbit large. Snout relatively elongate and protruding in nuptial males. Mouth terminal and oblique; lower jaw contained in upper, both extending to anterior margin of orbit. Caudal peduncle slender and elongate. Dorsal fin greatly expanded in breeding males; origin in both sexes slightly posterior to pelvic fin insertion.

Dorsal rays 8; anal rays 8–10 (9); pelvic rays 8; pectoral rays 14–18 (15 or 16); principal-caudal rays 17; dorsal procurrent rays 11–14 (12), ventral procurrent rays 10–13 (11).

Lateral scale margins higher than wide. Lateral-line scale rows 38–43 (39–40, slightly higher in eastern populations); total predorsal circumferential scales generally 26; scales above lateral line 11–15 (13), below lateral line 11; total caudal-peduncle scales usually 14, scales above and below lateral line 7 and 5, respectively.

Pharyngeal teeth 1, 4-4, 1, hooked, and with narrow grinding surfaces usually not serrated. Total gill rakers 7–9 (9). Total vertebrae 39–41 (40), precaudals 19–22 (20), caudals 19–21 (20). Dorsal insertion above vertebra 13 or 14 (13).

Lateral line complete. Supratemporal canal broadly interrupted, pores 2 per side. Supraorbital canal complete, pores 8. Infraorbital canal complete, pores 10 or 11. Preoperculomandibular canal complete, total pores 11–13 (12), mandibular pores 4.

Intestine with simple S-shaped loop, Type I. Peritoneum silvery with several melanophores.

Coloration in life.—Females and nonbreeding males olive to silver-blue dorsally and laterally to lateral stripe. Lateral stripe silver-blue and best developed posterior to dorsal origin, continued forward to opercle by broad, diffuse, dusky band delimited dorsally by narrow dark line. Lateral band darker and

broader on hypural plate and basal caudal fin rays, producing oval caudal spot. Caudal peduncle, procurent rays, and basals of uppermost and lowermost principal caudal rays unpigmented above and below caudal spot, producing two distinct white areas on tail. Dorsum of head darkly pigmented; melanophores, extending to lacrymal, lips, dorsal preopercle, and entire opercle. Gular stripe short and faint. Remainder of head and all of belly immaculate. Dorsolateral and lateral scales with margins darkly pigmented, producing diamond-shaped pattern. Dorsal fin dusky, especially posteriorly on last 2 membranes. Caudal fin dusky, except for unpigmented areas. Leading rays of pectoral fins outlined with melanophores. Anal and pelvic fins clear.

Breeding males more brightly colored. Iridescent steel-blue dorsally, bluish-silver to milky-white laterally, and white ventrally. Snout red. Lateral stripe well developed; expanded between dorsal fin and opercle into large, dark spot. Scapular bar well developed and separate from expanded lateral spot by broad, lightly colored (generally salmon-pink), rectangular region. Pelvic and anal fins white, most intense distally. Pectoral, dorsal, and caudal fins salmon-pink to red with white edges.

Tuberculation.— Dorsum of head with moderately large and antrorse tubercles in scattered pattern. Preorbital and supraorbital tubercles antrorse, numerous, and heavily concentrated. Snout organs grade from antrorse near nares to erect on snout; continuous with dorsal head organs. Mandibular tubercles moderately large and scattered. Small and erect organs present on branchiostegals, interopercle, preopercle, gular, and opercular membrane. Opercle, subopercle, and suborbital regions naked.

Body tuberculation similar to that of *C. camura*, except that scales along flanks have, in addition to subcentral organs, small tubercles located centrally in scattered pattern. Central tubercles on caudal peduncle largest of body tubercles.

Fin tuberculation as in *C. camura*, except first ray of pectoral fin with 2 organs per segment.

Distribution. Endemic to the Interior and Eastern Highlands of eastern North America. Western populations in the White and St. Francis rivers of the Ozark Plateaus. Eastern populations notably common in the Cumberland, Tennessee, upper Kanawha of the Ohio basin, and the Savannah and Santee rivers of the east coast; the latter two systems gained via stream capture. Prior to glaciation, this species most likely enjoyed a widespread distribution in these highland areas, as well as in the glaciated Central Lowlands (Mayden, 1985; Wiley and Mayden, 1985).

Ecology. Generally inhabits small to moderately large, high-gradient, clear streams with continuous flow. Typically found over clean gravel or rubble substrates. Common in raceways or near riffles and frequents deep pools in association with large boulders and rocky banks.

The biology of the whitetail shiner in the French Broad River, North Carolina, was examined by Outten (1958). Most individuals live a maximum of two years, but some can reach 3 or even 4 years. By the end of their first summer juveniles average about 34 mm, 55 mm at the end of the second, and 73 mm by the end of their third. The oldest specimen collected was an 80 mm, 4-year-old female; the largest was a 101 mm, 2-year-old male. Thus, as similarly observed by Pflieger (1975), males have a higher growth rate than females.

Maturity is attained by most individuals of both sexes by 2 years. At this age males develop breeding tubercles and bright coloration, and females are greatly distended with mature oocytes. Males are generally larger than females, 46–95 or 41–78 mm, respectively. The number of mature oocytes produced by 40 females 57–86 mm ranged from 404 to 1815; oocyte diameter averaged 1.6 mm. Fecundity is likely higher than these observed figures, since the whitetail shiner is a fractional spawner.

In Missouri the spawning season is pro-

tracted, spanning from early June to August (Pflieger, 1975). In North Carolina spawning lasts from late May to mid-July (Outten, 1958). Like other *Cyprinella*, males guard territories around nesting locations. Nest sites include crevices between rocks or logs, under bark, or on the undersurfaces of any object. Males swim continuously around the nesting location, defending it from other conspecific males and any potential predators of embryos. Once a female is attracted to the spawning location by displays, and perhaps sounds, the two approach the spawning surface, press their vents to the nesting surface, and deposit adhesive eggs for up to seven minutes. When nests are located on the undersurface of an object, spawning behavior is similar, but both sexes are inverted. A single nest may contain 127–382 embryos arranged in several individual clumps on the spawning surface.

The diet is very diverse, consisting primarily of drifting aquatic or terrestrial insects. This species is a voracious sight feeder, feeding equally on drifting midwater materials and floating items (Outten, 1958). Among aquatic insects, immature Ephemeroptera were most commonly eaten, varying seasonally with the particular taxon. Immature Diptera, oligochaetes, and Hemiptera were very common, but also varied seasonally. Other items less frequently ingested included larvae of Lepidoptera, Odonata, Hymenoptera, Nematoda, other fishes, and vascular plants.

Etymology. Derived from the Greek *galactos* for milk and *oura* for tail, in reference to the whitish region on the caudal peduncle and caudal fin.

Comments. Although this species consists of two widely disjunct groups of populations, Gibbs (1961) found little differentiation between the two. The two groups of populations varied only slightly in number of lateral-line scales, pectoral rays, and in certain morphometric features, but not enough to warrant taxonomic recognition.

CYPRINELLA PYRRHOMELAS (COPE)

Fieryblack Shiner

Plate III

Photogenis pyrrhomelas Cope, 1870: 463–464. [Orig. descr.; Type locality: trib. upper Catawba River, NC]

Diagnosis. Anal rays 10; mandibular pores 3; tail of breeding males red and white and tipped in black; breeding males with red snout and lips; *adductor mandibulae* A1 insertion on maxilla anterior to isthmus; posterior ramus of premaxilla straight; ascending wings of parasphenoid very broad; posterior and anterior wings of hyomandibular narrow; lateral commissure very narrow; anterior notch of vomer very deep; mentomeckelian short and cone-shaped; dermopterotic connected to frontals.

Description. A large and stout member of *Cyprinella*, attaining a maximum of about 90 mm SL. Body robust and deep, only slightly compressed. Head large, triangular, and deep. Orbit large. Mouth large, terminal, and oblique; upper jaw containing lower, both reaching to behind anterior margin of orbit. Snout blunt, slightly pointed in breeding males and protruding. Caudal peduncle thick and relatively short. Dorsal fin expanded in peak males; origin in both sexes posterior to pelvic fin insertion.

Dorsal fin rays 8; anal rays 9–11 (10); pelvic rays 8; pectoral rays 13–17 (15); principal caudal rays 17; dorsal procurrent rays 10–12 (12), ventral procurrent rays 10–12 (11).

Lateral scales with exposed margins higher than wide. Lateral-line scale rows 34–39 (35–36 in Santee and 37 in Peedee); total predorsal circumferential scales generally 26; scales above lateral line 11–15 (13), below lateral line 11; total caudal-peduncle scales generally 14; scales above and below lateral line 7 and 5, respectively.

Pharyngeal teeth 1, 4-4, 1, hooked, and with smooth or serrated cutting surfaces. Total gill rakers 6–7 (7). Total vertebrae 36–38 (37), precaudals 18, caudals 18–20 (19). Dorsal fin insertion above vertebrae 11–13 (12).

Lateral line complete. Supratemporal canal

complete or occasionally narrowly interrupted, pores 2 per side. Supraorbital canal complete, pores 6–7 (6). Infraorbital canal complete, pores 9–11 (10). Preoperculomandibular canal complete, total pores 9, mandibular pores 3.

Intestine simple, arranged in single S-shaped loop, Type I. Peritoneum with silver background color, overlain with speckling of melanophores.

Coloration in life.—Dorsum of females and nonbreeding males dark silver-blue, becoming lighter ventrally. Venter cream to white. Lateral stripe weakly developed, but best developed posteriorly where terminates at caudal base with large, distinct oval spot. Anterior to dorsal origin stripe indistinct and broader, continuing to opercle. Scapular bar well developed. Lateral and dorsal scales edged in black, producing crosshatched pattern. Dorsum of head plumbeous, continuing laterally to opercle, upper preopercle, lacrymal, and both lips. Ventrally, head immaculate, except for indistinct, short gular stripe. Dorsal fin dusky, darkest on last 2 or 3 membranes. Caudal dusky, edged posteriorly and on procurrent rays by heavy concentration of melanophores. First pectoral ray lightly pigmented. Anal and pelvic fins clear.

Breeding males brilliantly colored. Iridescent bluish-silver dorsum and upper lateral surfaces, darkest dorsally. Snout and lips bright red. Pectorals, pelvics, and anal fins milky-white. Base of anal dusky. Dorsal fin dark basally and subdistally; membranes heavily pigmented, strongest posteriorly with last 2 membranes jet-black. Anterior membranes red medially. White band well developed distally. Entire fin with milky-white hue. Caudal fin tricolored; narrow black band distally, broad red band medially, and white basally.

Tuberculation.—Dorsum of head with very large, antrorse organs arranged in 2 rows down midline, 1 row per side behind each orbit; development from erect to antrorse. Supraorbital tubercles also large, but not as large as dorsal head organs, ranging in number from 3–5; connected to preorbitals by single row of an-

trorse organs between naris and orbit. Preorbital organs few, moderately large, and antrorse. Snout tubercles equal in size to preorbital tubercles, scattered, and not separate from dorsal head organs by hiatus. Mandibles with single row of moderately large, erect organs. Remainder of head devoid of organs.

Predorsally, 1–5 rows of very large, antrorse tubercles; 1 tubercle per scale located centrally. No other organs formed. Midline scale row best developed, sometimes extending from dorsal origin to occiput; laterally, rows shorter. Flank scales without tubercles. Caudal-peduncle scales 3 rows above and below lateral line with very large, antrorse organs centered on scales. Single row developed above anal fin, beginning before anal fin and terminating about midway along fin base. No tubercles on dorsal or ventral midline scale rows. No edge or subcentral organs present on any body scales. Like dorsal head tubercles and tubercles on predorsal and caudal-peduncle scales, tubercles along body begin erect and transform into antrorse organs in development.

Dorsal fin with single row of tubercles and single organ per segment on medial portion of fin from second unbranched ray to second branched element. Anal fin with tubercles on most rays medially, composed of single row per ray and single organ per segment. Pelvic fins with rays 1–5 tuberculate; 1 row medially and 1 tubercle per segment. First ray of pectoral fin with single row of moderately large, retrorse organs, 1 per segment. Posteriorly, rays 2–7 with single row and single organ per segment. No ventral organs present on paired fins.

Distribution. The fieryblack shiner is an Atlantic Slope endemic in the Santee and Peedee rivers of North and South Carolina, above the Fall Line. Gibbs (1955) and Lee et al. (1980) provide distribution maps of this species.

Ecology. Virtually nothing is known of the life history of this species. It occurs primarily in small to moderate sized streams with clear, cool water. It may be found in quiet pools, but

also frequents deep riffles and raceways.

Etymology. The epithet *pyrrhomelas* is from Greek *pyrrhos*, meaning flame-colored, and *melas*, for black, describing the red-black coloration of caudal fins of breeding males.

Comments. Based primarily on differences in meristic and morphometric characters, populations from the Peedee River drainage were considered a separate, but undescribed subspecies by Gibbs (1955).

CYPRINELLA XAENURA (JORDAN)

Altamaha Shiner

Minnilus xaenurus Jordan, 1877a:79. [Orig. descr.; Type locality: S Fk. of Ocmulgee River, at Flat Shoals, Dekalb Co., GA]

Diagnosis. Anal rays 10; caudal-peduncle scales below lateral line 7; lacrymal long; anterolateral margin of lateral ethmoid concave; mesethmoid moderately long; frontal-sphenotic connection placed anteriorly; symplectic narrow; second infraorbital bone short; preethmoid socket of palatine long and narrow; dorsal margin of anguloarticular horizontal.

Description. A large *Cyprinella*, reaching a maximum of about 90 mm SL. Body deep, moderately robust. Head large and triangular. Mouth small, terminal, and oblique; jaws reaching to or before anterior margin of orbit; lower jaw smaller than upper and contained. Snout pointed and protruding slightly, especially in peak males. Orbit small. Caudal peduncle stout and relatively short. Dorsal fin slightly expanded in peak males; origin in both sexes slightly posterior to pelvic fin insertion.

Dorsal rays 8; anal rays 10 or 11 (10); pelvic rays 8; pectoral rays 13–17 (15–16); principal caudal rays 17; dorsal procurrent rays 10–13 (13), ventral procurrent rays 10–12 (11 or 12).

Lateral scales higher than wide. Lateral-line scale rows 38–40 (38 or 39); total predorsal circumferential scales generally 26; scales above lateral line 11–13, below lateral line usually 11; total caudal-peduncle scales 16; scales above and below lateral line 7.

Pharyngeal teeth 1, 4-4, 1, hooked, and

with narrow serrated surfaces. Total gill rakers 5–6 (5). Total vertebrae 38–40 (39), precaudals 18 or 19, caudals 20–22 (20–21). Dorsal fin insertion above vertebrae 12–14 (13).

Lateral line complete. Supratemporal canal complete, total pores 5. Supraorbital canal complete, pores 8. Infraorbital canal complete, pores 10. Preoperculo-mandibular canal complete, total pores 9, mandibular pores 4.

Intestine short, forming single S-shaped loop, Type I. Peritoneum silver, overlain by speckling of melanophores.

Coloration in life.—Dorsum of females and nonbreeding males bluish-silver to light-tan down to lateral stripe. Below stripe silver to white. Belly immaculate. Lateral stripe poorly developed, strongest posterior to dorsal fin, terminating posteriorly in large, oval caudal spot. Anteriorly, lateral stripe very diffuse, but broader and continuing forward to opercle. Dorsal and dorsolateral scales to 1–2 rows below lateral line outlined with narrow, black borders, presenting diamond-shaped pattern. Scapular bar narrow and strongly developed. Dorsum of head olive to dark bluish-silver, extending to include lacrymal and dorsal half of ascending arm of preopercle and opercle. Remainder of head immaculate. Gular stripe dark. Dorsal and caudal fins dusky. Last two membranes of dorsal darkly pigmented. Pectoral, pelvic, and anal fins clear. Leading ray of pectoral fin with some melanophores. Anal fin with dusky base.

Breeding males dark plumbeous dorsally. Lateral stripe broader and strongly defined; dark iridescent and deep metallic blue, except for black caudal spot. Belly silver. Dorsal fin darkly pigmented, especially last 2 membranes which are jet-black. Medially, dorsal fin burnt-orange, best developed anteriorly. Caudal dusky with red-orange medial and distal regions. Dorsal and ventral procurrent rays and medial caudal fin dark.

Tuberculation.—Like *C. pyrrhomelas*, this species has very large, antrorse tubercles on dorsum of head in form of 2 rows extending down midline and single or double row parallel to these, only behind orbits. Snout covered

with slightly smaller tubercles, antrorse posteriorly and erect anteriorly, and not separate from those on top of head. Above orbits, single row of 5–6 moderately large, antrorse organs connected to group of tubercles at anterior edge of lacrymal. Only occasionally are tubercles present in preorbital region. Area immediately anterior to orbit devoid of organs. Anterior lacrymal organs equal in size to snout tubercles and antrorse. Mandibular rami with single row of erect, moderately large tubercles. Remainder of head without tubercles.

Predorsal region with 1–5 rows of very large, antrorse organs; no other tubercles present. Single organs centered on each scale and rows graded in size, as in other species with predorsal rows, with central row longest. Caudal-peduncle scales also with large, antrorse organs in center of each scale; generally 3 rows above and below lateral line. Single row above anal fin absent. This species and *C. pyrrhomelas* share the unique condition among species with large caudal-peduncle tubercles of having scale rows above and below lateral line with tubercles. Other taxa only have large organs on ventral caudal-peduncle scales; dorsal scales with tubercles equal in size to other body tubercles. These two species also share the lack of other body scale tubercles.

Dorsal fin without tubercles. Anal fin tuberculate on first 4–5 rays medially, with single row and single organ per segment. On pelvic fin, first unbranched ray naked, but next 3 rays with single row and 1 per segment medially. First ray of pectoral fin with single row and tubercle per segment. Posteriorly, rays 2–6 armed with single row and single element per segment. Ventral tubercles on paired fins few, erect, and small.

Distribution. Endemic to the Altamaha River system of the Atlantic Slope, above the Fall Line. Gibbs (1955) and Lee et al. (1980) provide distribution maps of this species.

Ecology. Nothing known about life history. Habitat includes small to moderately sized, clear, and cool streams where individuals are typically found in pools near undercut banks and boulders.

Etymology. The epithet is Greek, *xaino* for scratch and *oura* for tail, presumably referring to the large tubercles on the upper and lower caudal peduncle.

CYPRINELLA CAERULEA (JORDAN)

Blue Shiner

Plate IV

Photogenis caeruleus Jordan, 1877b: 338–339. [Orig. descr.; Type locality: tribs. of Oostanula River (primarily Rocky Creek), above Rome, Floyd Co., GA]

Diagnosis. Anal rays 8; predorsal circumferential scales below lateral line 9; caudal-peduncle scales below lateral line with several centrally located tubercles; caudal-peduncle scales above lateral line without central tubercles; dorsal head tubercles develop from linear to scattered pattern; fourth and fifth membranes of dorsal fin uniformly pigmented with melanophores; caudal-peduncle tubercles present on dorsal and ventral scale rows; coronoid process of dentary vertical; premaxillary process of maxilla short; vomer with long neck; posterior subopercle greatly elevated; ceratobranchial 1 with a straight neck; anterior margin of frontals with mesial extension over supraethmoid; symplectic narrow; posterior wing of hyomandibular curled.

Description. A moderately sized species, reaching about 70 mm SL. Body nearly terete, narrow, elongate, and only slightly compressed. Head triangular and relatively small. Snout pointed, especially in breeding males where it protrudes. Orbit moderately large. Mouth terminal to subterminal and oblique; lower jaw contained in upper, both extending to anterior margin of orbit and longer than orbit. Caudal peduncle slender and moderately long. Dorsal fin greatly expanded in nuptial males; origin in both sexes above to slightly posterior to pelvic fin insertion.

Dorsal fin rays 8; anal rays 8–9 (8); pelvic rays 8; pectoral rays 13–16 (14); principal caudal rays 17–18 (17); dorsal procurrent rays 11–13 (11 or 12), ventral procurrent rays 10–12 (10–11).

Exposed margins of lateral body scales taller than wide. Lateral-line scale rows 37–39 (38); total body circumferential scales generally 22; scales above lateral line 11–13 (11), below lateral line 9; total caudal-peduncle scales generally 14; scales above lateral line 7, below lateral line 5.

Pharyngeal teeth 1, 4-4, 1, hooked, and with narrow grinding surfaces. Total gill rakers 6. Total vertebrae 38–40 (39), precaudals 18–20 (19), caudals 19–21 (20). Dorsal fin insertion above vertebrae 12–14 (13).

Exposed margins of lateral body scales taller than wide. Lateral line complete. Supratemporal canal broadly interrupted, pores 2 per side. Supraorbital canal complete, pores 8. Infraorbital canal complete, pores 11. Preoperculo-mandibular canal complete, total pores 11, mandibular pores 4.

Intestine in single S-shaped loop, Type I. Peritoneum silvery with scattered melanophores.

Coloration in life.— Nonbreeding males and females plain. Body steel-blue to dark silver above lateral stripe, white, or silver-white below. Margins of dorsal and lateral scales darkly pigmented, presenting cross-hatched pattern. Bluish lateral stripe present, best developed posteriorly, but extending from opercle to caudal base, where slightly expanded into wider and darker oval spot. Lateral stripe bordered dorsally by narrow depigmented line. Dorsum of head, lacrymal, lips, and dorsal opercle and preopercle plumbeous. Venter of head immaculate, except for short gular stripe. Dorsal fin of large specimens with some melanophores in last two membranes. Pelvic and anal fins clear. Anal fin base pigmented, pigment extending to ventral caudal peduncle. Rays of caudal and pectoral fins edged with melanophores.

Breeding males as above, except more brilliant. Dorsum and dorsolateral body brilliant blue. Lateral stripe bright bluish-green and continuous from opercle to caudal base. Fins bright yellow or orange and edged in milky-white pigments. Dorsal fin membranes dark except for last two, which are jet-black. Cau-

dal diffusely pigmented with melanophores.

Tuberculation.— Dorsum of head covered with antrorse, moderately large organs arranged in a scattered-clumped pattern, as in *C. whipplei*, *C. analostana*, and *C. chloristia*. Tubercles extend from occiput to anterior border of nares and laterally to, but not including, dorsal margin of operculum. Preorbital region covered with several moderately large, antrorse organs connected to supraorbital tubercles by series of 2–4 rows. Supraorbital tubercles antrorse and arranged in scattered pattern. Snout organs separate from dorsum of head by wide hiatus. Antrorse mandibular organs arranged in 2 rows. All other regions of head devoid of tubercles.

Predorsally, scales generally with 1–3 central and occasionally 1 or 2 subcentral antrorse organs. Central tubercles generally about equal in size to dorsal head organs. Pattern similar to that of *C. galactura*, *C. analostana*, *C. chloristia*, *C. venusta*, and *C. spiloptera*. No edge organs present. Along flanks, above lateral line, some scales with weak development of 1–4 subcentral, erect tubercles; many dorsolateral scales on anterior body without tubercles. Below lateral line, posterior to depressed pectoral fins, each scale with 1–8 subcentral, antrorse organs. Caudal-peduncle scales with antrorse organs around margin subcentrally (generally 1–8) and series of centrally located, antrorse organs of equal size. Pattern best developed ventrally on 2 scale rows below lateral line. For 3 scale rows above lateral line only subcentral, antrorse organs present. Dorsal and ventral scale rows of caudal peduncle devoid of tubercles.

Dorsal fin with weak tubercle development; anterior few rays with single row medially and single tubercle per segment. Anal fin with single row along each ray, 1 tubercle per segment. Anteriorly, anal rays completely covered, but posteriorly rows restricted to medial portions of rays. First 3 rays of pelvics with single row and 1 organ per segment. First ray of pectoral fin with single row of retrorse tubercles, 1 tubercle per segment and extending most of length of ray; posteriorly, rays 2–7

with single file basally; after segmentation 2 tubercles per segment. After branching, main row continues along posterior branch, first with 2 organs per segment and distally with 1 tubercle per segment. Anterior branch with 1 tubercle per segment. No tubercles observed on ventral surfaces of paired fins.

Distribution. Endemic to the Mobile Bay Basin, above the Fall Line in the Coosa River system. Distribution maps of this species are provided in Gibbs (1955), Lee et al. (1980) and Pierson and Krotzer (1987).

Ecology. Almost nothing is known of the biology of this rare species. Jordan and Evermann listed it as common in 1896. Since then, it has apparently been extirpated from much of its range (Lee et al., 1980). This species is apparently common today only at a few locations in southeastern Tennessee, northwestern Georgia, and eastern Alabama. The blue shiner is disappearing from Alabama. Habitat includes sand, gravel, or rubble pools in medium to small, clear, cool stream (Pierson and Krotzer, 1987).

Etymology. The name *caerulea* is Latin for blue, referring to the lateral stripe and presumably the overall coloration of breeding males.

CYPRINELLA GIBBSI (HOWELL AND
WILLIAMS)
Tallapoosa Shiner
Plate IV

Notropis gibbsi Howell and Williams, 1971:55–64, figs. 1, 2a,e,g. [Orig. descr.; Type locality: Enitachope Creek, trib. Hillabee Creek, 3.2 mi SSW Ashland, along St. Hwy. 9, Clay Co., AL]

Diagnosis. Anal rays 9; breeding males with tubercles in rows on branchiostegals, subopercle, cheek, and along ventral margins of orbit; dorsum of head with tubercles arranged in a scattered-clumped pattern; predorsal scales with several central tubercles; ascending process of premaxilla elongate and narrow; posterior ramus of premaxilla strongly decurved; pharyngeal process of basioccipital

deep and triangular in shape; horizontal plate of urohyal broad; supraethmoid very broad and with entire lateral edges; posterior process of quadrate deep and heavy.

Description. A moderately sized *Cyprinella*, reaching about 80 mm SL. Body elongate to moderately deep, robust, and stout; only slightly compressed. Dorsal profile arched, greatest body depth between dorsal origin and midway between occiput and dorsal fin; ventral profile more horizontal. Head moderately large and triangular. Snout moderately long and pointed, especially in breeding males where it protrudes. Orbit large. Mouth large, terminal, and oblique; lower jaw contained in upper and both extending slightly beyond anterior margin of orbit. Caudal peduncle stout and relatively short. Dorsal fin not greatly expanded in breeding males; origin in both sexes slightly posterior to pelvic fin insertion.

Dorsal fin rays 8; anal rays 8–10 (9); pelvic rays 8; pectoral rays 13–16 (14 or 15); principal caudal rays 17; dorsal procurrent rays 10–12 (11), ventral procurrent rays 9–11 (10).

Exposed margins of lateral scales higher than wide. Lateral-line scale rows 37–42 (38–40); total predorsal circumferential scales 23–27 (24–26); scales above lateral line 12–16 (13–15), below lateral line 9–11; total caudal-peduncle scales 14; scales above lateral line 7, below lateral line 5.

Pharyngeal teeth 1, 4-4, 1, hooked, and with narrow serrated grinding surfaces. Total gill rakers 5–6 (5). Total vertebrae 37–40 (38), precaudals 18–20 (19), caudals 18–21 (19). Dorsal fin insertion above vertebra 13 or 14 (13).

Lateral line complete. Supratemporal canal complete, pores 5, or broadly interrupted, pores 2 per side. Supraorbital canal complete, pores 8. Infraorbital canal complete, pores 11. Preoperculomandibular canal complete, total pores 10 or 11, mandibular pores 4.

Intestine simple S-shaped loop, Type I. Peritoneum silvery with speckling of melanophores.

Coloration in life.—Females and nonbreeding males bluish-silver to olive dorsally and

dorsolaterally, lighter ventrally before bluish-black lateral stripe. Lateral stripe separate from darker dorsum by cream to silver narrow band. Margins of scales not heavily pigmented; diamond-shaped pattern not well developed laterally. Lateral stripe extending from snout to caudal base, where expanded into large, oval spot. Anteriorly, lateral stripe 2–3 scale rows wide and more diffuse, especially ventrally. Posteriorly, stripe narrows to 1 row before spot. Belly immaculate. Dorsum of head plumbeous to olive, extending to lateral stripe on dorsal opercle, preopercle, lacrymal, and upper lips. Venter immaculate except for short, dark gular bar.

Males more brilliantly colored. Dorsum bluish-black to steel-blue and separate from bluish lateral stripe by narrow copper stripe (1–2 scale rows wide); narrow stripe extending from orbit to caudal base. Lateral surfaces with light blue cast. Belly cream. Dorsal fin red-orange anteriorly with white overcast of entire fin. First few membranes heavily pigmented basally, narrowing posteriorly to produce a basal wedge; last 4 interradiial membranes black, producing dark posterior spot. Anterior 2–4 membranes of pectoral, pelvic, and anal fins red-orange, remainder of fins milky-white. Leading ray of pectoral fin also outlined with melanophores. Caudal suffused with milky-white pigment, especially basally; rays and membranes red-orange, except distally where greyish-black.

Tuberculation.— Dorsum of head with moderately large, antrorse tubercles in pattern consisting of 2 clumps of scattered organs on either side of midline; tubercles smaller and distributed in regions normally occupied by rows of large tubercles in other species. Supraorbital tubercles arranged in scattered pattern and approximately equal in size as dorsal head organs. Supraorbitals connected to preorbital tubercles by 2–3 rows of antrorse organs. Preorbital tubercles moderately large, scattered, and antrorse; slightly connected to suborbital organs. Snout organs equal in size to other head organs, antrorse posteriorly, and erect anteriorly; separate from dorsal organs.

Antrorse organs present on many surfaces of lower head. Preopercles with several organs of equal size as dorsal tubercles in scattered pattern and connected to suborbitals and preorbitals. Branchiostegals all with single row of tubercles. Subopercles with few tubercles in row along ventral margin. Interopercle with single row. Gular region with single tubercle at symphysis in peak males. Opercle and opercular membrane naked. Mandibles with 2 rows of tubercles.

Predorsally, each scale with 1–3 centrally located organs and 1–4 antrorse, smaller, subcentral organs surrounding these. Along flanks, both above and below lateral line, 1–2 central, erect and 2–6 subcentral, erect organs per scale. Along caudal peduncle, both above and below lateral line, each scale with 1 central and 2–3 subcentral organs.

All rays of dorsal and anal fins with single row of tubercles, and 1 organ per segment medially and distally. Pelvic fins with single row on first unbranched ray and next 2 branched rays. Leading ray of pectoral fin with single row and 1 retrorse organ per segment. Posteriorly, rays 2–7 each with single row of retrorse organs, 1 per segment. No ventral organs observed on paired fins.

Distribution. Endemic to the Tallapoosa River system, above the Fall Line, of the Mobile Bay Basin. Howell and Williams (1971) considered the single specimen from the Coosa River system (Boschung, 1961) to be a case of accidental bait introduction. Howell and Williams (1971) and Lee et al. (1980) provided distribution maps of this species.

Ecology. No published information is available on the life history, except for habitat notes. Although very restricted in range, this is the most abundant *Cyprinella* in the Tallapoosa system. Howell and Williams (1971) found it to be most common in medium-sized tributaries (20–40 ft) over sand, silt, and/or gravel substrates. Most frequently associated with swift current in raceways and deep riffles, but also found in slow to moderate current in pools and eddies.

Etymology. This species was named after

Dr. Robert Henry Gibbs, United States National Museum, in recognition of his outstanding studies on species of the genus *Cyprinella*.

Comments. Prior to 1971 (Howell and Williams) this species was referred to as *Notropis trichroistius*.

CYPRINELLA TRICHOISTIA (JORDAN
AND GILBERT)
Tricolor Shiner
Plate IV

Codoma trichroistia Jordan and Gilbert in Jordan and Brayton, 1878:50–51. [Orig. descr.; Type locality: trib. Etowah River, GA (probably near Rome, Floyd Co., GA)(after Gilbert, 1978a)]

Diagnosis. Anal rays 9; lateral stripe silver-grey; dorsum of breeding males bright orange; fins yellowish orange; scales below lateral line not appearing strongly diamond-shaped; tubercle connection between preorbital and supraorbital regions narrow; supraorbital tubercles in a single row; epibranchial 4 with short mesial to dorsal process; posterior ramus of premaxilla straight; posterior process of vomer narrow; anterior neck on ceratobranchial 2 long and thin; supraethmoid short; anterior notch of vomer very shallow; interoperculum deep posteriorly; branchiostegal 1 very narrow.

Description. A moderately sized species of *Cyprinella*, attaining a maximum of about 80 mm SL. Body elongate and slightly compressed; greatest body depth at and slightly anterior to dorsal origin. Head triangular and moderately large. Snout pointed and long, especially in peak males. Mouth large, terminal, and oblique; upper jaw containing lower, both extending posteriorly past anterior margin of orbit. Orbit large. Caudal peduncle robust and relatively short. Dorsal fin not greatly expanded in nuptial males; origin in both sexes above pelvic fin insertion.

Dorsal fin rays 8; anal rays 8–10 (9); pelvic rays 8; pectoral rays 12–16 (generally 14 or 15 in Coosa, 13 or 14 in Cahaba, and 15 in Alabama); principal caudal rays 19; dorsal

procurent rays 10–11 (11), ventral procurent rays 10–11 (10).

Exposed edges of lateral scales taller than wide, especially anterior, near lateral line. Lateral-line scale rows 36–44 (40–41 in Coosa, 38–39 in Cahaba, 39–40 in Alabama); total predorsal circumferential scales generally 24–26; scales above lateral line 11–15 (13), scales below lateral line 8–12 (11); total caudal-peduncle scales generally 14; scales above and below lateral line 7 and 5, respectively.

Pharyngeal teeth 1, 4-4, 1, hooked, and with narrow, sometimes serrated cutting surfaces. Total gill rakers 6–7 (7). Total vertebrae 38–40 (39), precaudals 18–20 (19), caudals 19–21 (20). Dorsal fin insertion above vertebrae 12–14 (13).

Lateral line complete. Supratemporal canal broadly interrupted, pores 2 per side. Supraorbital canal complete, pores 8–9 (8). Infraorbital canal interrupted behind orbit, pores 10–12 (12). Preoperculomandibular canal complete, total pores 10–11 (11), mandibular pores I.

Intestine simple S-shaped loop, Type I. Peritoneum silvery with scattered melanophores.

Coloration in life.— Body coloration of nonbreeding males and females like that of *C. gibbsi* (Howell and Williams, 1971). Breeding males differ in having a more blue-grey lateral stripe and a narrow yellow stripe above. Fins typically yellowish-orange instead of red-orange.

Tuberculation.— Dorsum of head with large, antrorse tubercles arranged in 2 rows anterior to posterior margin of orbit. Posterior to orbits, antrorse organs arranged in semiscattered pattern, no obvious rows formed. Prenuptial males with linear pattern. Above orbits, single row of large, antrorse organs connects with preorbital tubercles by single row. Preorbital tubercles few, antrorse, moderately large, and scattered. Snout tubercles antrorse posteriorly grading to erect anteriorly and smaller than any tubercles on head. Mandibular organs antrorse posteriorly, arranged in 2 rows. Remainder of head devoid of organs.

Predorsal region with 1–3 rows of large,

antrorse tubercles; each scale with single tubercle located centrally. Midline row first to develop and strongly developed anteriorly. Lateral to midline, 1–2 rows present, but shorter. No other organs present on predorsal scales. One erect, central tubercle per scale along flanks. No edge or subcentral organs present on body scales. Caudal-peduncle scales all with single tubercle per scale; those on scales below lateral line very large and antrorse. Above lateral line, central tubercles antrorse, but only slightly larger than body tubercles. No tubercles present on upper or lower midline scale rows.

All dorsal and anal fin rays with single row of organs per ray and single tubercle per segment. Anterior rays with more tubercles. Pelvic fin tuberculate medially and distally. Unbranched ray and next 3 branched rays tuberculate with single row of tubercles and 1 tubercle per segment. First ray of pectoral fin with single row of retrorse organs, 1 per segment. Posterior rays 2–9 with single row of tubercles each and 1 organ per segment, extending almost to edge of fin. No ventral organs observed on paired fins.

Distribution. Endemic to the Mobile Bay Basin. Found in the Cahaba, Coosa, and Alabama rivers. One population in Black Warrior system believed to be the result of stream capture.

Ecology. Very little known for this common species. Inhabits cool, clear, continuous flowing, small to medium-sized streams and is associated with deep riffles and raceways. Less common in pools.

Etymology. The name *trichroistia* is from Greek *treis*, meaning three, *chros* for color, and *histon* for sail, describing the tricolored dorsal fin (black, red, and white) of breeding males.

CYPRINELLA CALLISTIA (JORDAN)

Alabama Shiner

Plate IV

Photogenis callistius Jordan,
1877b:337–338. [Orig. descr.; Type locality:

tribs. Etowah and Oostanaula rivers, near Rome, GA (most specimens from Silver Creek, trib. Etowah River)]

Diagnosis. Anal rays 8; caudal-peduncle scales below lateral line 7; no large centrally located tubercles on caudal-peduncle scales above and below lateral line; tubercle hiatus between snout and dorsum of head absent; tubercle connection between supraorbital and preorbital region composed of two rows; preorbital tubercles restricted to single row along dorsal margin of lacrymal; mandibular tubercles absent; caudal-peduncle tubercles present on ventral and dorsal scale rows; pigmentation on scales above and below lateral line in diffuse diamond-shaped pattern; lateral stripe not strongly developed; epibranchial 4 short mesial to dorsal process; single ligament connecting palatine to ecto- and endopterygoids; anterior preethmoid socket of palatine elongate and shallow; ascending wings of parasphenoid very broad; lacrymal tilted ventrally; supraorbitals narrow anteriorly and posteriorly; anterior notch of urohyal shallow; horizontal urohyal plate broad and without posterior notch; vertical plate of urohyal deep; posterior hyomandibular wing curled; mesial neck of epibranchial 2 straight; anterior parasphenoid short; ceratobranchial 1 with restricted neck.

Description. A moderately large *Cyprinella*, reaching about 80 mm SL. Body stout, moderately elongate; only slightly compressed. Dorsal profile elevated and arched; venter more or less horizontal; greatest body depth from dorsal fin origin to just posterior to occiput. Head moderately large, deep, and triangular. Snout protruding, especially in breeding males. Orbit large. Mouth large, horizontal, and inferior. Lower jaw smaller than upper and contained within the latter. Caudal peduncle heavy and moderately long. Dorsal fin expanded in breeding males; origin in both sexes above pelvic fin insertion.

Dorsal fin rays 8; anal rays 7–9 (8); pelvic rays 8; pectoral rays 13–17 (15–16); principal caudal rays 17; dorsal procurrent rays 11–13 (11 or 12), ventral procurrent rays 10–11 (11).

Exposed margins of dorsal and lateral scales taller than wide. Lateral-line scale rows 37–41 (38–39); total predorsal circumferential scales generally 24; scales above lateral line 11–15 (11), below lateral line 11; total caudal-peduncle scales usually 16; scales above and below lateral line 7.

Pharyngeal teeth 1, 4-4, 1, hooked, and with narrow serrated or entire grinding surfaces. Total gill rakers 8–9 (8). Total vertebrae 39 or 40, precaudals 18–20 (19), caudals 20–21 (20); dorsal fin insertion above vertebra 12 or 13 (13).

Lateral line complete. Supratemporal canal broadly interrupted, pores 2 per side. Supraorbital canal complete, pores 8. Infraorbital canal complete, pores 10–11 (11). Preoperculo-mandibular canal complete, total pores 9, mandibular pores 3.

Intestine with single S-shaped loop, Type I. Peritoneum silvery with scattered melanophores.

Coloration in life.— Body bicolored. Dorsal half of body from lateral line darkly pigmented; venter white to cream. Dorsum of nonbreeding males and females silver-blue to olive. Lateral stripe diffuse, best developed posteriorly where terminates at large, oval dark caudal spot. Weakly developed diamond-shaped pattern on lateral and dorsolateral body scales. Dorsal scales darkly pigmented and often obscuring pattern; ventral scales just below lateral line with wide, anteriorly directed chevrons. Dorsum of head darkly pigmented, extending laterally down to middle of opercle, ascending arm of preopercle, lacrymal, and upper lip. Venter immaculate, except for short, dark gular stripe. Fins generally clear, except for dusky and reddish caudal, lightly pigmented first few rays of pectoral, and distal margin of dorsal which may be lightly pigmented with light reddish hue.

Breeding males dark, steel-blue dorsally and dorsolaterally, with dark blue-black caudal spot and posterior lateral stripe. Cream to silver ventrally. Fins with milky-white cast. Dorsal fin bright red medially, dorsally and anteriorly; with large black blotch posteriorly

and basally. Distal margin of dorsal milky-white. Pelvics and anal immaculate, except for milky-white pigments. Pectorals white; leading ray yellowish, outlined with melanophores. Caudal bright red; white distally and yellowish basally.

Tuberculation.— Dorsum of head with 2 rows of large, antrorse organs down midline and single postorbital row per side. Preorbital areas devoid of tubercles, except for single row of moderately large, antrorse organs beneath nares, connecting tubercles of supraorbital region and snout. Supraorbital area with single row of large, antrorse tubercles. Snout tubercles erect and smaller than dorsal head organs by half. Hiatus between snout and dorsal head tubercles essentially nonexistent in peak males. Mandibles without tubercles. Remainder of head devoid of tubercles.

Scales of predorsal region each with single large, centrally located, antrorse organ. Rows present down midline and on 1 or 2 scale rows laterally, producing up to 5 rows from dorsal fin to occiput. In peak males, central row best developed, extending full length of predorsal region. Lateral rows stepped in length, with lateralmost rows shortest. Flank scales with 10–15 small, retrorse edge tubercles per scale on all scales except in belly and breast regions.

Tubercles on dorsal fin well developed beyond branching, with 1 tubercle per segment. Anal fin tubercles found on all rays medially and distally; 1 tubercle per segment. Pelvic fins with first ray devoid of organs and rays 2–6 with single row each, best developed medially and distally and with single organ per segment. First ray of pectoral fin with single row of retrorse organs, 1 tubercle per segment. Posteriorly, rays 2–10 with single row basally and on branches, each with single retrorse organ per segment. Ventrally, both pectoral and pelvic fins without organs.

Distribution. Endemic to the upper Mobile Bay Basin, generally above the Fall Line. Mettee et al. (1987) reported this species from below the Fall Line in the lower Tombigbee River. At least two disjunct populations are known, those in the Alabama River and those

in the Tombigbee River system. A distribution map is provided by Lee et al. (1980).

Ecology. Other than habitat characteristics, nothing is known of the biology of this very common species. Most frequently inhabits small to moderately large, high-gradient, cool, and clear streams. Typically associated with raceways and pools over a gravel and rubble substrate.

Etymology. The name *callistia* is from the Greek *kallos* for beautiful and *histion*, meaning sail, describing the brilliantly colored, large dorsal fin of breeding males.

CYPRINELLA NIVEA (COPE)

Whitefin Shiner

Plate IV

Hybopsis niveus Cope, 1870:460–461.
[Orig. descr.; Type locality: Upper waters of Catawba River, NC]

Diagnosis. Anal rays 8; prominent black lateral stripe present; tubercle development on dorsum of head from linear to scattered pattern; suborbital tubercles present; second membrane of dorsal fin uniformly pigmented with melanophores; connection of ligament from epibranchial 1 to 2 lateral to uncinat process of epibranchial 2; pharyngobranchial 1 elongate and narrow; sphenotic-frontal connection placed forward.

Description. A moderately large *Cypripinella*, reaching about 70 mm SL. Body elongate, not deep but terete, only slightly compressed. Dorsal profile more arched than ventral. Head short and subconical. Snout blunt, moderately long and protruding. Orbit moderately large. Mouth inferior, lower jaw contained in upper. Caudal-peduncle moderately long, but robust. Dorsal fin expanded in breeding males; origin over pelvic fin insertion in both sexes.

Dorsal fin rays 8; anal rays 7–9 (8); pelvic rays 8; pectoral rays 13–16 (15). Principal caudal rays 17, dorsal procurrent rays 11–14 (12), ventral procurrent rays 10–13 (11).

Exposed margins of lateral scales taller than wide. Lateral-line scale rows 35–41

(37–38 in Tar to Santee, 39 in Savannah); total predorsal circumferential scales generally 26; scales above lateral line 13–15 (13), below lateral line usually 11; total caudal-peduncle scales generally 14; scales above and below, 7 and 5, respectively.

Pharyngeal teeth 1, 4-4, 1, hooked, and with or without serrations on narrow cutting surfaces. Total gill rakers 7–10 (9). Total vertebrae 36–39 (38), precaudals 17–19 (18), caudals 18–20 (19). Dorsal fin insertion above vertebra 11 or 12 (12).

Lateral line complete. Supratemporal canal complete with 5 pores or incomplete with pores 2 per side. Supraorbital canal complete, pores 9–10 (10). Infraorbital canal complete, pores 11–12 (11). Preoperculo-mandibular canal complete, total pores 9, mandibular pores 3.

Intestine simple S-shaped loop, Type I. Peritoneum silvery, but heavily coated with melanophores.

Coloration in life.—Dorsum of nonbreeding males and females light olive-tan to silver-grey, continuing to belly but becoming much lighter. Belly immaculate. Midlateral stripe bluish, separating dark dorsum from light venter. Stripe strongest posteriorly on caudal peduncle where terminates at caudal base in elongate caudal spot. Anterior to dorsal origin, stripe diffuse, but wider and continuing to operculum. Scales above lateral line and 1–2 scale rows below lateral line with heavily outlined margins, creating crosshatched pattern. Scapular bar narrow and not strongly developed. Dorsum of head like body dorsum, only darker; extending laterally to include lacrymal, upper opercle, and preopercle; lips colored as snout. Venter of head immaculate, except for well-developed, short gular stripe. Dorsal fin dusky, darkest posteriorly. Caudal dusky. Anal, pectoral, and pelvics clear.

Breeding males with all fins milky-white. Dorsum dark steel-blue; laterally diffuse light silver-blue. Lateral stripe more intense, continuing from opercle to caudal spot. Dorsal fin dusky, except for last 2 membranes that are jet-black; some peak males have most membranes heavily pigmented. Caudal rays outlined with

melanophores, appearing dusky. Pectoral, anal, and pelvic fins unpigmented, except for leading ray of the former, which is outlined with melanophores.

Tuberculation.— Dorsum of head covered with antrorse, moderately large tubercles arranged in 2 rows anterior to postorbital margins and in semiscattered pattern posterior to orbits. Tubercles extend anteriorly to anterior margin of nares and laterally to dorsal margin of opercles. Occasionally, single organ present on dorsal margin of opercle. Snout covered with tubercles of equal size, antrorse posteriorly and grading to erect anteriorly. Preorbital area covered with many small antrorse tubercles connected to single supraorbital row by wide band. Mandibular tubercles antrorse and arranged in 2 fairly well-defined rows, sometimes appearing scattered. Remainder of head devoid of tubercles. Occasionally, single tubercle present on suborbital region.

Predorsal scales each with single large, antrorse tubercle. Generally single row occurs down midline and bordered laterally by 1–2 shorter rows. No subcentral or edge organs present. Along flanks, both above and below lateral line, each scale with 1–6 erect and small subcentral tubercles and 1–4 central erect and small tubercles, all of equal size. Caudal-peduncle scales directly above and below lateral line with small, erect tubercles in center and along subcentral margins. Scale rows above and below these with 1, occasionally 2, larger, antrorse central tubercles and series of 1–6 subcentral, erect tubercles.

Distally, dorsal and anal fin rays each with tubercles arranged in single row, 1 per segment. Pelvic fin rays all tuberculate, 1 row per ray and 1 tubercle per segment. First pectoral ray with single row of retrorse tubercles arranged 1 per segment and extending almost to edge of fin. Rays 2–7 tuberculate; anterior rays with best development, single row and single tubercle per segment on main branch and both branches after branching. Small, erect organs present on ventral surfaces of paired fins.

Distribution. This species is an Atlantic Slope endemic, found only in the Montane,

Piedmont, and parts of the Coastal Plain Provinces from the Neuse to the Savannah rivers. Gibbs (1955) and Lee et al. (1980) provide distribution maps of this species. The map provided by Gibbs lacks populations from the Neuse and includes an erroneous locality from the upper Tar River, not included in Lee et al. (1980).

Ecology. Until recently, little known other than habitat association. Cloutman and Harrell (1987) studied food habits, age and growth, reproduction, and length-weight relationships of the whitefin shiner. The species was considered to be omnivorous, but most food items included insects. Males generally attain maturity at 3 years. Females, however, generally mature at 4 years. Spawning presumably occurs between June and August. During this period gonadosomatic index values are greatest and females contain ripe ova. Fecundity ranges from 112 to 545 in single females. Although not documented, the whitefin shiner is believed to be a fractional and crevice spawner like other members of the genus. Habitat includes moderate to large rivers and reservoirs. In rivers, the species is commonly associated with areas of current and found near the sand and gravel substrate.

Etymology. The name *niveus* is Latin for snow or snowy, referring to the white pigment in fins of breeding males.

Comments. This species is a composite of 2 distinct forms, which Gibbs (1955) considered to be subspecifically distinct. The description of the undescribed form has not been published. One form is found from the Neuse to Santee and the other is endemic to the Savannah River system. Both forms may be separated by lateral-line scale count and some morphometric characteristics.

CYPRINELLA LEEDSI (FOWLER)

Bannerfin Shiner

Notropis leedsi Fowler, 1942:2–4, Figs. 3, 4. [Orig. descr.; Type locality: Ochopee River, ca. 2.5 mi N Oak Park, Emanuel Co., GA]

Diagnosis. Anal rays 8; peritoneum brown; third membrane of dorsal fin with pigment

restricted to distal half; pigment on scales above and below lateral line in diffuse pattern; posterior hyoideal foramen of ceratohyal located mesially; ascending process of premaxilla short and triangular; nasal canal with a single pore; epiphyseal bar located anteriorly; mesial neck of epibranchial 2 straight; anterior neck of parasphenoid short; ligament connecting epibranchials 1 and 2 attached lateral to uncinat process of epibranchial 2; pharyngobranchial 1 narrow and elongate; sphenotic and frontal connection anteriorly placed; dorsal margin of anguloarticular horizontal.

Description. A moderately sized *Cypripinella*, reaching about 80 mm SL. Body elongate, moderately deep, and slightly compressed. Dorsal profile more strongly arched than ventral. Head moderately large and subconical. Snout long and pointed, protruding over lips. Orbit moderately large. Mouth inferior and small; lower jaw contained in upper and both short of anterior margin of orbit. Caudal peduncle relatively long and slender. Dorsal fin greatly expanded in nuptial males; origin in both sexes over pelvic fin insertion.

Dorsal fin rays 8; anal rays 8–9 (8); pelvic rays 8; pectoral rays 12–16 (14–15). Principal caudal rays 17, dorsal procurrent rays 12–13 (12), ventral procurrent rays 10–11 (10).

Midlateral scales with exposed surfaces higher than wide, especially anterior to dorsal fin. Lateral-line scale rows 35–39 (36–37); total predorsal circumferential scales generally 26–28; scales above lateral line 13–15, below lateral line 11; total caudal-peduncle scales generally 14, scales above and below lateral line 7 and 5, respectively.

Pharyngeal teeth 4–4, hooked, and with narrow, sometimes serrated cutting surfaces. Gill rakers long and slender, numbering 5. Total vertebrae 37–38 (38), precaudals 18–19 (19), caudals 18–20 (19). Dorsal fin insertion above vertebra 11 or 12 (11).

Lateral line complete. Supratemporal canal broadly interrupted, pores 2 per side. Supraorbital canal complete, pores 8. Infraorbital canal generally complete, pores 11. Preoperculo-mandibular canal complete, total pores 8–9

(9), mandibular pores 3.

Intestine simple S-shaped loop, Type I. Peritoneum brown.

Coloration in life.— Dorsum of females and nonbreeding males olive-tan to light steel-blue, extending to lateral stripe. Flanks, below lateral stripe, cream to silver. Stripe steel-blue, moderately broad, and extending from caudal base, where expanded into oval spot, to opercular membrane; broader and more diffuse anterior to dorsal fin. Scapular bar diffuse. Diamond-shaped pigment pattern on lateral scales not strongly developed. Scales with broad, heavily pigmented margins, obscuring cross-hatched pattern. Diamond-shaped pigment pattern present on scales of lateral line and 1–2 scale rows below. Dorsum of head darkly pigmented, including snout, lips, and upper half of preopercle and opercle. Dorsal fin light orange; rays outlined with melanophores, and with well-developed spot on membrane behind first rudimentary ray. Anal and pelvic fins clear, except for dusky base of former. Leading ray of pectoral outlined with melanophores, otherwise clear.

Breeding males with milky-white fins, especially ventrals. Dorsal fin orange and black medially and distally; basally with clear wedge, widest anteriorly. Most fin membranes jet-black. Caudal yellowish-orange with dark leading rays. Lateral stripe dark blue-black.

Tuberculation.— Dorsum of head with large, antrorse tubercles arranged in 2 parallel rows down midline and single row laterally, posterior to each orbit. Dorsal postorbital region of head occasionally with some tubercles in scattered pattern. Preorbital areas with moderately large, antrorse organs connected to single row of antrorse supraorbital tubercles by 1 or 2 rows of antrorse tubercles between nares and orbit. Snout with smaller tubercles grading from antrorse posteriorly to erect anteriorly, and separate from dorsal organs by wide hiatus. Mandibles with single row of erect organs along outermost margin. Remainder of head devoid of tubercles.

Dorsalmost 3 or 4 predorsal scales with single, large, antrorse tubercles on scale, form-

ing rows; edge tubercle on each scales absent. Flank scales anterior to dorsal fin insertion and above lateral line usually with single, small, antrorse organ. Below lateral line, scales usually devoid of tubercles. No edge organs present on any body scales. Occasionally, lateral-line scales and one row above and below lateral line with 2 small, antrorse tubercles each arranged vertically in center of scale. Caudal-peduncle scales each with single, antrorse tubercle in center. Those developed below lateral line as large or larger than predorsal organs. No tubercles developed on midline row dorsally or ventrally. Tubercles formed above lateral line smaller than those below, about the size of lateral body organs.

Dorsal fin tuberculation consisting of few organs on first rudimentary ray and distal portion of first branched ray. Rays of anal and pelvic fins tuberculate medially, each with single row per ray and single tubercle per segment. First ray of pectoral fin with single file row of moderately large, retrorse organs. Rays 2–7 with single row and single organ per segment, extending almost to edge of fin. No organs on ventral surfaces of paired fins.

Distribution. *Cyprinella leedsi* is confined to rivers of the southern Atlantic Slope and eastern Gulf Slope; inhabiting most large rivers from the Savannah to the Ochlocknee and Suwannee rivers of South Carolina, Georgia, and Florida. See Gibbs (1955) and Lee et al. (1980) for distribution maps.

Ecology. Little information is available on the life history of this species other than habitat notes and laboratory observations of breeding behavior (Rabito and Heins, 1985). Adults of the bannerfin shiner are difficult to capture, usually being associated with large rivers in open channels over a sand substrate. Juveniles, however, are more easily captured and are often near shore (C. R. Gilbert, pers. comm.). Rabito and Heins (1985) observed spawning of this species and noted the crevice spawning behavior typical of other species of *Cyprinella*. Males defend territories around crevice substrates where the eggs are deposited. A single male may use the same crevice

nesting site in mating with several females. Clutch sizes ranged from 26 to 228 eggs per nest. The adhesive eggs ranged from 1.2 to 1.6 mm in diameter. A single hybrid of this species with *C. venusta* has been collected by C. R. Gilbert from the Alapaha River in northern Florida.

Etymology. Named after Arthur N. Leeds of Philadelphia who was present at the type locality when the type series was collected.

CYPRINELLA CALLISEMA (JORDAN)

Ocmulgee Shiner

Plate IV

Episema callisema Jordan, 1877b:363–364. [Orig. descr.; Type locality: S. Fk. Ocmulgee River, Flat Rock, DeKalb Co., GA]

Diagnosis. Anal rays 8; pattern of dorsal head tubercles develops from linear to scattered; pharyngeal teeth 4-4; second membrane of dorsal fin with melanophores uniformly distributed; supraorbital bones moderately long; basibranchial 1 with no median constriction; symplectic narrow; posterior wing of hyomandibular terminating near ventral tip; margin of anterior wing of hyomandibular smooth; anterior neck of parasphenoid short.

Description. An elongate, moderately large member of the genus, reaching a maximum of about 75 mm SL. Body slender, only slightly compressed. Dorsal profile much more highly arched than ventral. Venter subhorizontal. Head moderately large, narrow, and subconical. Snout moderately elongate, protruding, and tapering to blunt tip. Orbit moderately large. Mouth small, inferior, slightly oblique. Lower jaw shorter than upper and contained, neither reaching anterior margin of orbit. Caudal peduncle elongate and relatively slender. Dorsal fin greatly expanded in breeding males; origin in both sexes above pelvic fin insertion.

Dorsal fin rays 8; anal rays 7–9 (8); pelvic rays 8; pectoral rays 11–18 (14–15); principal caudal rays 17; dorsal procurrent rays 10–11 (11), ventral procurrent rays 9–11 (10).

Lateral and dorsolateral scales with exposed margins higher than wide, especially

anteriorly near lateral line. Lateral-line scale rows 37–40 (38–39); total predorsal circumferential scales generally 26–28; scales above lateral line 13–16 (generally 13 or 15), below lateral line 11; total caudal-peduncle scales 14; scales above and below lateral line 7 and 5, respectively.

Pharyngeal teeth 4–4, well hooked, and with or without serrated grinding surfaces. Total gill rakers 6–7. Total vertebrae 39–40 (40), precaudals 18–20 (19–20), caudals 20 or 21. Dorsal fin insertion above vertebra 12 or 13 (13).

Lateral line complete. Supratemporal canal broadly interrupted, pores 2 per side. Supraorbital canal complete, pores 9. Infraorbital canal complete, pores 11. Preoperculo-mandibular canal complete, total pores 9, mandibular pores 3.

Intestine simple S-shaped loop, Type I. Peritoneum silvery with scattered and large melanophores.

Coloration in life.—Females and nonbreeding males lightly colored. Dorsum olive-tan to light silver-blue down to 1–2 scale rows above lateral line, where lighter. Venter immaculate, except for pigmented anal base and lower caudal peduncle. Lateral stripe silver-blue and extending from caudal base, where expanded into an elongate oval, to opercle; narrow and diffuse anterior to dorsal fin. Margins of dorsal and dorsolateral scales down to 2 scale rows below lateral line darkly outlined, presenting a strong diamond-shaped pattern. Scapular bar absent. Dorsum of head, down to upper third of opercle and preopercle, entire lacrymal, and lips like dorsum of body but slightly darker; ventral and ventrolateral surfaces of head silver-white. Gular stripe short and dark. Dorsal fin lightly pigmented except for dark membrane behind first rudimentary ray. Posterior membranes of dorsal fin dark. Pelvics and anal fins clear. Caudal rays outlined with melanophores, appearing dusky to slightly yellow-orange; procurrent rays darkest. Pectoral fins clear, except for darkly outlined leading ray.

Breeding males more colorful. Dorsal and dorsolateral surfaces down to and including

lateral stripe iridescent bluish-purple; scale edges dark blue, centers purple. Lateral stripe dark blue-black; caudal spot distinct. Fins with milky-white pigments. Dorsal and caudal fins burnt-orange. Dorsal heavily pigmented on upper $\frac{2}{3}$ with melanophores on all membranes and with dark spot anteriorly. Basally, each membrane of dorsal fin only lightly pigmented or clear, narrowing posteriorly and presenting a clear, basal wedge. Pectoral and pelvic fins white, the former with a dark leading ray. Anal fin white, except for dusky leading rays and basally, where lightly dusted with yellow-orange.

Tuberculation.—Dorsum of head covered with moderately large, antrorse organs scattered over top of head in 2 clusters, 1 on either side of midline. Development of antrorse tubercles proceeds from erect to antrorse. Early season males or young males with linear tubercle pattern over dorsum of head. Preorbital region with small, antrorse tubercles thickly distributed over lacrymal. These organs are connected to scattered supraorbital organs by 3 rows of equal-sized antrorse organs between nare and orbit. Snout tubercles antrorse posteriorly, erect anteriorly, and separate from dorsal head organs by large hiatus. Mandibles with single row of small, erect organs on outer edge. Remainder of head devoid of tubercles.

Predorsal scales each with single, moderately large, antrorse tubercle forming 1–5 rows. Rows developed on each scale down midline and generally 1, occasionally 2, rows laterally. No other tubercles present on predorsal scales. Flank scales with 1–3 sub-central tubercles, best developed above lateral line, but also occurring below, posterior to depressed pectoral fins. Caudal-peduncle scales below lateral line each with single, moderately-large antrorse tubercle in center, forming rows. Caudal-peduncle scales may also develop 1–3 subcentral, erect tubercles surrounding central organ. Above lateral line, tubercle development rarer and consisting only of central organs.

No tubercles found on dorsal fin. Anal fin with tubercles medially, arranged in single

row on first 4 branched rays. Medially, first 3 branched rays of pelvic fins with single row and 1 tubercle per segment. First pectoral fin ray with single file row of retrorse tubercles. Rays 2–9 each with single row and tubercle per segment, extending to edge of fin. No ventral organs observed on paired fins.

Distribution. *Cyprinella callisema* is endemic to the Altamaha and Ogeechee rivers of the southern Atlantic Slope in Georgia. Gibbs (1955) and Lee et al. (1980) provide complete distribution maps of this species.

Ecology. No life history data are available for this common species. Habitats most frequently include moderately large streams with continuous current. Typically associated with open channels over a sand and/or gravel substrate, although generally over sand.

Etymology. Derived from the Greek *kalos* for beautiful and *sema* for sign or sail, in reference to the expanded and colorful dorsal fin of peak breeding males.

CYPRINELLA CALLITAENIA (BAILEY AND GIBBS)
Bluestripe Shiner

Notropis callitaenia Bailey and Gibbs, 1956:1–14, fig. 1. [Orig. descr.; Type locality: Flint River, about 1 mi S Radium Springs outlet, 5.5 mi S Albany, Dougherty Co., GA]

Diagnosis. Anal rays 8; prominent steel-blue lateral stripe with dark basicaudal spot, not separate from lateral band and slightly wider; lower margin of lacrymal outlined by narrow, dark row of melanophores; single tooth in secondary tooth row of at least one pharyngeal arch; parietals invade dermopterotic; posterior process of vomer narrow; metapterygoid articulation with interhyal narrow; ectopterygoid short and broad.

Description. An elongate, moderately large *Cyprinella*, reaching up to 70 mm SL. Body slender and slightly compressed. Head small. Orbit moderately large. Mouth small, inferior, and slightly oblique; upper jaw longer than lower, both short of anterior margin of orbit. Snout long, blunt, and slightly protruding.

Caudal peduncle moderately deep and long. Dorsal fin expanded in breeding males; origin over pelvic fin insertion.

Dorsal fin rays 8; anal rays 7–8 (8); pelvic rays 8; pectoral rays 13–17 (14 or 15); principal caudal rays 17–18 (17); dorsal procurent rays 11–12 (12); ventral procurent rays 10–11 (11).

Exposed margins of lateral scales taller than long. Lateral-line scale rows 37–40 (38 or 39); total circumferential scales 26; scales above lateral line 13, below lateral line 11. Total caudal peduncle scales 14; scales above lateral line 7, below lateral line 5.

Pharyngeal teeth 1, 4-4, 1, hooked, and with poorly developed grinding surfaces. Total gill rakers 5–7 (6). Total vertebrae 38–39 (39), precaudals 19–20 (20), caudals 18–19 (19). Dorsal fin insertion over vertebra 12 or 13 (13).

Lateral line complete. Supratemporal canal broadly interrupted, pores 2 per side. Supraorbital canal complete, pores 8. Infraorbital canal complete, pores 10–11 (11). Preoperculo-mandibular canal complete, total pores 9, mandibular pores 3.

Intestine simple S-shape loop, Type I. Peritoneum silvery, overlain by scattered melanophores.

Coloration in life.— Dorsal and dorso-lateral surfaces of females and nonbreeding males plumbeous to olive, becoming lighter ventrally to lateral stripe. Lateral stripe metallic blue, extending from caudal base to opercle. Stripe more diffuse and broader anterior to dorsal origin, formed mainly by a narrow, dark line extending forward as a continuation of dorsal margin of posterior portion of stripe and bordered ventral to lateral line by diffuse and dusky region. Lateral stripe expanded slightly and darker at caudal base, forming caudal spot, but not separate from stripe. Venter light cream or white. Dorsum of head down to lips, lower lacrymal, and upper opercle plumbeous; light ventrally. Lower margin of lacrymal bordered by dark narrow line of melanophores. Mandibles with scattered melanophores laterally. Dorsal fin with melanophores lining rays and

heavy concentration on posterior membranes. Other fins generally clear.

Breeding males as above but more brightly colored. Dorsum of body steel-blue, spotted with metallic pink flecks, changing to salmon-pink above steel-blue lateral stripe. Dorsal fin iridescent green centrally, blue subdistally, and milky-white distally over a background of heavy melanophores. Caudal lobes, pectorals, and pelvic fins fringed in white. Anal bright greenish-yellow, tipped in white.

Tuberculation.—Early males with 2 semi-linear rows of tubercles on top of head; peak males with rows anterior to posterior margin of orbit and semiscattered pattern posteriorly. Dorsal head tubercles moderately large and antrorse. Preorbital region with several scattered, antrorse, and moderately large organs connected to single row of supraorbital organs by 1–2 rows of antrorse organs. Snout tubercles antrorse posteriorly and erect anteriorly, separate from dorsal head organs by wide hiatus. Mandibles with 2 rows (occasionally 1) of small, erect organs. Remainder of head devoid of tubercles.

Predorsal region with 1–5 rows of large, antrorse tubercles. Rows formed from 1 tubercle per scale. Median predorsal scale row always first to develop organs. No edge tubercles present. Lateral body scales with single, small antrorse organ in center of scale, as in *C. leedsi*. Caudal peduncle tuberculation like that species.

Dorsal fin devoid of tubercles. Anal fin with organs present medially on first rudimentary ray and first 4 branched rays. Pelvic fin rays 1–5 with tubercles on medial and distal portions. First pectoral fin ray with single row of retrorse organs, 1 tubercle per segment. Rays 2–6 with single file row, developing 1 tubercle per segment. Each ray with organs extending close to fin edge. No ventral paired fin tubercles noted.

Distribution. The bluestripe shiner is endemic to the Apalachicola River System, including the Apalachicola, Chattahoochee, and Flint rivers. Bailey and Gibbs (1956) provisionally listed a second record from the Es-

cambia River. This record is not considered valid (Gilbert, 1978b, 1980). Distribution maps are presented by Bailey and Gibbs (1955) and Gilbert (1980).

Ecology. Some aspects of the biology of this species are well known (Wallace and Ramsey, 1981). Habitat includes areas of current in large rivers over a sand and/or gravel substrate. Much of this habitat type is and has been lost through impoundment projects (Gilbert, 1978b, 1980).

Reproduction in Uchee Creek, Alabama, probably spans from late April to August (Wallace and Ramsey, 1981). GSI began to increase in March, reached a peak in June, and maintained a high level until August. Eggs numbered 88–230 per female. Total eggs produced by a female may be much greater since *C. callitaenia* is probably a fractional spawner, like other members of the genus.

Spawning occurs in June and is similar to other *Cyprinella*. Males maintain territories near crevices and swim back and forth in the current with fins erect to attract females. If unsuccessful, some males may swim as much as 3 m or more from the crevice to obtain a female and may return with as many as three. After the male displays in the typical *Cyprinella* “figure-8” pattern around the crevice, both sexes press their vents in the crevice and vibrate, spraying eggs and milt into the cavity. Afterwards the female moves into fast current and the male continues to seek additional mates. Nesting areas are used by several males; eggs found in a cavity may number several hundred and are arranged in several layers at several stages of development. Fertilized eggs range in size from 1.2 to 1.7 mm and are located 3 or more cm from the outer edge of the crevice.

Cases of hybridization with the bluestripe shiner are few and limited to other species of *Cyprinella*. Bailey and Gibbs (1956) reported a case of hybridization with *C. venusta*, and Wallace and Ramsey (1982) noted a hybrid with the red shiner. All three species are now known to be crevice spawners, and *C. venusta* and *C. lutrensis* are known to have distinctive sounds for species and sex recognition (Delco,

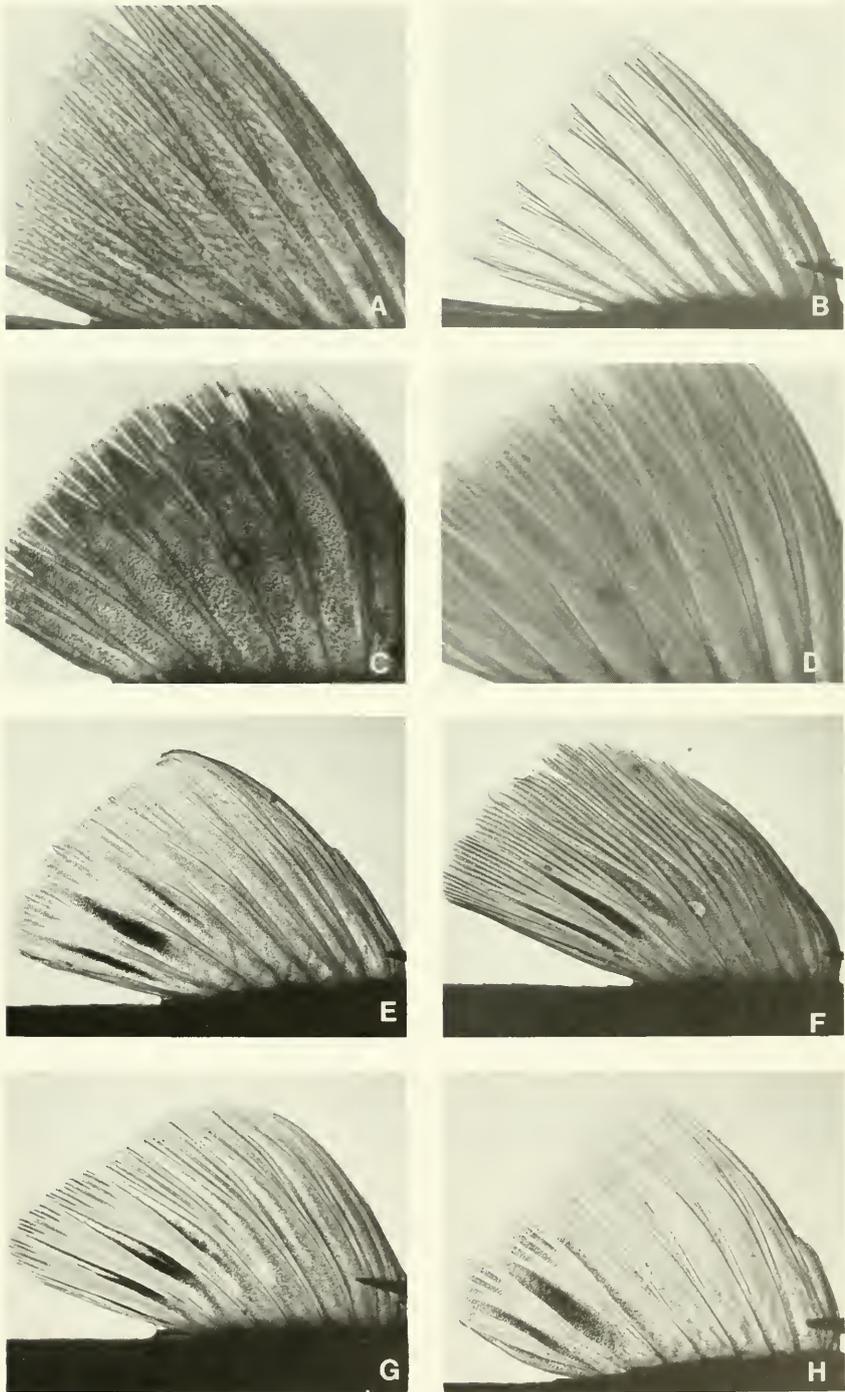


Fig. 41. Dorsal fin pigmentation patterns in male *Cyprinella* and close relatives. A) *Lythrurus umbratilis*, 52 mm, KU 9547. B) *Luxilus cornutus*, 96 mm, KU 7296. C) *Cyprinella ornata*, 49 mm, ASU 9629. D) *C. proserpina*, 56 mm, TNHC 9771. E) *C. spiloptera*, 59 mm, KU 14561. F) *C. whipplei*, 80 mm, KU 11357. G) *C. camura*, 84 mm, KU 10734. H) *C. analostana*, 68 mm, TU 25867.

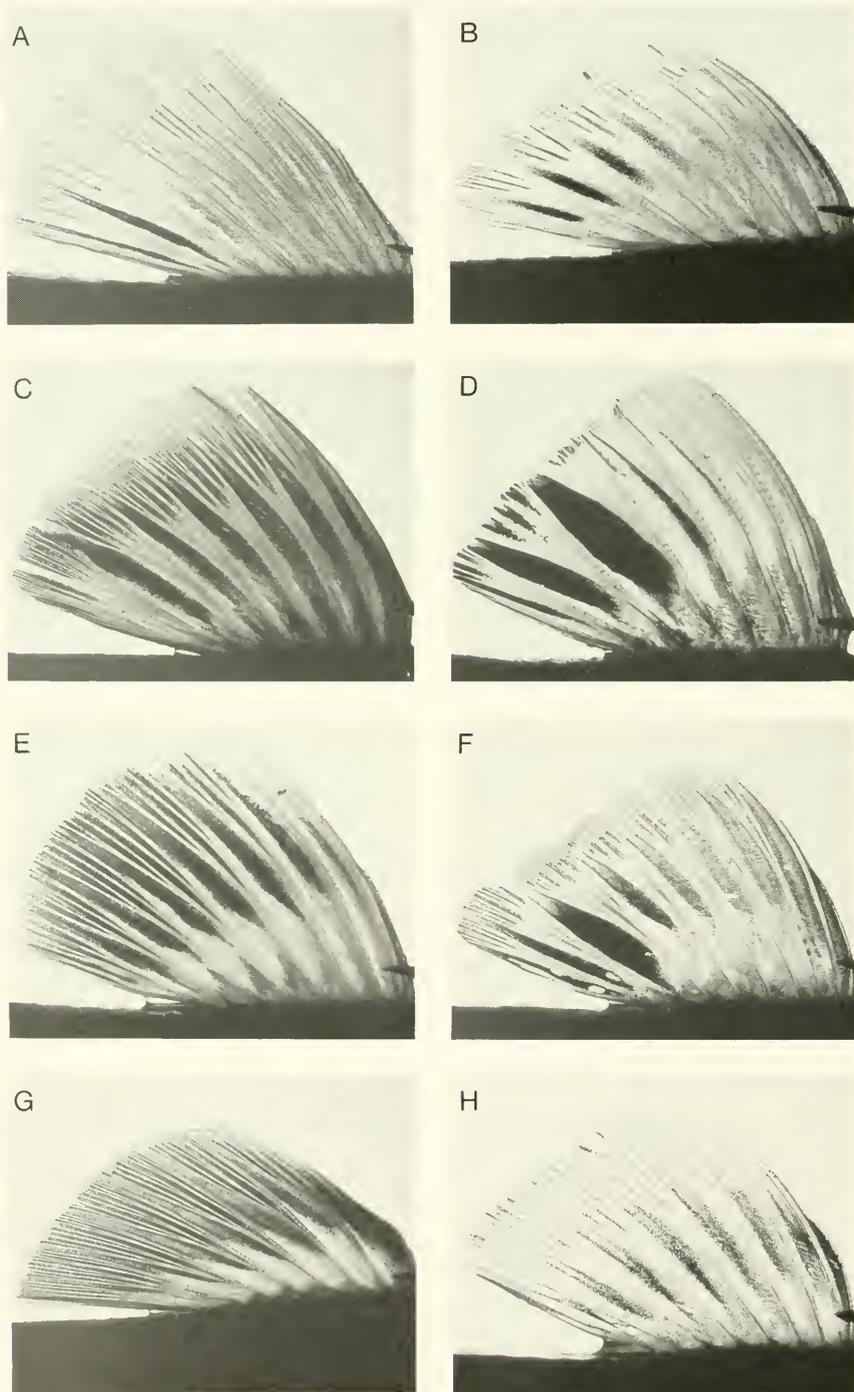


Fig. 42. Dorsal fin pigmentation patterns in male *Cyprinella*. A) *C. galactura*, 98 mm, KU 19732. B) *C. venusta*, 94 mm, KU 19698. C) *C. pyrrhomelas*, 83 mm, UAIC 2550.05. D) *C. trichroistia*, 71 mm, KU 5292. E) *C. callistia*, 84 mm, KU 19697. F) *C. nivea*, 77 mm, TU 38616. G) *C. leedsi*, 74 mm, UAIC 3127.01. H) *C. callisema*, 58 mm, KU 19653.

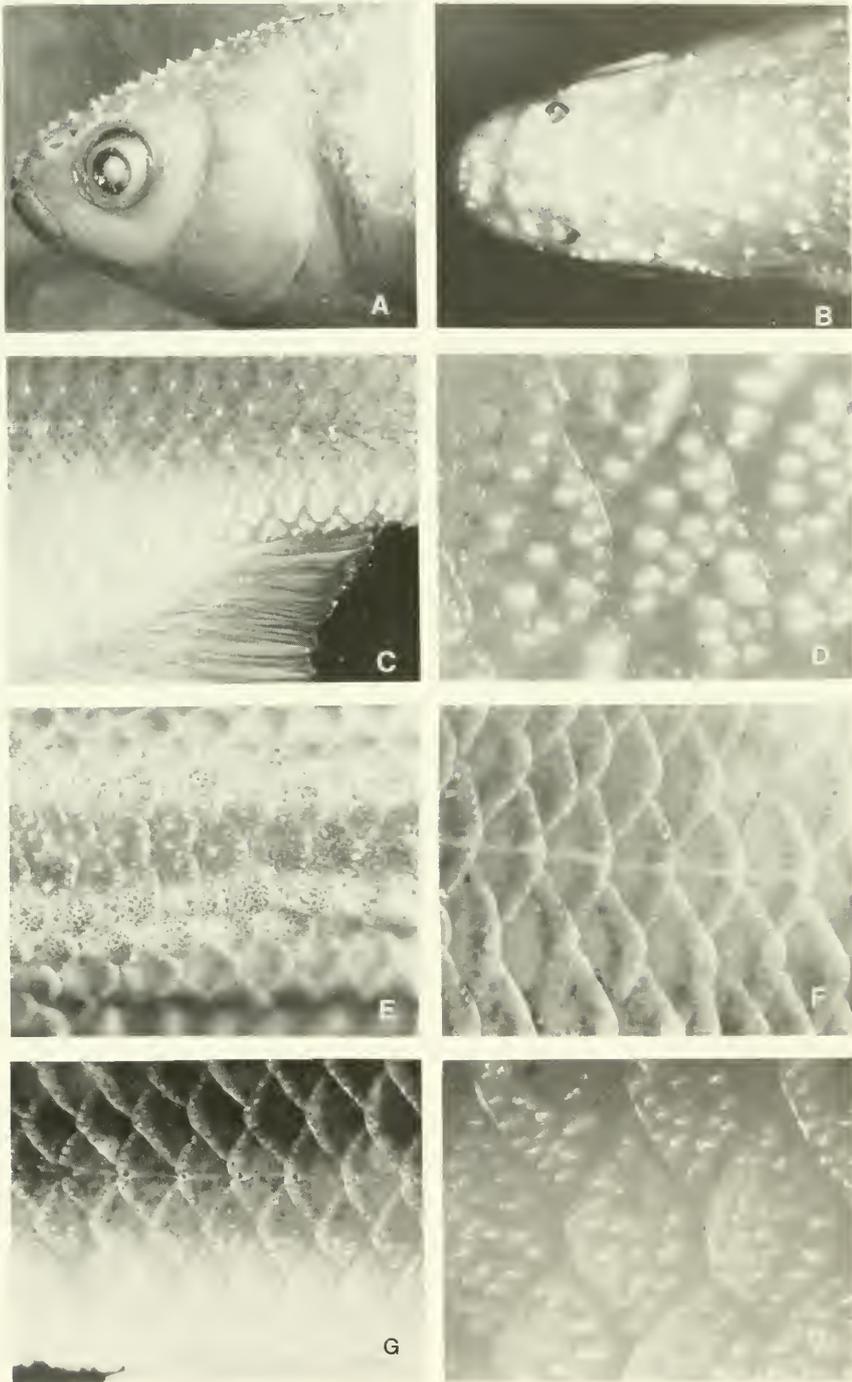


Fig. 43. Tuberculation patterns in male *Cyprinella*. A-D) *C. garmani* (50 mm, KU 20164): lateral view of head, dorsal view of head, lower caudal-peduncle and above anal fin, and ventral caudal-peduncle. E-H) *C. formosa* (42 mm, KU 8399): nape scales, lateral body scales, lower caudal-peduncle and scales above anal fin, and ventral caudal-peduncle scales.

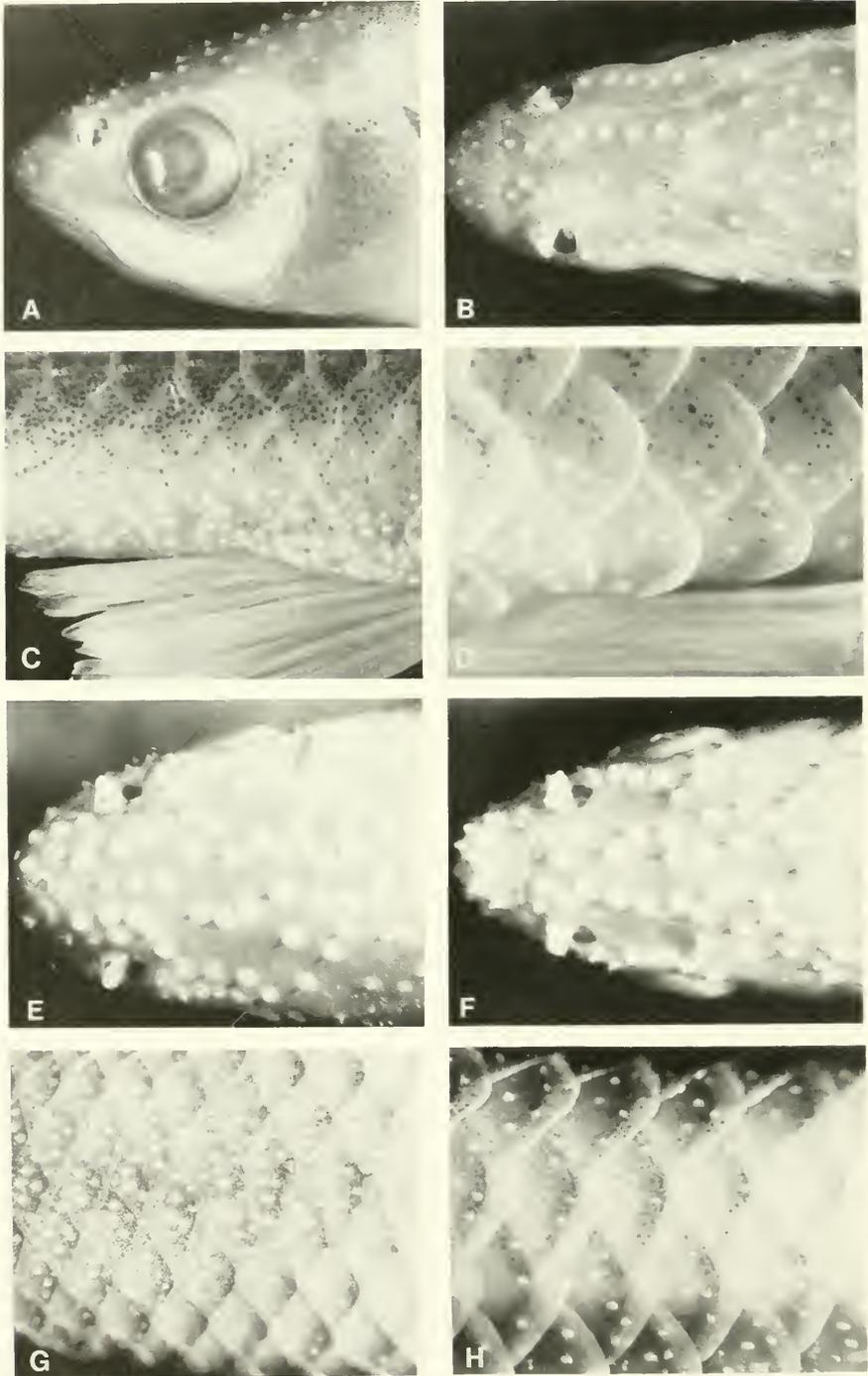


Fig. 44. Tuberculation patterns in male *Cyprinella*. A-C) *C. rutila* (49 mm, ASU 5982): lateral view of head, dorsal view of head, and lower caudal-peduncle and scales above anal fin. D) lower caudal-peduncle scales and scales above anal fin in early breeding male of *C. rutila* (46 mm, ASU 5982). E) dorsal view of head of *C. camura* (60 mm, KU 10734). F-H) *C. chloristia* (64 mm, KU 20041): dorsal view of head, nape scales, and dorsal caudal-peduncle scales.

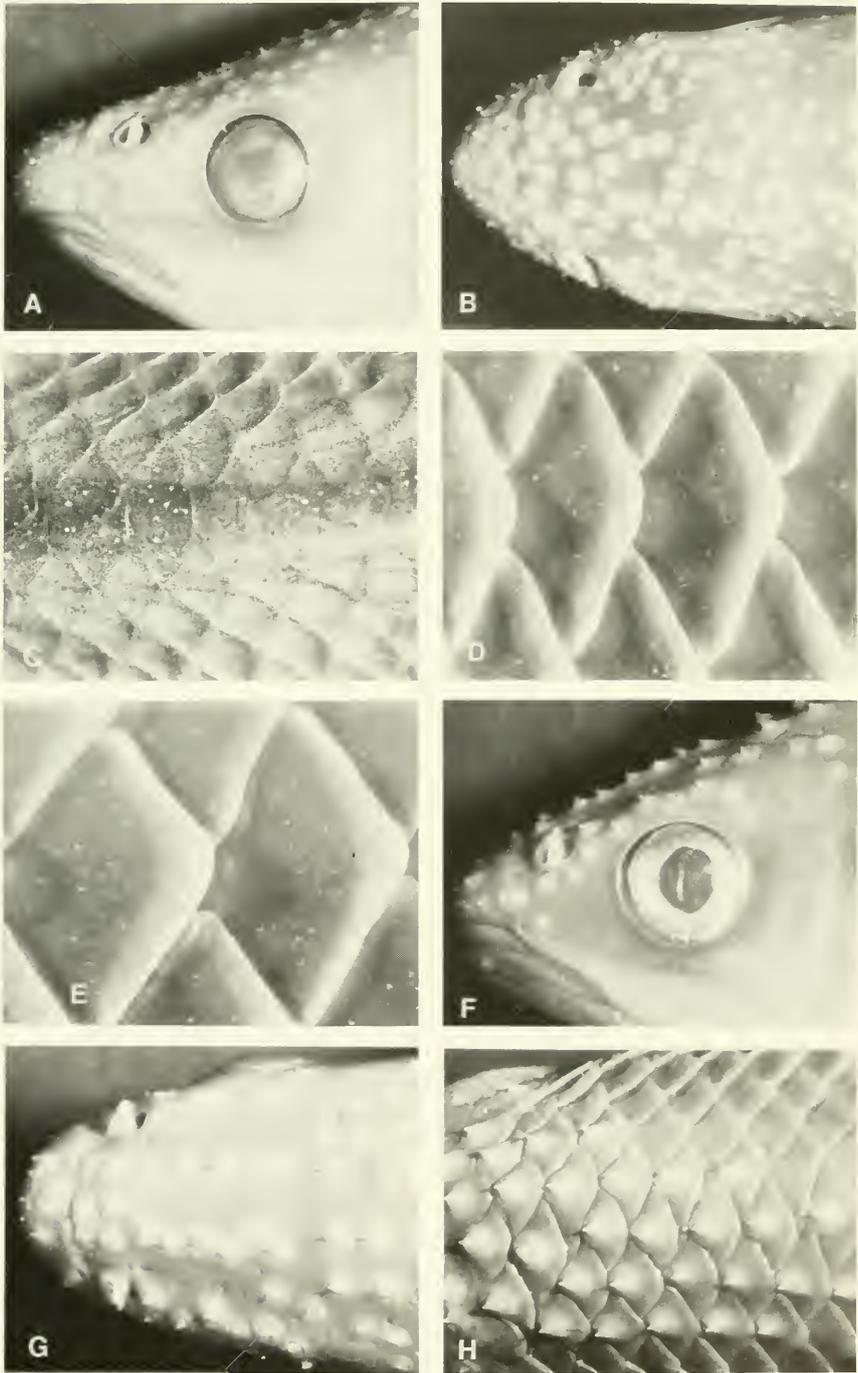


Fig. 45. Tuberculation patterns in male *Cyprinella*. A-E) *C. galactura* (108-120 mm, KU 16461): lateral view of head, dorsal view of head, nape scales, lateral body scales, and caudal-peduncle scales. F-H) *C. xaenura* (100 mm, TU 29458): lateral view of head, dorsal view of head, and nape scales.

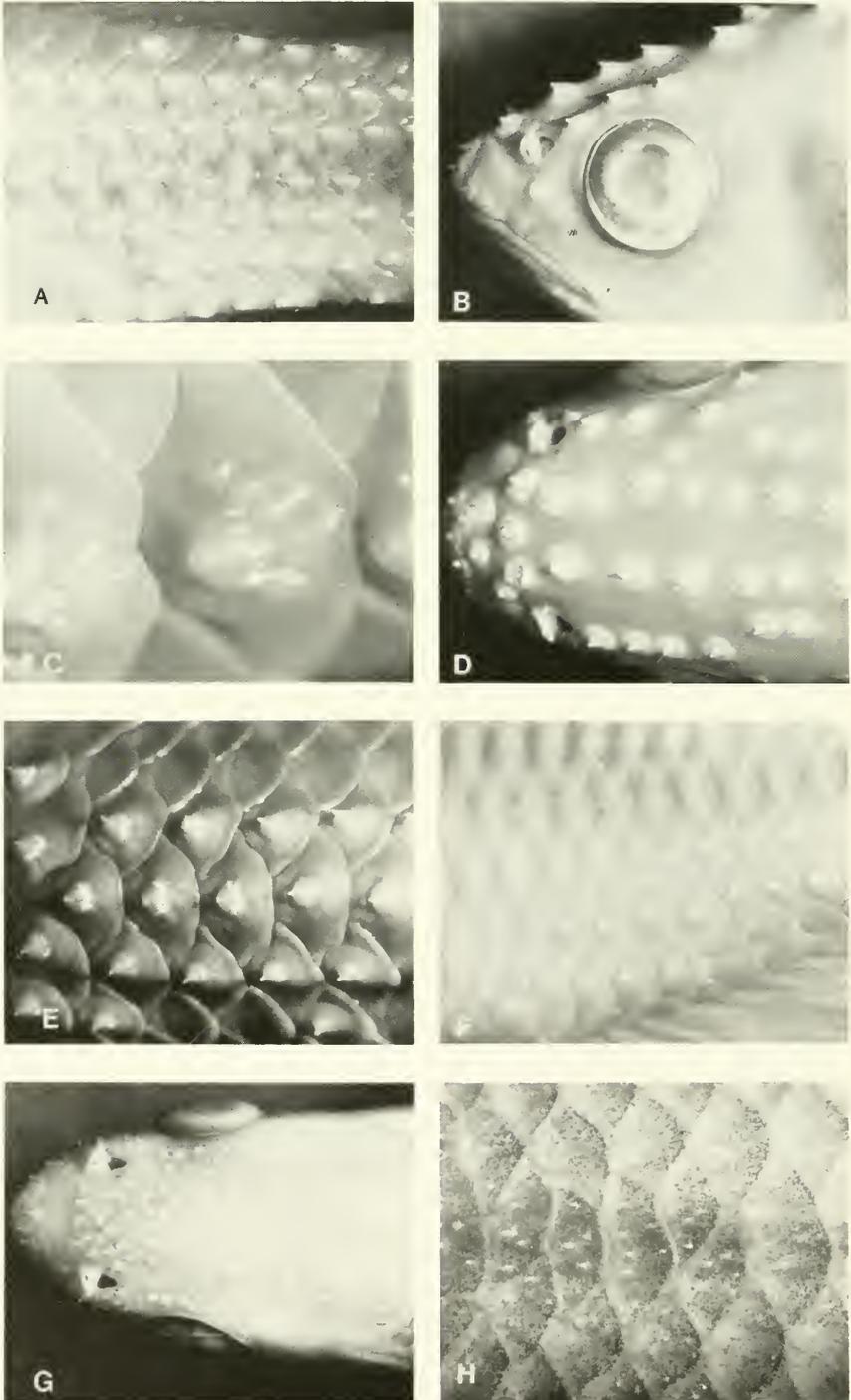


Fig. 46. Tuberculation patterns in male *Cyprinella*. A) caudal-peduncle scales of *C. xaenura* (100 mm, TU 29458). B-F) *C. pyrrhomelas* (84-85 mm, UAIC 2550.05): lateral view of head, caudal-peduncle scales, dorsal view of head, nape scales, and lower caudal-peduncle scales. G-H) *C. caerulea* (60 mm, UAIC 2580.13): dorsal view of head and nape scales.

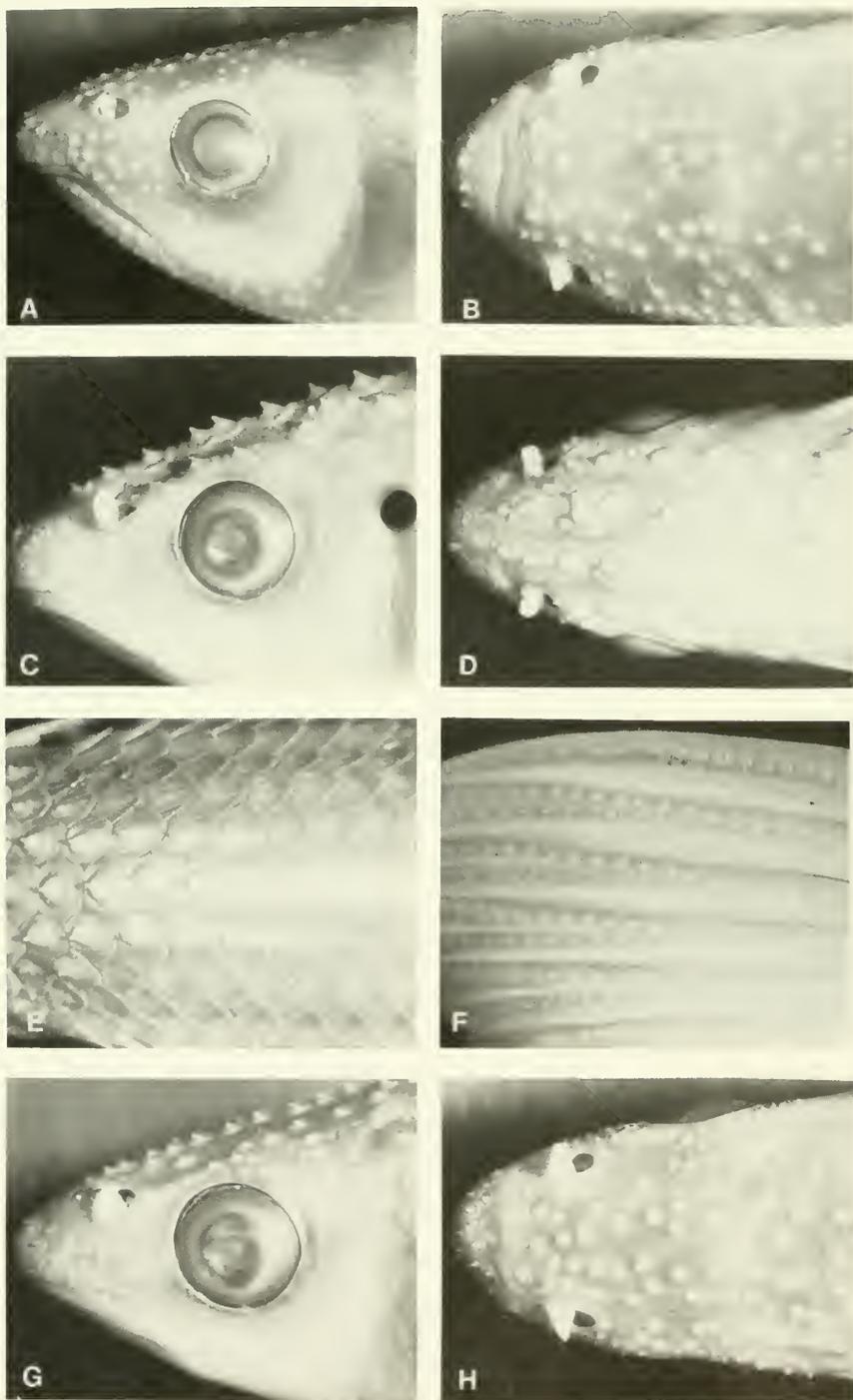


Fig. 47. Tuberculation patterns in male *Cyprinella*. A-B) *C. gibbsi* (82 mm, TU 40670): lateral view of head and dorsal view of head. C-F) *C. callistia* (84 mm, KU 19697): lateral view of head, dorsal view of head, nape scales, and left pectoral fin. G-H) *C. callisema* (62 mm, KU 19653): lateral view of head and dorsal view of head.

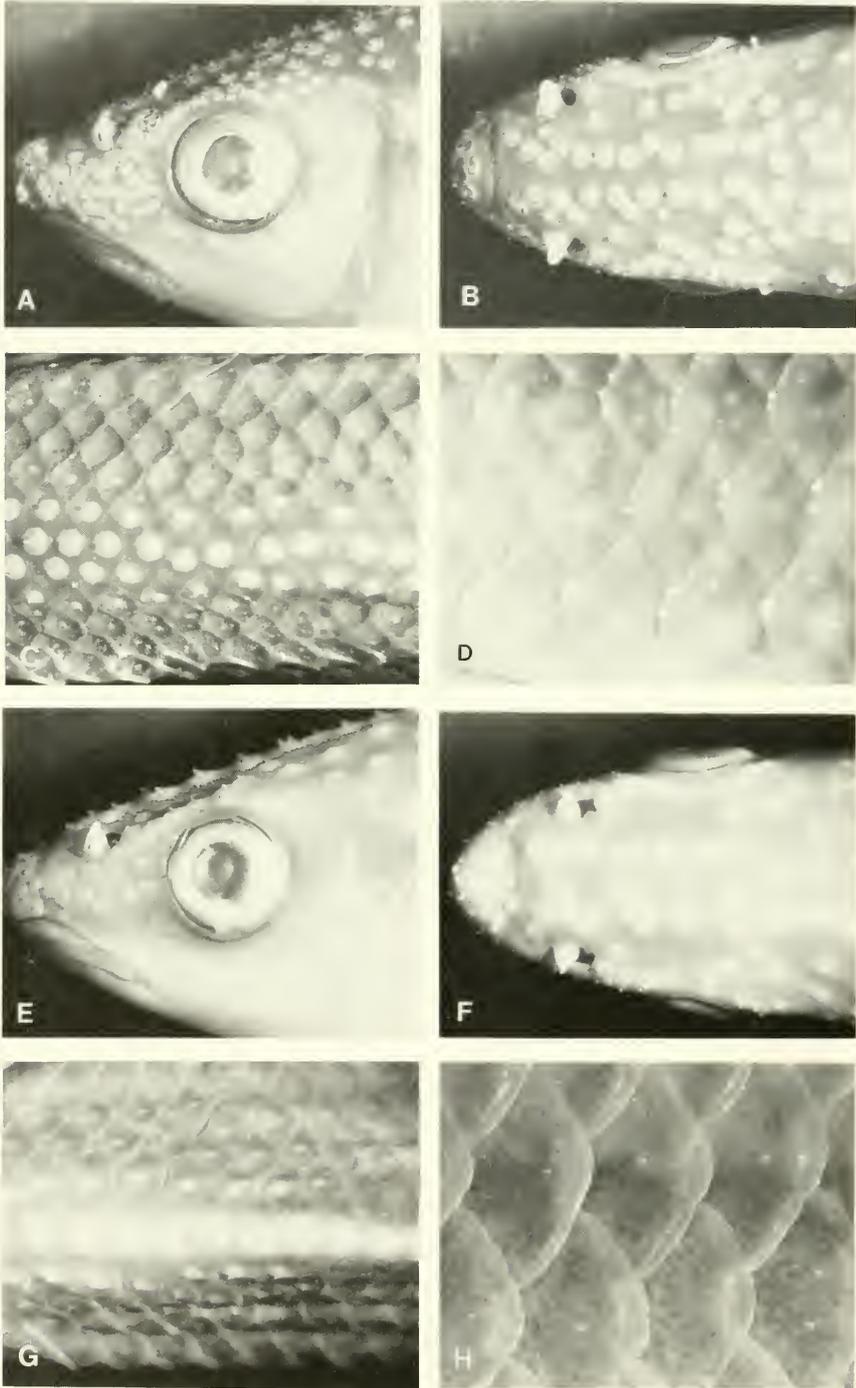


Fig. 48. Tuberculation patterns in male *Cyprinella*. A-D) *C. nivea* (78-82 mm, TU 38616): lateral view of head, dorsal view of head, nape scales, and ventral caudal-peduncle scales. E-H) *C. leedsii* (74.5 mm, UAIC 3127.01): lateral view of head, dorsal view of head, nape scales, and lateral body scales.

1960). Although Wallace and Ramsey (1981) observed a male spottail shiner attempting to swim into the nesting crevice of the bluestripe shiner, it is unlikely in this clear stream that hybridization would have resulted. Most cases of hybridization can be correlated with ecological disturbances (Hubbs and Strawn, 1956).

More likely, the crevice habitat was an attractive spawning site for *C. venusta*.

Etymology. The name *callitaenia* is derived from the Latin *calli* for beautiful and *taenia* for band or ribbon, in reference to the lateral blue stripe.

OSTEOLOGY

This section contains an osteological description of species of *Cyprinella*, as well as comparisons to other North American cyprinids. Below, the skeleton of these fishes is divided into 15 separate sections. Under each section, included bones are discussed in detail with respect to their developmental origins and systematic variation of several potential morphological variables. Characteristics examined for variation included the shape and relative size of a bone and its articulation with adjacent elements. Variations in bones noted only in individual specimens, and hence of limited use systematically, are not discussed. Only those skeletal variations noted to be consistent for a species and hypothesized to be potential characters are included. In this study, many morphological variations were noted from the skeletons of these fishes, especially from certain anatomical regions, but these variations were not consistent within a species and were thus not considered further. Some variations hypothesized below to represent systematic characters are subtle differences in the shape or relative size of the bone or perhaps the type or degree of articulation with adjacent bones. Although these characters may appear to be of minor significance, they were in almost all cases, verified with one or more additional specimens of a taxon to guard against individual variation. Numerous illustrations of variations discussed are presented to aid the reader in descriptions and interpretations. Abbreviations used in all illustrations and text are listed and explained in the Methods section of this paper.

group taxa (and variation) and the primitive and derived morphologies within *Cyprinella* are considered. In most cases, the nearest outgroups to *Cyprinella* were used to determine character polarities and are discussed most thoroughly. The derived morphologies are used and discussed later under systematic species relationships.

ETHMOID REGION

The ethmoid region (Figs. 49–58) of the skull is complex and composed of elements of dermal, endochondral, and perichondral origin. Included are the mesethmoid, lateral ethmoids, preethmoid cornua, supraethmoid, vomer, kinethmoid, and nasals. The last four elements are of dermal origin and only the nasals are paired. The first three elements are cartilage bones. The mesethmoid is single and perichondral, the preethmoids are paired and endochondral, and the paired lateral ethmoids are dermal, endochondral, and perichondral.

Most of these elements form surfaces surrounding the nasal cavities. The supraethmoid and nasals are dorsal, lateral ethmoids are posterior and ventral, the mesethmoid is anterior, dorsal and ventral, and the vomer is ventral. The preethmoids and kinethmoid are not in the nasal cavity and are anterior. The kinethmoid articulates via ligaments to the anterior supraethmoid and mesethmoid and the preethmoids lie between the anterolateral mesethmoid and vomer.

Penetrating much of the ventral ethmoid region is the cartilaginous *planum ethmoidale*. This cartilage block extends between the mesethmoid and vomer anteriorly and is expanded posteriorly to the orbitosphenoid and laterally into the lateral ethmoids. Dorsally, it

Following the discussion of osteological variation of a particular bone among species of *Cyprinella*, the variation is compared to out-

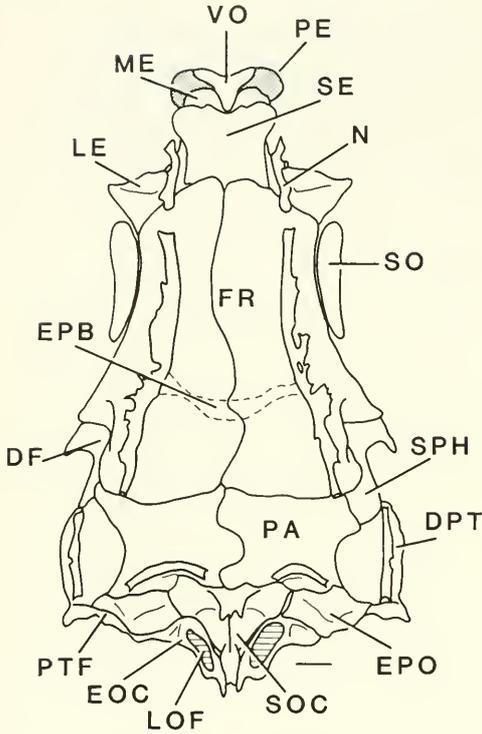


Fig. 49. Dorsal view of cranium of *Luxilus coccogenis* (72 mm, INHS 79254). Stippled regions represent cartilage. Lateral occipital foramina identified by lined pattern. Horizontal bar equals 1 mm.

invades much of the ventral half of the mesethmoid. In adults, the *planum ethmoidale* becomes ossified laterally in the lateral ethmoids, dorsally in the mesethmoid, and ventrally and anteriorly between the mesethmoid, preethmoids, and vomer.

Mesethmoid (ME, Fig. 57). Resting on the cartilaginous *planum ethmoidale*, this semi-circular bone is the largest anterior element of the ethmoid region. Medially it is constricted, forming a waist near the olfactory foramen. Dorsally and anteriorly it is roughly convex. Posteriorly, it is laterally compressed and oriented vertically, forming the nasal septum. The posterior margin is roughly vertical where it articulates with the lateral ethmoids. Together these bones contain the olfactory foramen. Anteriorly, dorsally, and ventrally the mesethmoid is expanded from the median waist, producing dorsal and ventral cavities.

The lateral surfaces thus form the respective faces of the nasal cavity. The ventral cavity is invaded by the *planum ethmoidale* like the lateral ethmoids, while the dorsal is generally hollow although some endochondral ossification may occur. The dorsal surface is covered by the dorsally convex supraethmoid. Anteriorly the mesethmoid produces bony anterolateral projections for ligament connections to the kinethmoid. Anteroventrally it serves as the dorsal receptacle for the preethmoids.

The length of the mesethmoid is variably developed in *Cyprinella*. *Cyprinella xaenura* has a short mesethmoid block (Fig. 57E), while in *callitaenia*, *callisema*, *leedsii*, and *nivea* it is elongate (Fig. 57F). All other species have similarly sized mesethmoids (Fig. 57D), as in outgroups examined. In *xaenura*, *pyrrhomelas*, *trichroistia*, *gibbsii*, and *caerulea* the olfactory foramen is large and bounded entirely by a laterally directed shelf produced by the mesethmoid and lateral ethmoids (Fig. 57E). In all other taxa no shelf is formed and both bones slope gradually into the foramen.

The shelf around the olfactory foramen is considered derived in this genus since no other species examined develops this structure. The short mesethmoid of *xaenura* and long mesethmoid of species of the *nivea* group are independently derived relative to other species of *Cyprinella* and the outgroups *Luxilus* and *Lythrurus*, all of which have similarly sized elements.

Lateral Ethmoid (LE, Figs. 49–58). These paired bones are complex structurally and developmentally, having dermal, endochondral, and perichondral portions. They articulate with the mesethmoid anteriorly, supraethmoid, frontals, and orbitosphenoid dorsally, and parasphenoid and vomer ventrally (Fig. 57). They form the posterior face of the nasal cavity anteriorly and the anterior face of the orbits, anterior neurocranium, and myodome posteriorly. Viewed ventrally, each bone is roughly triangular, broadest mesially and narrowing laterally, producing a long lateral wing. The ventral surface is somewhat con-

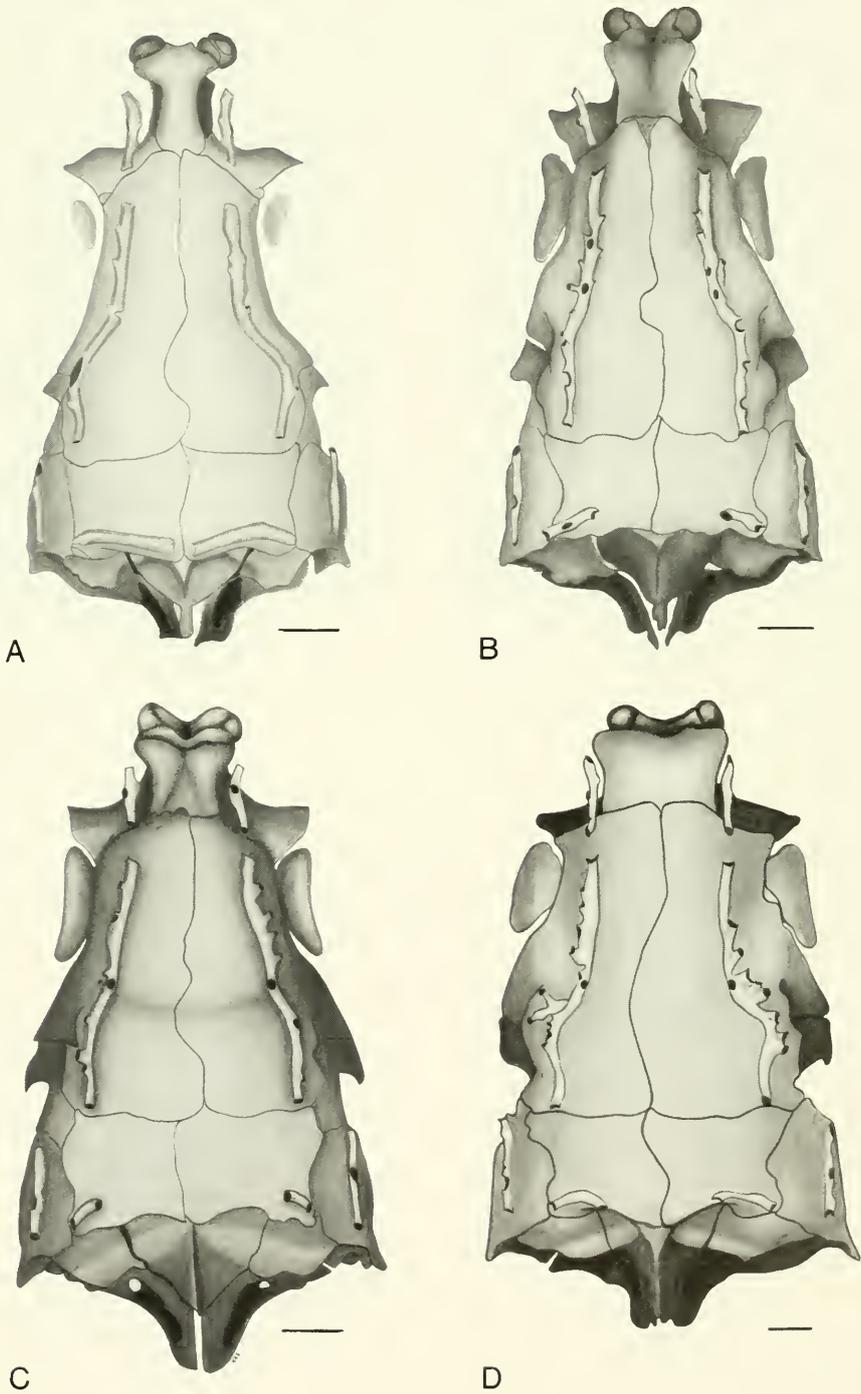


Fig. 50. Dorsal view of cranium of *Cyprinella* and close relatives. A) *Rhinichthys falcatus*, 41 mm, KU 18912. B) *Notropis atherinoides*, 55 mm, KU 18935. C) *Lythrurus funeus*, 55 mm, KU 6244. D) *Cyprinella spiloptera*, 65 mm, KU 17776. Horizontal bar equals 1 mm.

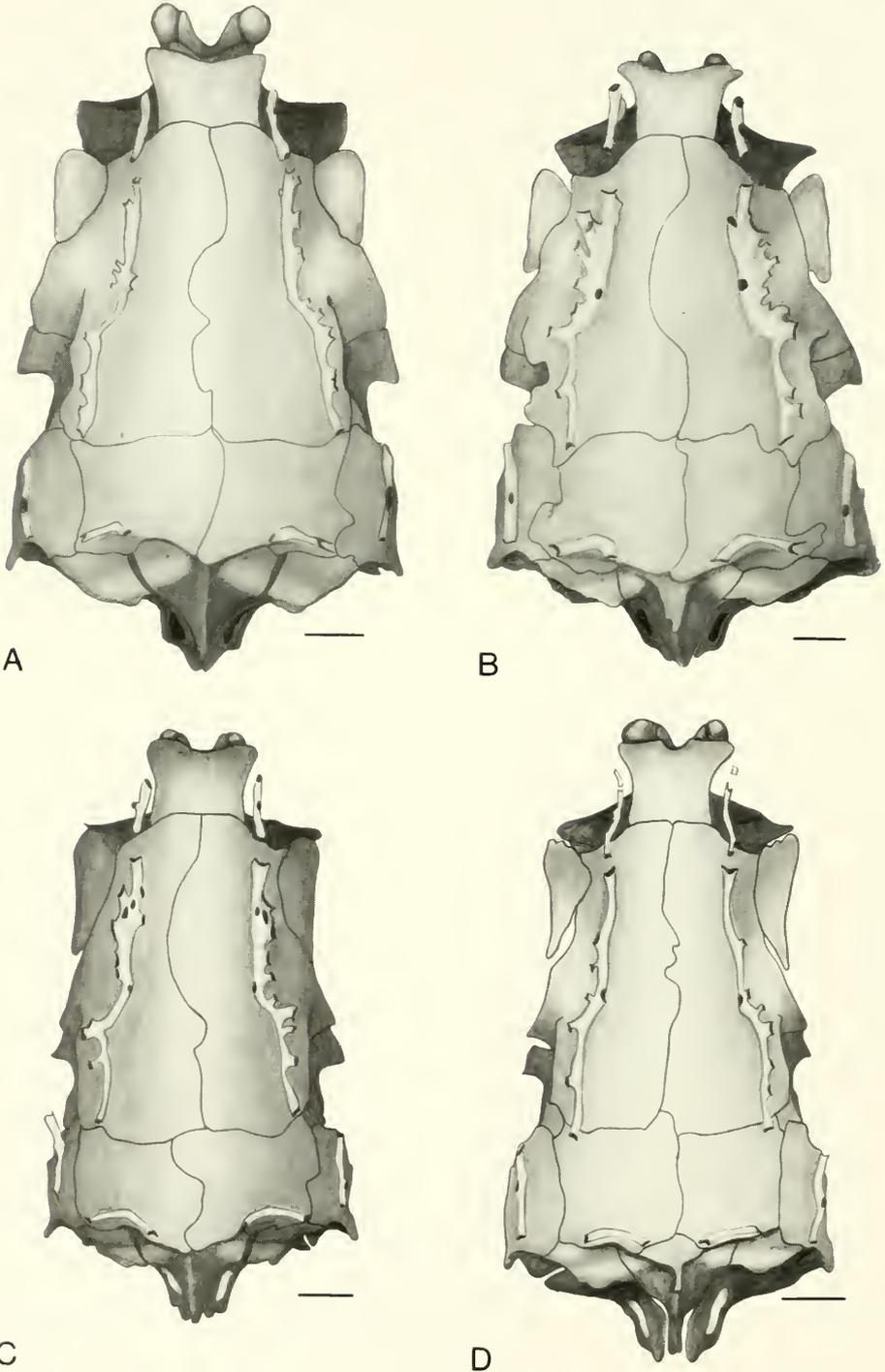


Fig. 51. Dorsal view of cranium in *Cyprinella*. A) *C. lutrensis*, 55 mm, KU 19431. B) *C. ornata*, 56 mm, KU 8405. C) *C. proserpina*, 58 mm, TNHC 3262. D) *C. ruila*, 65 mm, ASU 5982. See Figure 49 for identification of elements. Horizontal bar equals 1 mm.

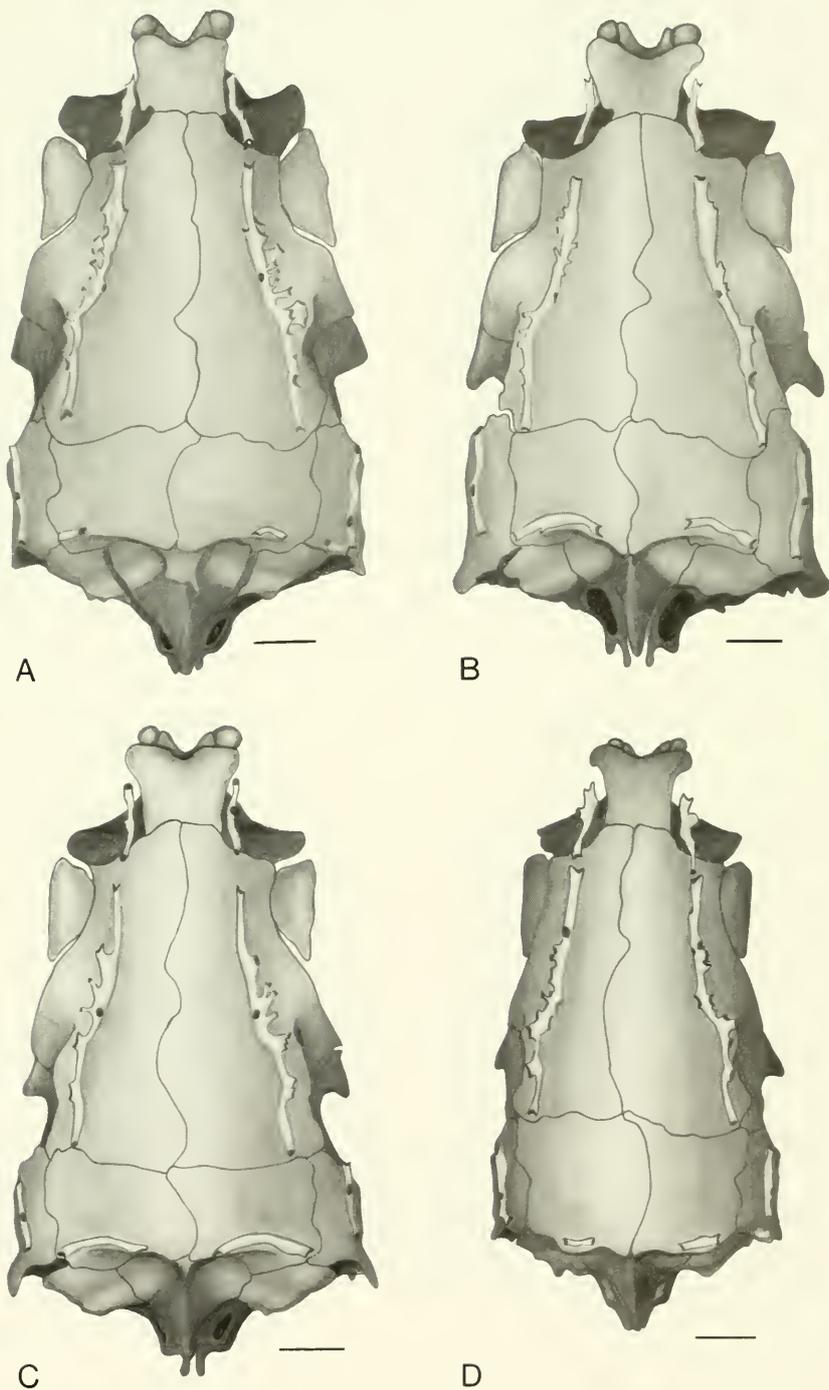


Fig. 52. Dorsal view of cranium in *Cyprinella*. A) *C. garmani*, 46 mm, KU 5416. B) *C. formosa*, 47 mm, KU 8399. C) *C. lepida*, 50 mm, KU 55189. D) *C. panarcys*, 45 mm, UMMZ 208212. See Figure 49 for identification of elements. Horizontal bar equals 1 mm.

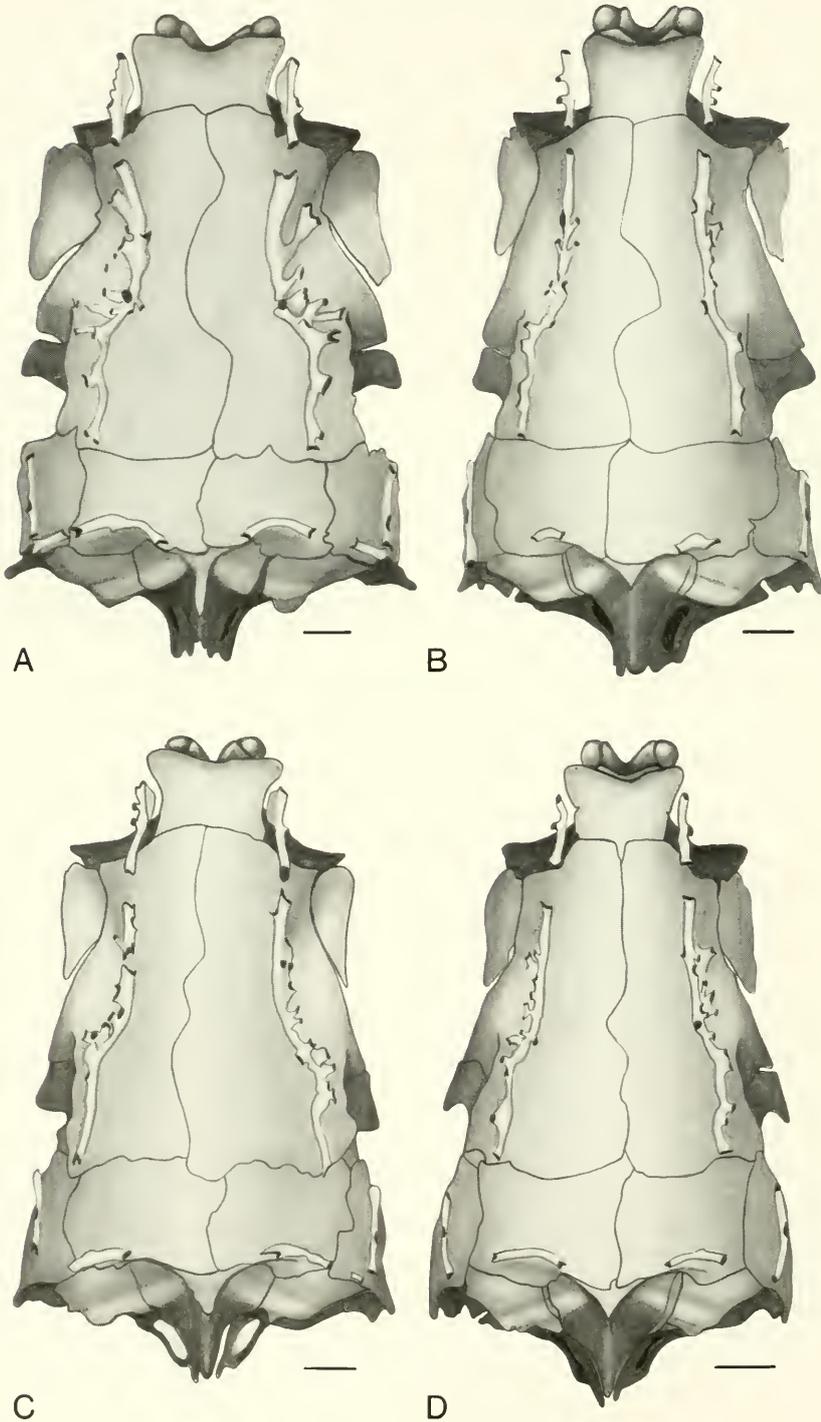


Fig. 53. Dorsal view of cranium in *Cyprinella*. A) *C. camura*, 60 mm, KU 15792. B) *C. whipplei*, 55 mm, KU 14211. C) *C. analostana*, 60 mm, INHS 77855. D) *C. chloristia*, 55 mm, KU 8882. See Figure 49 for identification of elements. Horizontal bar equals 1 mm.

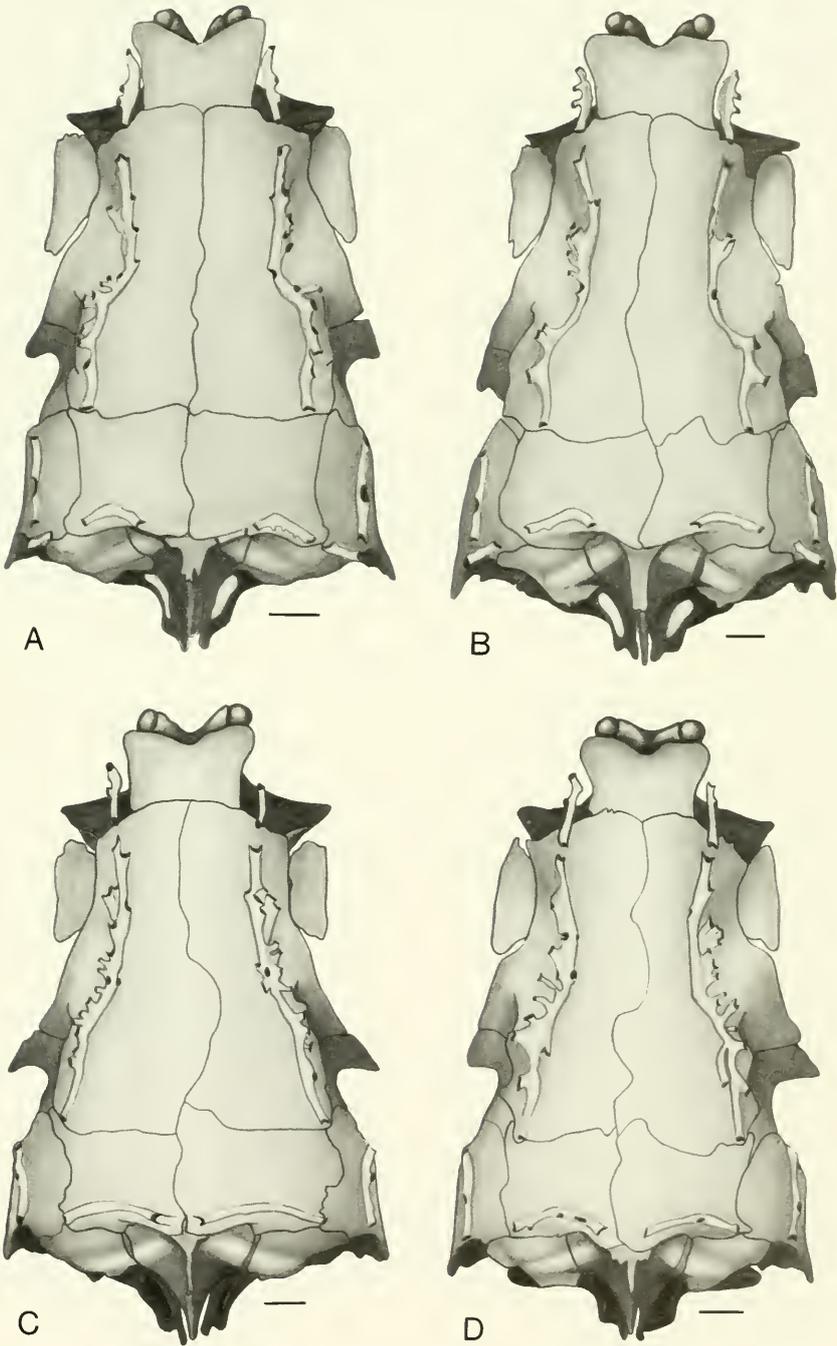


Fig. 54. Dorsal view of cranium in *Cyprinella*. A) *C. galactura*, 67 mm, KU 12029. B) *C. venusta*, 85 mm, KU 8810. C) *C. pyrrhomelas*, 79 mm, INHS 76839. D) *C. xaenura*, 74 mm, KU 18994. See Figure 49 for identification of elements. Horizontal bar equals 1 mm.

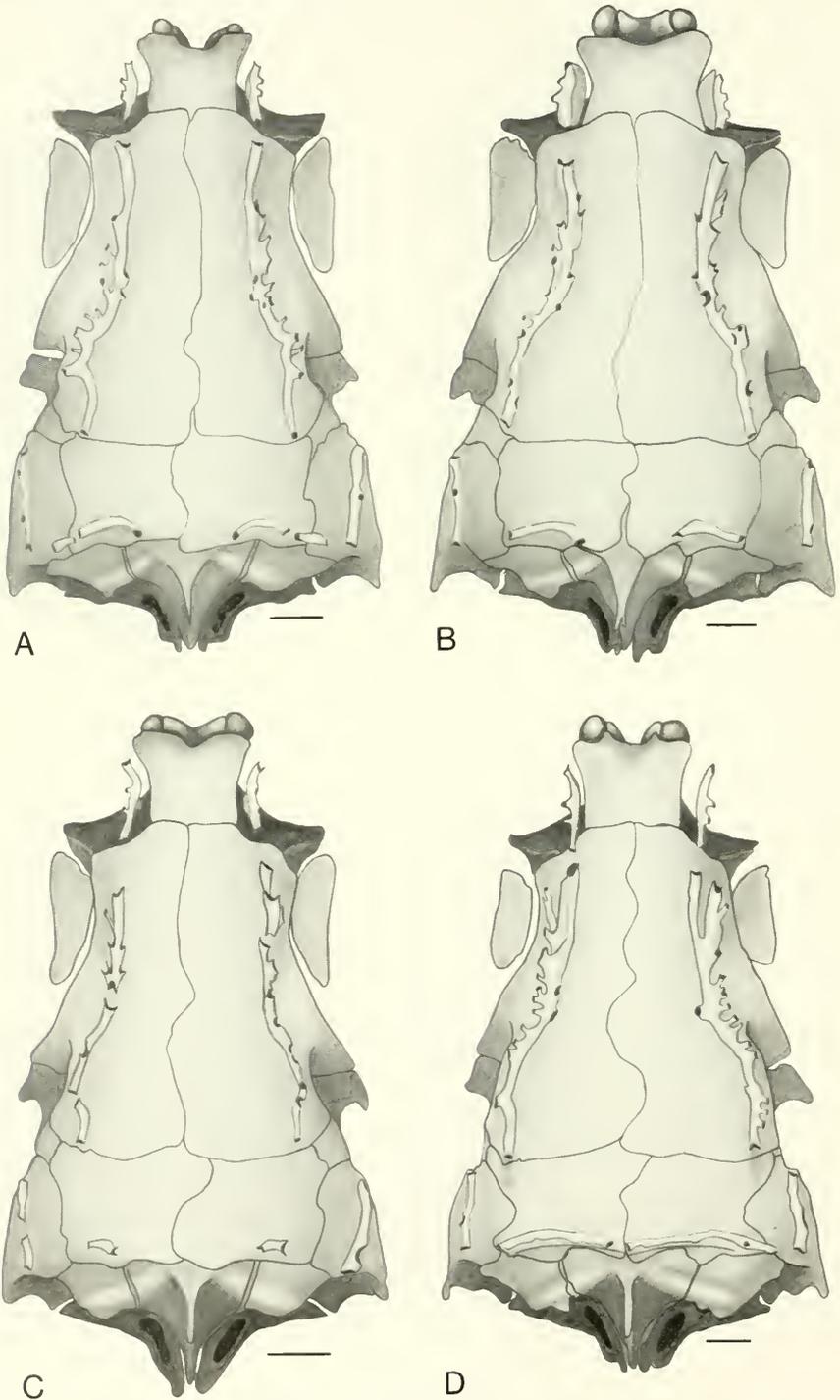


Fig. 55. Dorsal view of cranium in *Cyprinella*. A) *C. trichroistia*, 60 mm, KU 18853. B) *C. gibbsi*, 59 mm, KU 18892. C) *C. caerulea*, 60 mm, KU 18978. D) *C. callistia*, 74 mm, KU 18842. See Figure 49 for identification of elements. Horizontal bar equals 1 mm.

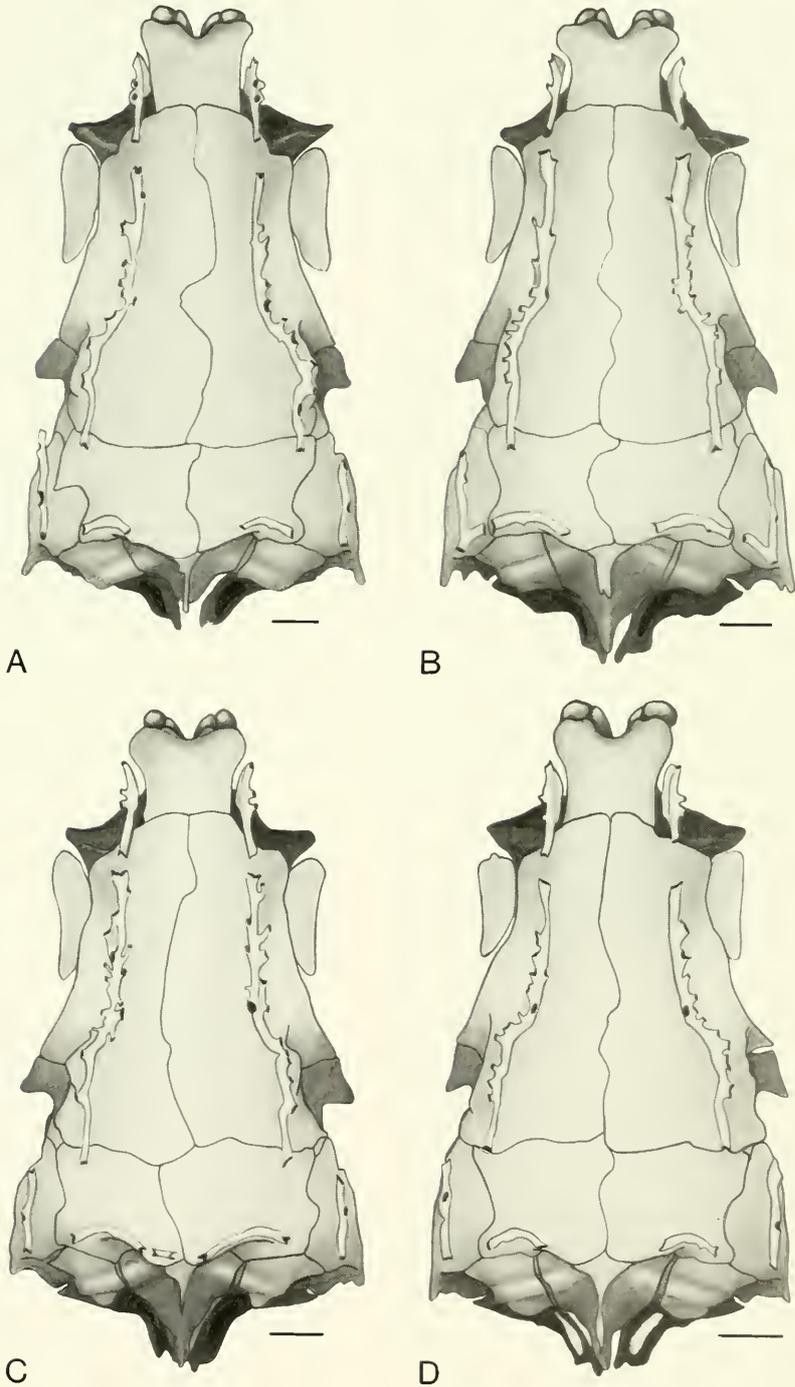


Fig. 56. Dorsal view of cranium in *Cyprinella*. A) *C. nivea*, 60 mm, KU 18987. B) *C. leedsii*, 51 mm, KU 18985. C) *C. callitaenia*, 59 mm, TU 92770. D) *C. callisema*, 52 mm, KU 8842. See Figure 49 for identification of elements. Horizontal bar equals 1 mm.

cave, depressed or slightly dished anteriorly and elevated along the posterolateral margin, forming a ridge. This elevated ridge supports the palatine-endopterygoid articulation.

Medially these bones are constricted, primarily with the development of the olfactory foramen. Each produces a posteromesially directed shelf that forms the floor of the anterior neurocranium (Fig. 57). The mesially directed shelves, together with a medial notch in each bone below the shelf, form the anterior myodome for the insertion of the *inferior* and *superior oblique* eye muscles. Posteriorly, below the anterior myodome, the lateral ethmoids, together with the orbitosphenoid, form the anterior wall of the orbit, while anteriorly they form the posterior face of the nasal cavity. Anteriorly they articulate with the mesethmoid and together border the olfactory foramen.

Dorsal to the medially constricted region the lateral ethmoids consist of two parallel and mesially curving walls that form the sides of the *taenia marginalis anteriorus*. These dorsal walls are broadly separated from their counterparts posteriorly and only narrowly separated anteriorly. Thus, the mesial concave walls form the anterior and ventral surfaces of the anterior neurocranium and the lateral walls form the dorsoposterior face of the nasal cavity. The dorsoposterior face forms the anterior wall of the orbit (Fig. 57).

Morphology of the lateral ethmoid varies among species of *Cyprinella* with respect to the shape of the ventral and mesial surfaces, the complexity of the olfactory foramen, and ossification of the investing cartilaginous ventral *planum ethmoidale*. In species of the *lutrensis* clade and outgroups, the ventral surface of the lateral ethmoids of adults is not completely ossified. Only the anterior and anterolateral surfaces become ossified and a large mesial portion extending laterally into the bone remains cartilage (Fig. 58A–E). When maximum ossification occurs a large cartilage pad generally remains posteromedially. This pad may be separate from the mesial *planum ethmoidale*.

In the *whipplei* clade most of the lateral ethmoid becomes ossified at an early age. Cartilage is present only as a thin line or spot posteromesially or laterally, isolated from the mesial cartilage separating the two lateral ethmoids (Fig. 58F–L).

Some *Cyprinella* develop a strongly triangular ventral surface to the lateral ethmoid with oblique anterior and relatively straight posteroventral edges. In others the anterior margin is concave when viewed from below, such that a slight anteromesial process is developed and the bone is roughly L-shaped. All species of the *lutrensis* group, except *proserpina* and *panarcys*, and *spiloptera*, *camura*, *whipplei*, *analostana*, and *chloristia* have the concave anterior margin. *Cyprinella panarcys* and *proserpina* have straight margins to the lateral ethmoids, unlike any other species of the genus. *Cyprinella galactura*, *venusta*, and *xaenura* have intermediate triangular lateral ethmoids ventrally, but with a slightly curved anterior margin (Fig. 58I). All other species have the triangular morphology (Fig. 58J–L).

Further influencing the shape of this bone is the shape of the ventromesial edge where the two meet to form the floor and roof of the anterior neurocranium and myodome, respectively. It may be either convex or squared. All species of the *lutrensis* clade, *spiloptera*, *camura*, *whipplei*, *analostana*, and *chloristia* have a convex margin ventrally, like other cyprinids examined. Other *Cyprinella* have the blunt and squared margin.

In all species except *caerulea*, *gibbsi*, *trichroistia*, *xaenura*, and *pyrrhomelas*, the surrounding lateral ethmoid and mesethmoid slope gradually to the olfactory foramen, in a manner similar to other cyprinids examined. In the above listed species a laterally projecting shelf is formed by both the mesethmoid and anterior lateral ethmoids around the foramen (Fig. 57).

As discussed under the mesethmoid, the shelf around the olfactory foramen represents a derived condition. Based on outgroup comparison the triangular lateral ethmoid with a blunt mesial edge is derived in this group, as

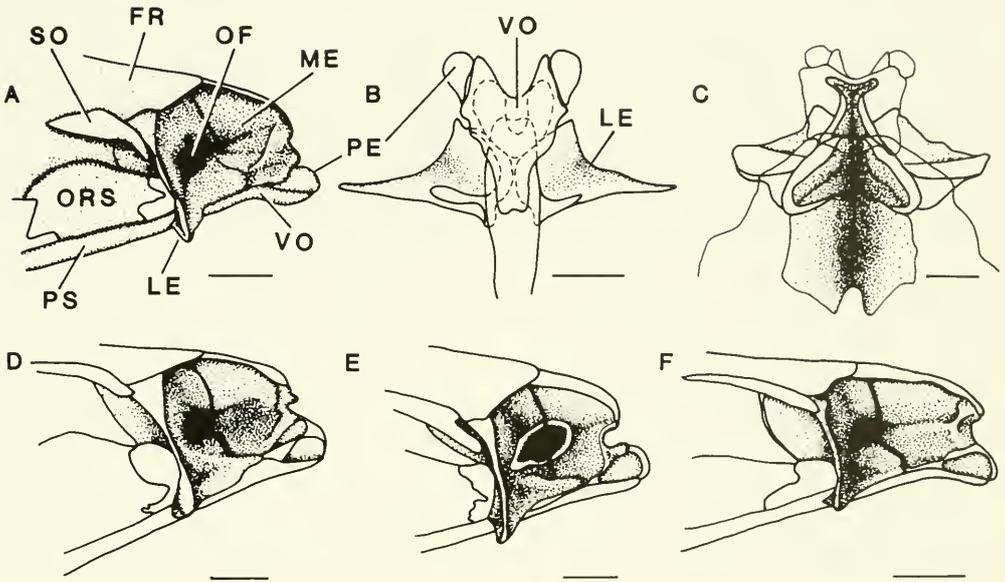


Fig. 57. Ethmoid region in *Cyprinella* and outgroup. A-C) Lateral, ventral, and dorsal view of ethmoid region of *Cyprinella lutrensis* (55 mm, KU 19431). In A the nasal cavity is illustrated with the centrally located olfactory foramen. In B the cartilage-filled mesethmoid and lateral ethmoids are illustrated beneath the vomer and parasphenoid. In C the anterior neurocranium formed by the anterior orbitosphenoid and posterior lateral ethmoids, and the internasal septum are illustrated beneath the frontals and supraethmoid. D) Lateral view of ethmoid region of *Luxilus cardinalis* (65 mm, KU 15281) illustrating primitive olfactory foramen and mesethmoid size. E) Lateral view of ethmoid region in *Cyprinella xaenura*, illustrating shelf formed around olfactory foramen and short mesethmoid. F) Lateral view of ethmoid region of *C. callisema* (52 mm, KU 8842) illustrating elongate mesethmoid and primitive olfactory foramen. Horizontal bar equals 1 mm.

well as the nearly completely ossified ventral surface. All other cyprinids examined, except for some *Pteronotropis*, have a basically L-shaped lateral ethmoid with a convex mesial margin and the *planum ethmoidale* extends laterally into this bone and generally remains in adults. The conical shape of the lateral ethmoids in *panarcys* and *proserpina* is unique to these species and is derived.

Vomer (VO, Figs. 49, 57, 58). This single, medial dermal bone lies horizontally beneath the ethmoid complex and the anterior end of the parasphenoid, and is visible only when viewed from below or laterally. It is broadest and thickest anteriorly where forked into two anterolateral processes, each forming a shallow bowl where the mesial preethmoid is formed. Separating these two processes is a variably developed notch. Medially, the vomer is flat and thin and forms a short, broad

neck separating the preethmoids from the anterior extent of the lateral ethmoids. Posterolaterally, where the medial neck ends the vomer is restricted to form a long, narrow posteriorly directed process. This process lies in a shallow trough against the ventral surfaces of the parasphenoid and may extend to the posterior margin of the lateral ethmoids.

In *Cyprinella*, interspecific variation in vomerine shape is expressed in the length of the posterior process, depth and width of the anterior notch separating the preethmoid processes, and length of the medial neck (Fig. 58). Some species have little or no medial neck developed between the preethmoids and lateral ethmoids. These include *spiloptera*, *lutrensis*, *garmani*, and *ornata*. Others have a medial neck developed that may be either short or long. Species with a long neck include *analostana*, *chloristia*, *caerulea*, *nivea*, *leedsii*,

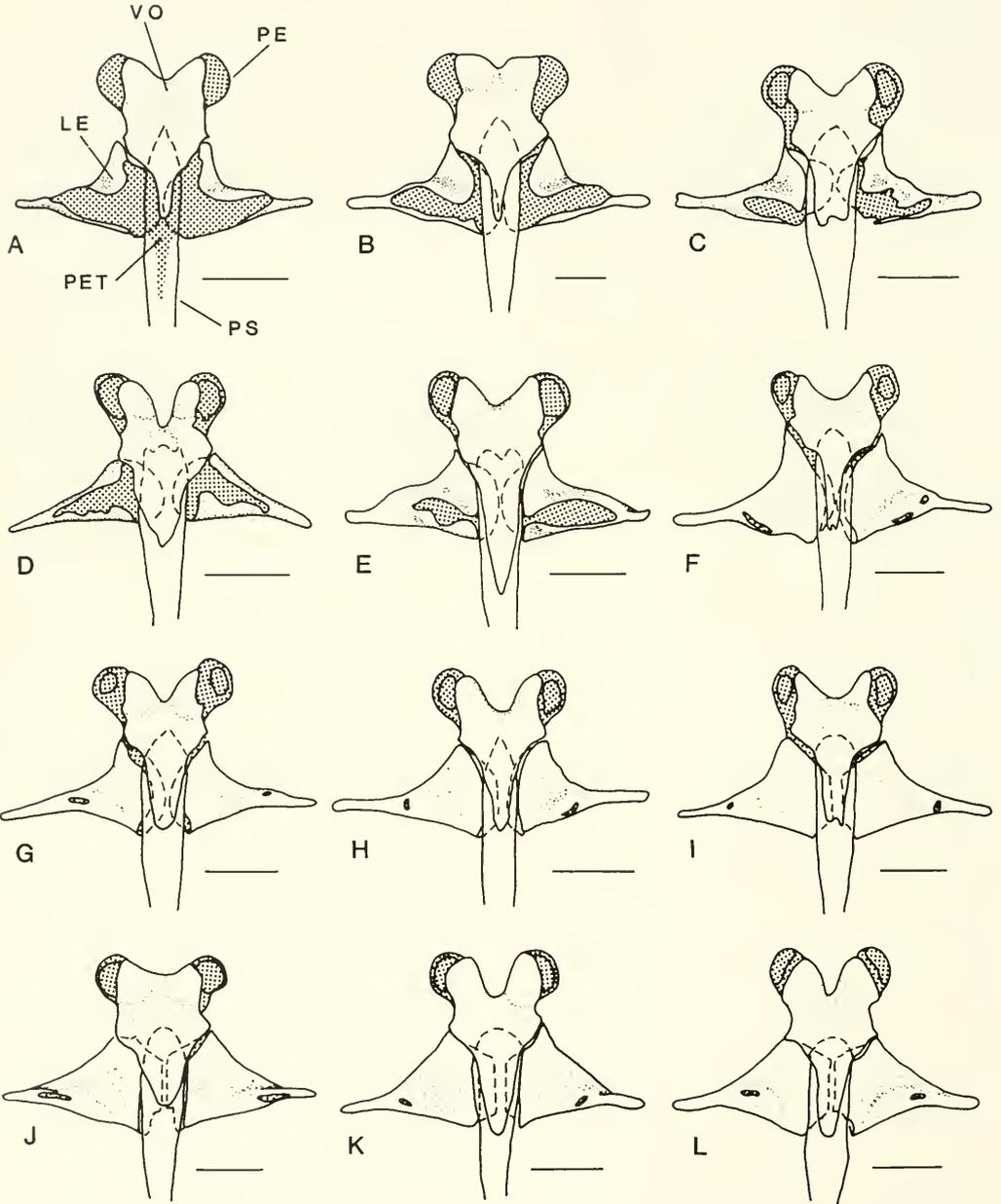


Fig. 58. Ventral view of ethmoid region in some species of *Cyprinella* and outgroups. A) *Notropis atherinoides*, 53 mm, KU 18935. B) *Luxilus coccogenis*, 72 mm, INHS 79254. C) *Cyprinella garmani*, 50 mm, KU 5416. D) *C. panarcys*, 44 mm, UMMZ 208212. E) *C. rutila*, 57 mm, ASU 5982. F) *C. spiloptera*, 56 mm, KU 17776. G) *C. whipplei*, 55 mm, KU 14211. H) *C. camura*, 45 mm, KU 15792. I) *C. venusta*, 58 mm, KU 8810. J) *C. caerulea*, 60 mm, KU 18978. K) *C. leedsii*, 53 mm, KU 18985. L) *C. callitaenia*, 57 mm, TU 92770. Stippled pattern represents cartilage. In A the posterior distribution of the planum ethmoidale is illustrated. In all others only that portion visible ventrally is illustrated in the lateral ethmoids and between the vomer and lateral ethmoids. In C–L the ossified preethmoids are illustrated with the cartilaginous preethmoid comua. Horizontal bar equals 1 mm.

callitaenia, and *callisema*. The anterior notch is broad and moderately shallow in all species, except *nivea*, *leedsi*, *callitaenia*, *callisema*, *pyrrhomelas*, *lutrensis*, *xanthicara*, *panarcys*, and *proserpina*, in which it is relatively deep. Species of the *nivea* group also differ in having the preethmoid processes closer together, producing a more narrow notch. No notch is developed in *caerulea* and *gibbsi*; in *xaenura* and *trichroistia* the notch is very shallow.

The posteriorly directed process of the vomer is variable in length and width. Generally, the posteriormost extent of the vomer is at the posterior edge of the lateral ethmoids, as in most outgroups examined. In *caerulea*, *gibbsi*, *trichroistia*, *pyrrhomelas*, and *xaenura* the process terminates well before the edge of the lateral ethmoids, and in *rutila*, *xanthicara*, *panarcys*, and *proserpina* it extends beyond the lateral ethmoids. Of these latter four species it is longest in *rutila* and *proserpina*. The posterior process is narrow in *spiloptera*, *galactura*, *venusta*, *analostana*, *trichroistia*, *callitaenia*, *rutila*, and *xanthicara* and broad, as in most outgroups, in all other species of the genus.

Development of a medial neck on the vomer is derived in *Cyprinella*. Most members of the genera *Luxilus* and *Lythrurus* lack any neck development. Outside this clade several other taxa are known to develop an elongate to short neck. Having a moderately shallow anterior notch in the vomer is primitive in this genus. The deep, shallow, and no notch conditions are derived, as well as the narrow notch in the *nivea* group. A wide posterior vomerine process extending to the posterior margin of the lateral ethmoids is primitive in *Cyprinella*. This condition is common to the genera *Luxilus* and *Lythrurus*. The short and elongate conditions are derived for *Cyprinella*, as is the narrow posterior process.

Preethmoid (PE, Figs. 49–58). The preethmoid cornua are paired endochondral ossifications located laterally between the anteroventral mesethmoid and vomer. In *Cyprinella* a mesial and lateral ossification are

present. As adults, these ossifications fuse, forming a large single endochondral ball surrounded laterally by cartilage. No significant interspecific variation occurs in *Cyprinella*. The occurrence of these elements in the genus might be hypothesized as being diagnostic since the closest outgroups (*Lythrurus* and *Luxilus*) apparently do not develop these structures.

Supraethmoid (SE, Figs. 49–57). Anterior to and generally articulating with the paired frontals is the dorsoventrally compressed supraethmoid. This roughly square bone roofs the nasal capsules and is fused with the dorsal mesethmoid. Relative to species of the more distant and primitive clades of *Rhinichthys* and *Nocomis*, the supraethmoid of *Luxilus*, *Lythrurus*, *Notropis* (s.s.), and most *Cyprinella* is a shorter structure. Like *Rhinichthys* and *Nocomis*, however, most species of *Lythrurus* and *Notropis* (s.s.), have a supraethmoid that has a “butterfly” shape, similar to that described by Harrington (1955) for *N. bifrenatus* and Coburn (1982) for *Notropis* (s.s.). In these taxa the anterior- and posterior-most ends are broader than the median waist. Except for the *nivea* species group of *Cyprinella*, the genera *Luxilus* and *Cyprinella* share a broader and more square-shaped supraethmoid, compared to other species examined. In these two clades the median constriction is usually only slight and the anterior margin of the bone is generally only slightly and smoothly indented.

Within *Cyprinella*, several different derived conditions of the supraethmoid are found. Members of the *lutrensis* clade have the same broad and short supraethmoid found in *Luxilus*, except for *garmani*, *formosa*, *bocagrande*, *lepida*, *proserpina*, *panarcys*, *rutila*, and *xanthicara*. These species have a narrower condition (but broader than the *nivea* group), and have a slight constriction of the median waist, giving it a more “butterflylike” appearance. In the *whipplei* clade the supraethmoid is further broadened, representing the derived condition. All members of this group except *camura*, *pyrrhomelas*, and *xaenura* also have the bone

more elongate. *Cyprinella caerulea* and *trichroistia* have broad, but short supraethmoids. Species of the *nivea* group have a reduced width to their supraethmoids as in outgroups, but have retained the elongate condition.

Kinethmoid. This small dermal bone is elongate and crescentic in shape and somewhat ornate. It articulates via ligaments with the mesethmoid, maxillaries, and premaxillaries. The mesethmoid ligament is forked and attaches to the kinethmoid at a single dorsal bony tubercle and with the mesethmoid anterolaterally. The maxillary ligaments attach to the kinethmoid dorsolaterally at small lateral processes and with the maxillary at the expanded anterior bony tubercles, behind the premaxillary process. The premaxillary ligaments attach ventrally on the kinethmoid and to the ascending processes of the premaxillaries. No significant variation occurs among species of *Cyprinella*.

Nasal (N, Figs. 49–56). The nasals are lateral to the supraethmoid and dorsal to the nasal cavity. These are small and thin dermal bones and contain the anterior portion of the supraorbital canal. The canal may have one or two laterally directed pores. Species with two pores include *camura*, *galactura*, *venusta*, *whipplei*, *caerulea*, *trichroistia*, *gibbsi*, *nivea*, *callisema*, *callitaenia*, and *callistia*. All other species have the primitive condition for *Cyprinella*, a single lateral pore as in the immediate outgroups.

ORBITAL REGION

The orbit is bounded by 10 paired elements and one median bone, the orbitosphenoid (Figs. 59, 60). Both endochondral and dermal elements are included here. The orbitosphenoid forms the interorbital septum and much of the floor of the neurocranium. The orbitosphenoid and pterosphenoids are cartilage bones, whereas the frontals, supraorbitals, and infraorbital bones are dermal. Included in the infraorbital series are the lacrymal and five infraorbital bones located below and behind the orbit. The lacrymal is the first of the infraorbi-

tal series and borders the orbit anteriorly. The fifth or sixth infraorbital bone is sometimes referred to as the dermosphenotic.

Orbitosphenoid (ORS, Figs. 59, 60). This large, medial, and V-shaped endochondral element forms much of the floor of the anterior neurocranium and mesial wall of the orbit. It articulates with the lateral ethmoids and posterior *planum ethmoidale* anteriorly, with the frontals dorsally, with the pterosphenoids posteriorly, and with the parasphenoid ventrally. The dorsal articulation with the frontals is the most complex. The orbitosphenoid plates extend dorsolaterally and fit into a double-walled lamella of the frontal, surrounding the *taenia marginalis anteriorus*. This canal continues anteriorly into the dorsal lateral ethmoids. Ventrally, the articulation with the parasphenoid is with the vertical interorbital septum. This septum is shallow in all *Cyprinella* (Fig. 59D–I) and may have smooth or ornate anterior and posterior margins.

Comparison with outgroups indicates that the shallow interorbital septum in this group is derived. Species of the genera *Luxilus* and *Lythyrurus*, as well as species of many other genera have a deep interorbital septum (Fig. 59A–C). Also derived in *Cyprinella* is the increased proportion of the optic foramen bounded by the orbitosphenoid. This is discussed under the pterosphenoid.

Pterosphenoid (PTS, Figs. 59, 60). These ventrally concave and paired endochondral elements form most of the posterior face of the orbit. Each articulates with the orbitosphenoid anteriorly, frontal and sphenotic dorsolaterally, and prootic posteriorly. Mesially these two bones rarely connect, but form the margins of the large and centrally located optic foramen and part of the more posterior hypophyseal foramen. Posteroventrally each forms the anterior corner of the hyomandibular socket. Stout ventromesially directed struts are formed from this corner, bridging the trigeminal foramen and connecting, in some individuals, with the ascending wing of the parasphenoid and the prootic.

Two conditions of the pterosphenoid vary

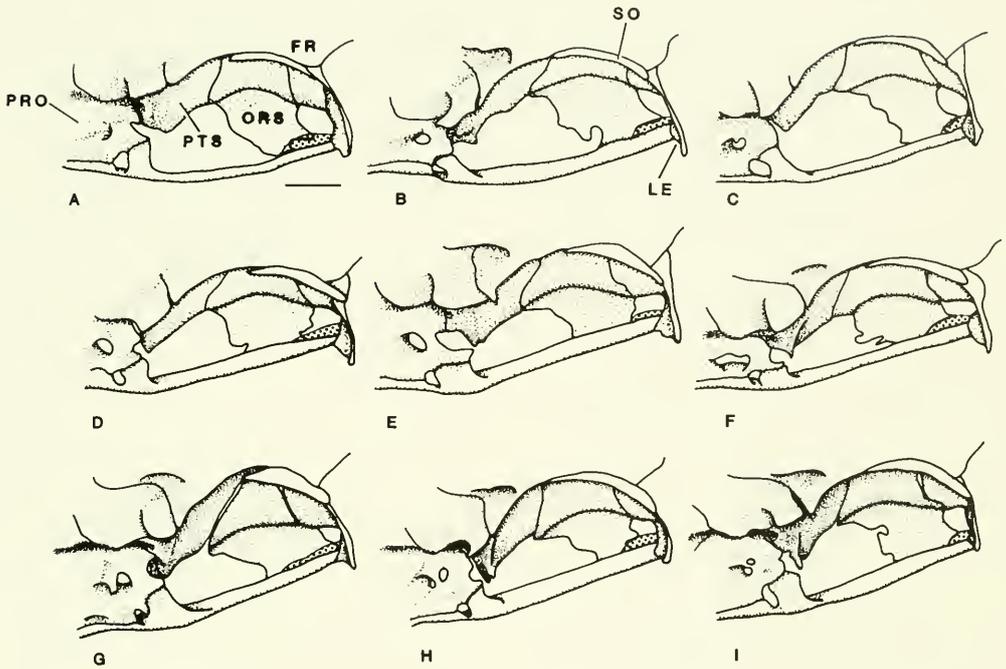


Fig. 59. Lateral view of orbital region in some *Cyprinella* and outgroups. A) *Notropis atherinoides*, 53 mm, KU 18935. B) *Lythrurus fumeus*, 55 mm, KU 6244. C) *Luxilus cardinalis*, 60 mm, KU 15281. D) *Cyprinella venusta*, 58 mm, KU 8810. E) *C. analostana*, 61 mm, INHS 77855. F) *C. nivea*, 59 mm, KU 18987. G) *C. ornata*, 56 mm, KU 8405. H) *C. rutila*, 57 mm, ASU 5982. I) *C. proserpina*, 58 mm, TNHC 3262. Stippled pattern at anterior end of parasphenoid represents posterior extent of planum ethmoidale. Horizontal bar equals 1 mm.

among species of *Cyprinella*, the proportion of the optic foramen formed by the pterosphenoid (and orbitosphenoid) and whether or not a posteromesial process divides the optic and hypophyseal foramina (Fig. 60). In members of the *lutrensis* clade a large proportion of the anterior optic foramen is formed by the orbitosphenoid (Fig. 60B, C), much more than other species of the genus or species of the outgroups (Fig. 60A, D–G).

Posteriorly, the pterosphenoid may or may not produce a mesial process of variable length, depending on the species (Fig. 60). All members of the *lutrensis* group, *spiloptera*, and outgroups lack a process dividing the anterior optic foramen from the posterior hypophyseal foramen (Fig. 60A–C). In members of the *whipplei* clade, excluding *spiloptera*, a process is present (Fig. 60D–G). *Cyprinella camura*, *whipplei*, *analostana*, and *chloristia* have a very small process, *galactura*, *venusta*,

pyrrhomelas, *xaenura*, *trichroistia*, *gibbsi*, *caerulea*, and *callistia* have a longer process, and species of the *nivea* group have an extremely long process, such that they meet medially and completely divide the two foramina.

The development of the mesial process of the pterosphenoid is derived in *Cyprinella* since none of the members of *Luxilus* and *Lythrurus* possess such a structure. The process is, however, in other *Notropis* (i.e., *atherinoides*), but is here considered independent. On a developmental basis, the elongation of the process until it meets its opposite is also considered derived. The decreased proportion of the contribution of the pterosphenoid to the optic foramen in some species is also derived since in closest outgroups the orbitosphenoid has little contribution to the foramen.

Frontal (FR, Figs. 49–60). In most *Cyprinella* the paired frontals are the largest bones

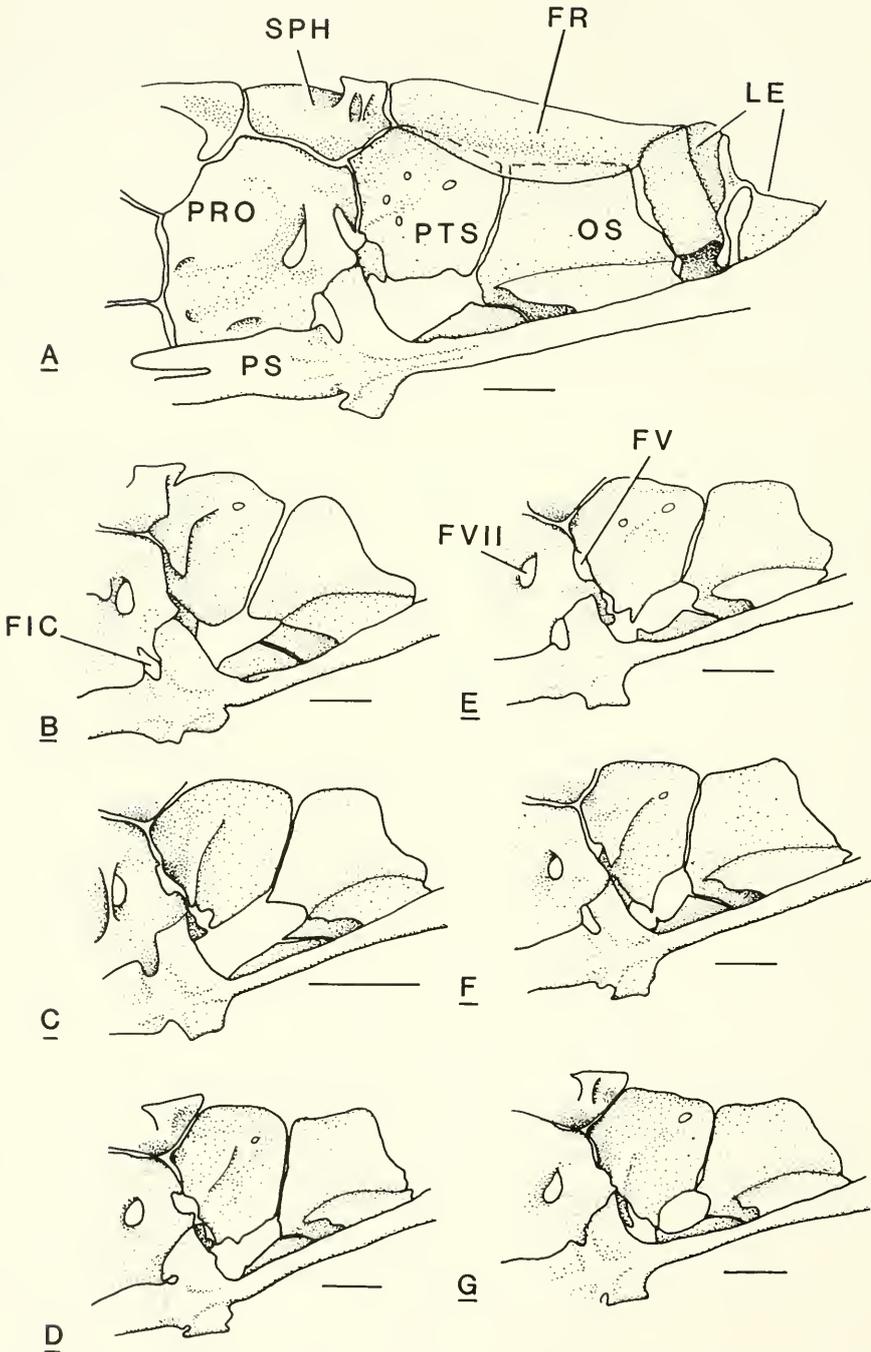


Fig. 60. Ventrolateral view of otic and orbital regions in species of *Cyprinella* and outgroups. A) Orientation view of orbital and otic regions in *Luxilus cornutus*, 60 mm, KU 8686, with primitive morphology. B) *Cyprinella ornata*, 56 mm, KU 8405. C) *C. bocagrande*, 32 mm, KU 20399. D) *C. chloristia*, 54 mm, KU 8882. E) *C. galactura*, 57 mm, KU 12029. F) *C. caerulea*, 60 mm, KU 18978. G) *C. leedsii*, 53 mm, KU 18985. Horizontal bar equals 1 mm.

of the cranium. Although some variation exists, the two bones broadly overlap medially and articulate with the supraethmoid, lateral ethmoids, supraorbitals, and orbitosphenoid anteriorly. Posterolaterally, each overlaps the sphenotic. Posteriorly, articulation occurs with the next largest skull roof bones, the parietals and dermopterotics (Fig. 49).

Shape of the paired frontals is of particular importance in *Cyprinella* and is unlike that of other cyprinids examined. Other cyprinids generally have frontals narrowing anteriorly, the widest aspect being where they contact the sphenotic (Figs. 49, 50A–C). The frontals of *Cyprinella* are typically very wide along their entire length (e.g., Fig. 50D). Little narrowing or mesial incurving of these bones occurs laterally above the orbits. Together with the supraorbitals, the expanded frontals produce a lateral margin of the cranium that is quasi-parallel to the body axis. This condition is modified to some degree in certain groups within *Cyprinella* where the skull is highly domed. In these forms (*proserpina*, *panarcys*, *rutila*, and *xanthicara*) a dorsal aspect of the frontals does not appear as wide (Fig. 51). A more primitivelike state appears in some species of the *nivea* species group. In these species the frontals are more narrow (Fig. 56). Generally, however, all *Cyprinella* have broad frontals, especially over the orbits where there is no constriction, typical of other cyprinids examined.

Also typical of species in this genus is the truncation of the anterior margins of the frontals where the supraethmoid articulation occurs (Figs. 50–56). The truncated anterior margins and broad frontal morphologies are derived in *Cyprinella*. The primitive condition is to have angled anterior margins (Fig. 50) and narrow frontals as in *Phenacobius*, *Rhinichthys*, *Nocomis*, *Hybopsis*, *Lythrurus*, *Notropis* (s.s.) and *Luxilus*.

Primitively within *Cyprinella*, the overall outline of the frontals, plus supraorbitals, is rectangular with squared-off front and sides. In some species of *Cyprinella* this overall outline is modified towards a more or less

rhomboidal shape. This is accomplished by broadening the occipital region of the cranium and angling the lateral margins of the frontals, such that the widest point is posterior. Moving anteriorly, the straight edges of the frontals (not incurved) narrow to a truncated anterior margin. Species with this pattern include *whipplei*, *analostana*, *chloristia*, *galactura*, *venusta*, *caerulea*, *pyrrhomelas*, *trichroistia*, *gibbsi*, *nivea*, *leedsi*, *callisema*, *callitaenia*, and *callistia*. *Cyprinella xanura* has a frontal morphology of parallel lateral margins, producing a more primitive morphology as in the *lutrensis* clade.

In most species the frontals are fairly flat dorsally with only slight decurving laterally to where they articulate with the orbitosphenoids. In lateral aspect, over the orbit and lateral to the orbitosphenoid connection they are slightly arched upward with the highest point being lateral and slightly anterior to the epiphyseal bar. Anterior and posterior to this point the bones curve downward with the lowest point being where they articulate with the sphenotic spine. In *lepida*, *xanthicara*, *rutila*, *proserpina*, and *panarcys* frontals are strongly domed over the orbits (Figs. 51, 59). This condition is most extreme in *panarcys* and *proserpina*, especially the former. The supraorbitals of these species are also strongly decurved (Fig. 59). Further, in these two species the skulls are highly domed mesially, the highest point being where the frontals unite. A similar condition, but less extreme, is found in *whipplei*, *analostana*, and *chloristia*. This highly arched orbit and domed cranial condition derived in *Cyprinella*, but independent in the two groups.

Posteriorly, the frontals may or may not contact the dermopterotics. Members of the *lutrensis* clade, except *rutila*, and *spiloptera*, *camura*, *whipplei*, *analostana*, *chloristia*, *pyrrhomelas*, *callisema*, and *callitaenia* have a connection between the frontals and dermopterotics. The remaining species have no connection, because either the dermopterotic or the frontals are not long enough (usually the former), or, as in species of the *nivea* group, the parietals extend some distance between the

frontals and dermopterotics. In the *nivea* group this is partially a function of the shape of the dermopterotic, with a convex mesial edge, and the parietals, with a concave lateral edge where they meet. The connection between the frontals and dermopterotics is derived for *Cyprinella*, but is reversed within the *whipplei* clade. Outgroup taxa and other species of this genus lack this connection (Fig. 50).

Supraorbital (SO, Figs. 49–56). There is one supraorbital per side situated lateral to the frontals. In *Cyprinella* these bones are generally long and broad with an acute posterior margin. The lateral margins are fairly straight and the mesial margins are convex, producing the broadest aspect anteriorly. This condition is derived for *Cyprinella*. Close outgroups typically have narrow supraorbitals with both the anterior and posterior ends being equal in width and both narrowing at their extremes. In more distant outgroups such as *Rhinichthys*, *Nocomis*, and *Hybopsis*, the supraorbitals are oval.

Narrowing of the supraorbitals has occurred secondarily in *panarcys*, *proserpina*, *rutila*, *xanthicara*, *chloristia*, *whipplei*, *caerulea*, *nivea*, *leedsi*, and *callitaenia*. *Cyprinella callisema* also has narrow supraorbitals, but they are shortened. *Cyprinella gibbsi*, *trichroistia*, and *camura* share extremely long and broad supraorbitals. *Cyprinella pyrrhomelas* and *xaenura* both have short and broad supraorbitals.

Association of supraorbitals with the lateral ethmoids and frontals is variable in *Cyprinella*. Species with no connection between the lateral ethmoid and supraorbital include *ornata*, *lutrensis*, *lepida*, *galactura*, *caerulea*, *xaenura*, *pyrrhomelas*, *trichroistia*, *gibbsi*, and species of the *nivea* species group. *Cyprinella camura*, *whipplei*, *analostana*, *chloristia*, *venusta*, and *formosa* have only a slight overlap. Most individuals of *spiloptera* and *garmani* have no overlap between these elements. Other individuals have overlap on one side but not the other. These species are considered to have a non-overlapping pattern. *Cyprinella rutila*, *xanthicara*, *proserpina*, and *panarcys* have

considerable overlap between the supraorbitals and lateral ethmoids, completely covering the dorsal edge.

Overlap of supraorbitals with the frontals varies between species from none to slight. Species with no overlap or with the supraorbitals abutting the edge of the frontals include *spiloptera*, *galactura*, *venusta*, *whipplei*, *trichroistia*, *gibbsi*, *nivea*, *leedsi*, *callistia*, *proserpina*, and *panarcys*. Species with slight overlap include *lutrensis*, *garmani*, *rutila*, *lepida*, *formosa*, *xanthicara*, *camura*, *analostana*, *chloristia*, *caerulea*, *xaenura*, *pyrrhomelas*, *callisema*, and *callitaenia*. *Cyprinella ornata* also has overlap of these bones, but in this species the frontals overlap the supraorbitals.

Overlap between the supraorbitals and the lateral ethmoids is derived in this genus. Close outgroups lack this condition. The overlap of the supraorbitals and frontals appears to be informative in *Cyprinella*, but variability in outgroups precludes determination of polarity at this time.

Infraorbital series (LA, IO 2–6, Figs. 61–63). This series of dermal, platelike bones extends from the nasal cavity posteroventrally down around the orbit and up to the sphenotic and pterotic, behind the orbit. Generally there are six elements in the series, each bearing part of the infraorbital canal as a bony tube fused to the lateral surface. The lacrymal (LA) (Fig. 61) is the first of the series and is the largest. This element is lateral to the nasal cavity, maxillary, and palatine, and is supported by the latter element mesially. The remaining five infraorbital elements (IO 2–6) are generally thinner and in some cases more elongate. The second is thin and may be short or long, depending on the species. The third is lunate in shape with anterior and ascending arms and may be broad. The fourth element is short and broad. The fifth and sixth elements are generally the smallest of the series and may be reduced to only the bony canal tube. These elements are not illustrated here, but are in line with the posttemporal canal and lateral to the temporal fossa (see Harrington, 1955).

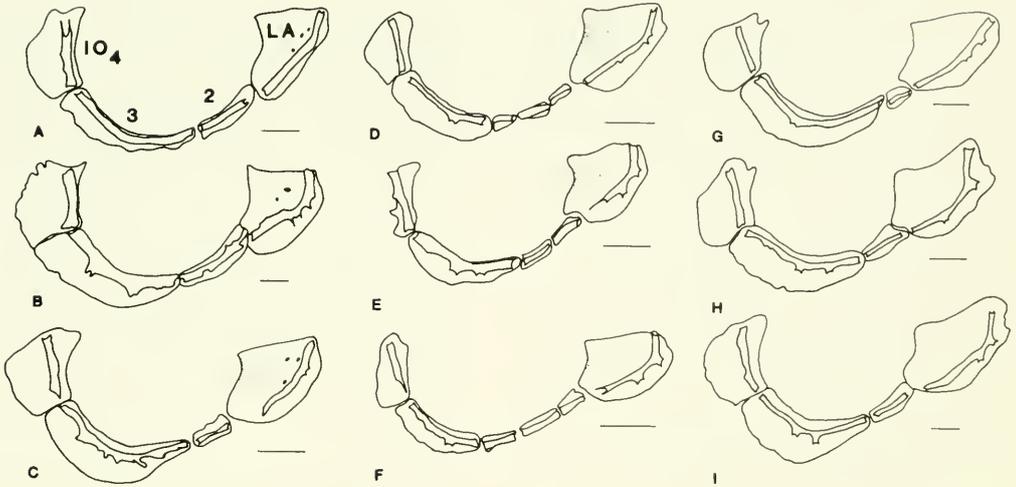


Fig. 61. Infraorbital series of some species of *Cyprinella* and close relatives. Infraorbitals 5 and 6 are not illustrated. A) *Lythrurus fumeus*, 56 mm, KU 6244. B) *Luxilus cardinalis*, 82 mm, KU 15281. C) *Cyprinella lutrensis*, 55 mm, KU 19431. D) *C. lepida*, 48 mm, TU 55189. E) *C. panarcys*, 43 mm, UMMZ 208212. F) *C. xanthicara*, 41 mm, ASU 3642. G) *C. spiloptera*, 68 mm, KU 17776. H) *C. galactura*, 73 mm, KU 12029. I) *C. venusta*, 84 mm, KU 8810. Horizontal bar equals 1 mm.

The origin of infraorbital 5 and 6 is controversial. Swift (1970) considered the fifth and sixth elements to be the dermosphenotic, while Harrington (1955) and Howes (1978) equated the fifth with this element. Because the sixth element is frequently attached to the dermopterotic and the fifth lies lateral to the sphenotic spine and carries the posterior curvature of the infraorbital canal, typical of the dermosphenotic, Coburn (1982) considered the fifth element and the dermosphenotic to be homologous. This argument is followed here.

Some elements of the infraorbital series are considerably variable between species of *Cyprinella*. Other elements vary, but intraspecific variation is as great as interspecific variation and is of no use systemically. Only the lacrymal and infraorbital 2, 3, and 4 varied systematically. Variation in the lacrymal includes length and contour of the bone and shape of the fused bony canal. Infraorbitals 2, 3, and 4 vary in width, length, and number of elements.

The lacrymal size is represented in *Cyprinella* by three conditions, short, long, and extremely long (Fig. 62). Short lacrymals are found in the *lutrensis* clade, *trichroistia*, *gibbsi*,

caerulea, and *pyrrhomelas* (Fig. 62). The long lacrymals are found in *spiloptera*, *xaenura*, and the *whipplei* and *venusta* species groups. The extremely long lacrymal is unique to the *nivea* species group. Perhaps correlated with the length of the lacrymal is the orientation of the lateral canal. In members of the *lutrensis* clade, *spiloptera*, the *whipplei* and *venusta* species groups, and the *pyrrhomelas* species pair the lateral canal is smoothly arched dorsally, like outgroup taxa. In the *caerulea* species complex the canal is straight and oblique and in the *nivea* species group it is L-shaped (Fig. 62).

In members of the *whipplei* clade the lacrymal is flat, while species of the *lutrensis* clade have a curled lacrymal, posterior to the canal. In all *Cyprinella* except *galactura* and *venusta* the dorsal margin of the lacrymal is fairly straight. These two species have an elevated dorsoanterior margin. Orientation of the lacrymal is consistent in the genus, except in *callistia*, *callitaenia*, and *callisema*. Typically it is nearly horizontal, like other cyprinids examined, but in these three species it is tilted ventrally (Fig. 63).

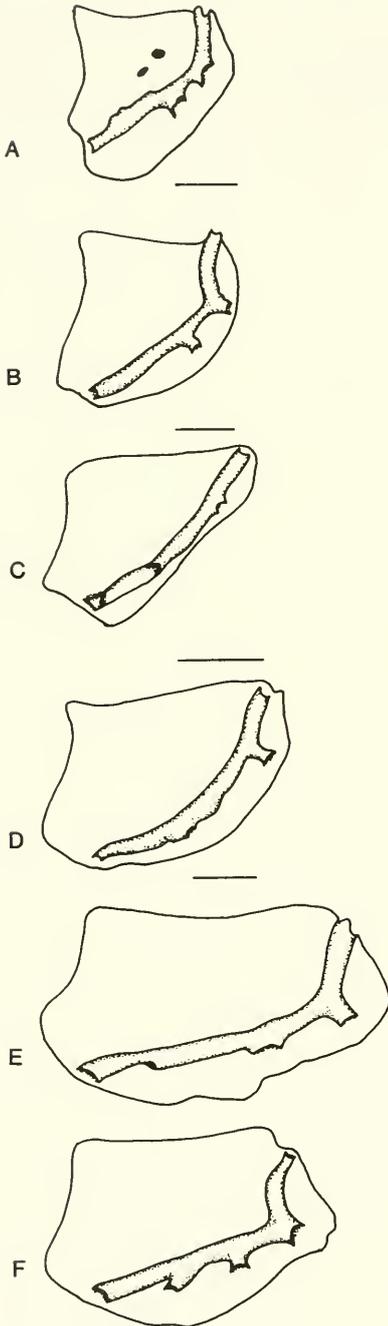


Figure 62. Lacrymal bone in some species of *Cyprinella* and close relatives. A) *Luxilus cardinalis*, 82 mm, KU 15281. B) *Cyprinella pyrrhomelas*, 70 mm, INHS 76978. C) *C. gibbsi*, 58 mm, KU 18892. D) *C. spiloptera*, 68 mm, KU 17776. E) *C. nivea*, 62 mm, KU 18987. F) *C. nivea*, 40 mm, KU 18987. Horizontal bar equals 1 mm.

Most species of the genus and outgroup taxa have an elongate second infraorbital. This bone is short in all members of the *lurensis* clade. Within the *lurensis* clade infraorbital 2 and the anterior arm of infraorbital 3 are broken into two or three smaller elements in the *lepida* species group (Fig. 61). Other members of this clade, species of the *whipplei* clade, and species of close outgroups all have a complete and long anterior arm to the third infraorbital. *Cyprinella panarcys* is unique in the genus in having a very thin infraorbital 4 (Fig. 61). In other species of *Cyprinella* this element is large and platelike, like members of the genus *Luxilus*.

Compared with close outgroups and some distant outgroups, all species of *Cyprinella* share an elongate lacrymal that is derived for the genus. Even species of *Cyprinella* with short lacrymals have lacrymals longer than immediate outgroups, relative to body length. Furthermore, within the genus the long and extremely long lacrymal morphologies are considered to be increasingly derived. This is supported developmentally. Young of species with the extremely long condition have lacrymals equal in length and shape to species with the long morphology (Fig. 62). The smoothly arched canal of the lacrymal is primitive in *Cyprinella*, since most species outside this group have this morphology. The straight and L-shaped canals are derived from this condition. The concave or curled lacrymal is derived within *Cyprinella*, based on outgroup and developmental criteria. In close outgroups and young of species with the curled lacrymal this element is flat. An elevated anterodorsal corner to the lacrymal and a ventrally tilted lacrymal are derived within the genus. No outgroup taxa examined thus far have either of these two conditions.

OTIC AND OCCIPITAL REGIONS

The 10 bones of the otic and occipital regions are of varied origin (Figs. 33, 59, 60, 64, 65). The supraoccipital is unpaired and all others are paired. The sphenotic (autosphentic), pterotic (autopterotic), exoccipital,

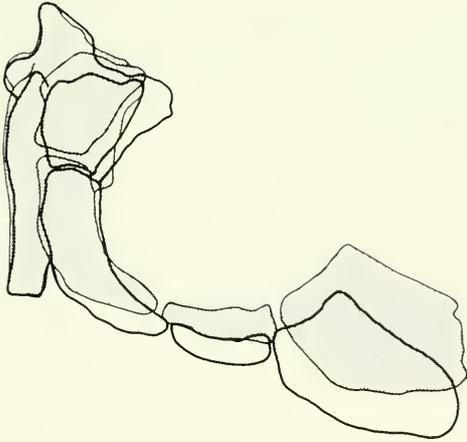


Figure 63. Ventrally deflected orientation of infraorbital series in *Cyprinella callistia*, *C. callisema*, and *C. callitaenia*. Stippled series and hyomandibular is *C. nivea* (58 mm, KU 18987) and represents primitive condition. Outlined infraorbital series and hyomandibular is *C. callisema* (56 mm, KU 8842) and is the derived condition.

epiotic, and the main bone of the supraoccipital are all cartilage bones. The dermosphenotic is dermal, free from the sphenotic, and represents the fifth element of the infraorbital series. The dermopterotic is dermal and fused to the pterotic. The parietals are dermal and the intercalar and crest of the supraoccipital are membrane bones. The bones from these regions form the posterior neurocranium ventrally, ventrolaterally, and posteriorly.

A characteristic shared by all species of *Cyprinella* is a compressed and vertical occipital region, when viewed laterally (Fig. 33B,C). Members of the *lutrensis* clade are most extreme in this morphology. Species of the close outgroups *Luxilus* and *Lythrurus*, and those of the more distant outgroups *Notropis* (s.s.), other unresolved *Notropis*, *Alburnops*, *Phenacobius*, *Hybopsis*, and *Rhinichthys* all have a more elongate occipital region, principally due to the elongation of the supraoccipital, exoccipitals, pterotics, and epiotics (Fig. 33A).

Sphenotic (SPH, Figs. 49–56, 64). These paired endochondral elements are located laterally, behind the orbit and articulate with four

or five surrounding elements. Anteriorly they articulate with the frontals and pterosphenoid, dorsally with the frontals and sometimes with the parietals, posteriorly with the pterotic, and mesoventrally with the prootic. Located lateral to the sphenotic are the last two elements of the infraorbital series, the penultimate element representing the dermopterotic. This element is discussed under the infraorbital section. The most obvious feature of the sphenotic is the posteroventrally directed process. The dorsal surface of this sphenotic process and the lateral surface of the sphenotic form part of the origin surface of the *dilatator operculi*. Ventrally, the entire mesial surface forms the lateral half of the anterior and much of the posterior hyomandibular sockets. No significant interspecific variation of the sphenotic morphology occurs in this genus.

Prootic (PRO, Figs. 59, 60, 64). The prootics are large, irregularly shaped endochondral elements that form much of the ventral neurocranium. Posteriorly on each side, each is in contact with the exoccipital and pterotic and together the three surround the subtemporal fossa. Posteromesially, the prootic is expanded ventrally and articulates with the anterior margin of the basioccipital, forming the anterior end of the *recessus sacculi*. Laterally, the prootic contributes to the anterior and posterior hyomandibular sockets. Mesially it is in contact with the parasphenoid ventrally and its opposite dorsally, contributing to the roof and side walls of the posterior myodome and part of the floor of the neurocranium. Anteromesially the prootic projects dorsally and together with the pterosphenoid forms the margins of the centrally located hypophyseal foramen. These bones also surround the anterolateral trigeminal foramen (FV), the prootic forming the posterior margin and the pterosphenoid generally forming the anterior rim.

The ventral surface of the prootic is very irregular and complex. Anteriorly, lateral to the ascending wings of the parasphenoid, is the lateral commissure, a broad lamella of bone forming a ventrally depressed bridge separating the facial and trigeminal chamber.

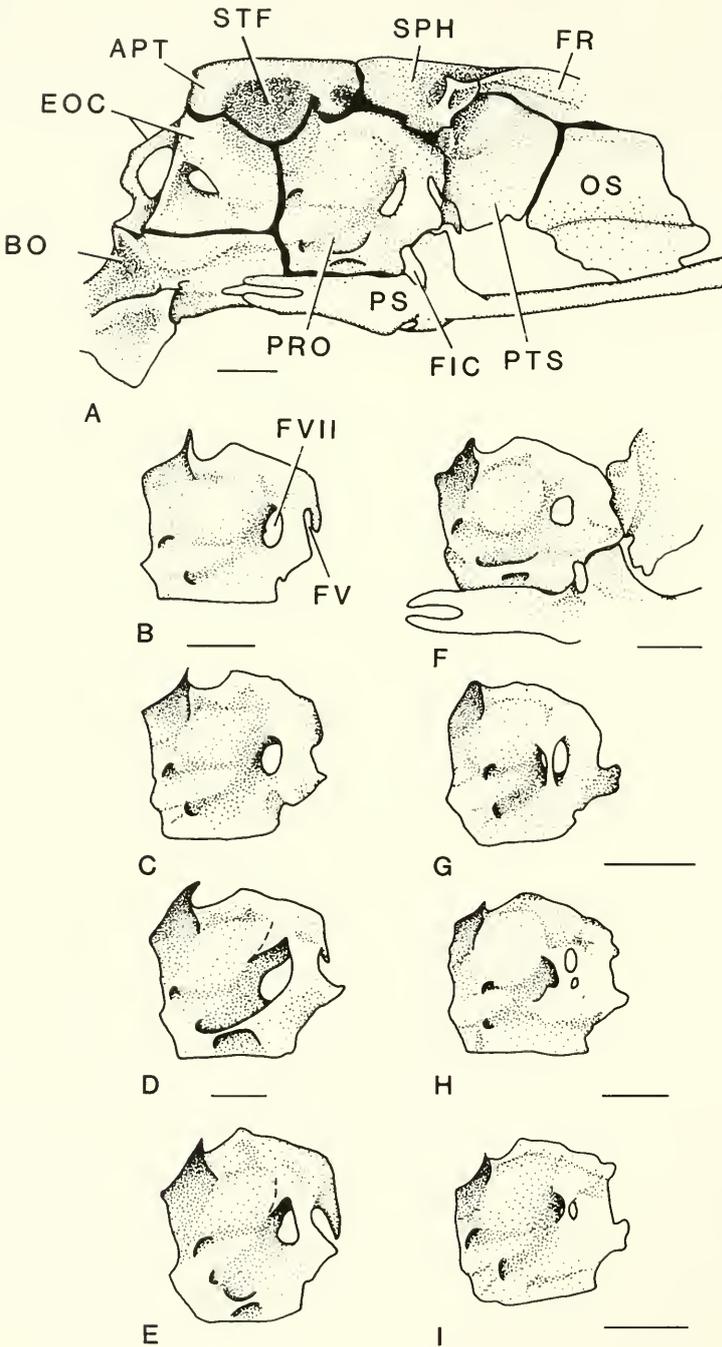


Fig. 64. Ventrolateral view of prootic in species of *Cyprinella* and outgroups. A) Ventrolateral view of otic and occipital regions of *Luxilus cornutus*, illustrating position of prootic and primitive morphology. B) *Lythrurus fumeus*, 55 mm, KU 6244. C) *Cyprinella spiloptera*, 56 mm, KU 17776. D) *C. xaenura*, 75 mm, KU 76978. E) *C. pyrrhomelas*, 70 mm, INHS 76978. F) *C. callisema*, 52 mm, KU 8842. G) *C. bocagrande*, 32 mm, KU 20399. H) *C. ruila*, 57 mm, ASU 5982. I) *C. xanthicara*, 49 mm, ASU 3642. Horizontal bar equals 1 mm.

Laterally, it is raised to contribute to the hyomandibular socket and posteriorly much of the surface is expanded ventrally to form the

bulla acoustica utricularis which contains the lapillus otolith.

No variation in overall shape occurs in

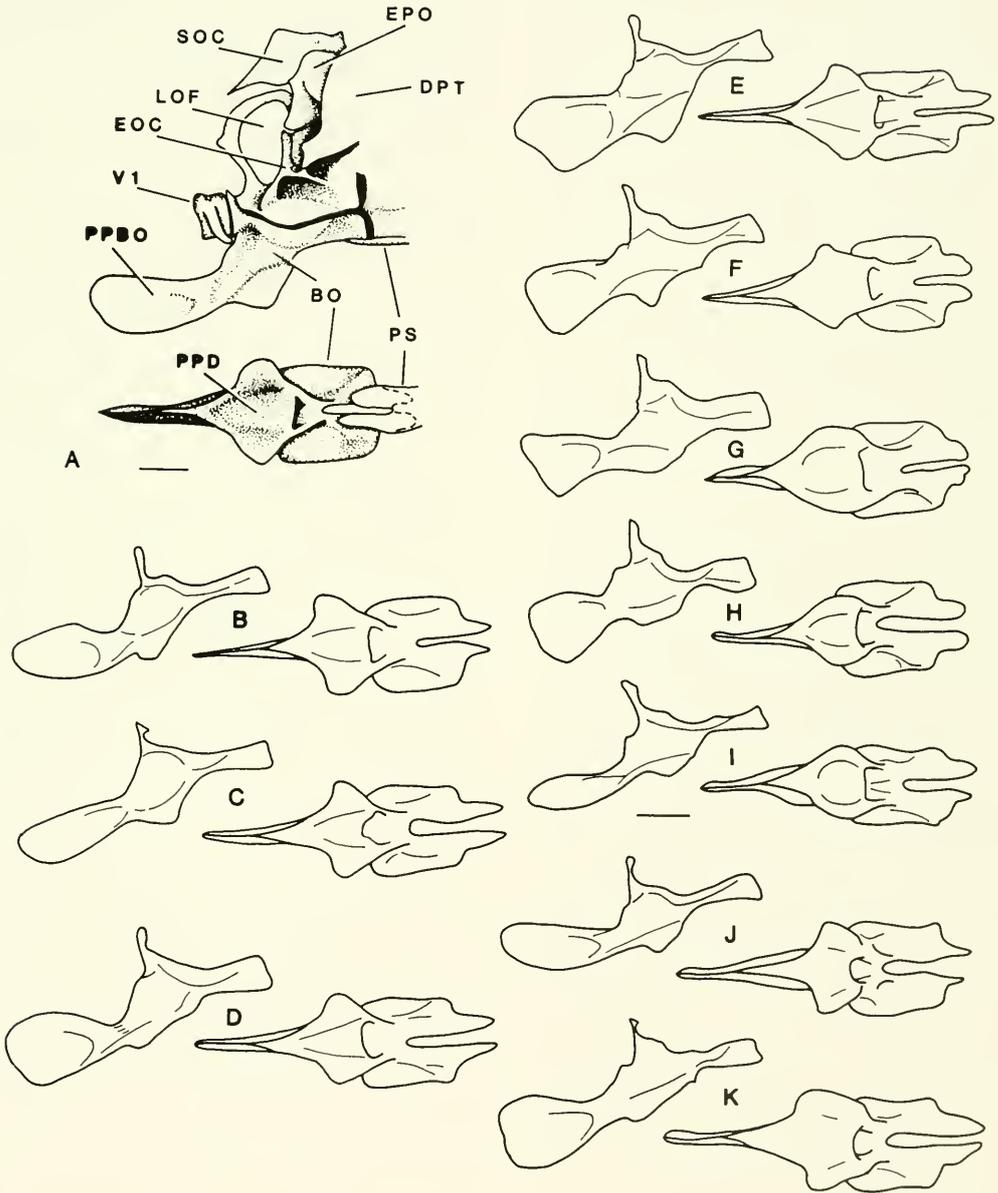


Fig. 65. Lateral and ventral views of the basioccipital of species of *Cyprinella* and related taxa. A) lateral view of basicranium and ventral view of basioccipital of *Luxilus cornutus*, 60 mm, KU 8686. B) Basioccipital of *Cyprinella camura*, 45 mm, KU 15792. C) *C. chloristia*, 54 mm, KU 8882. D) *C. analostana*, 61 mm, INHS 77855. E) *C. lutrensis*, 55 mm, KU 19431. F) *C. garmani*, 50 mm, KU 5416. G) *C. formosa*, 47 mm, KU 8399. H) *C. panarcyis*, 44 mm, UMMZ 208212. I) *C. rutila*, 57 mm, ASU 5982. J) *C. trichroistia*, 60 mm, KU 18853. K) *C. gibbsi*, 57 mm, KU 19982. Horizontal bar equals 1 mm.

Cyprinella. Some species develop a variably sized lateral commissure. In others a narrow, internal jugular strut (Howes, 1979) is developed which bridges the facial foramen. Species with the jugular strut include *bocagrande*, *formosa*, *lepida*, *rutila*, *xanthicara*, *proserpina*, and *panarcys*. In all these species, except *rutila*, the strut is narrow (Fig. 64). In *rutila* it is broad, covering most of the trigeminal foramen (FV). Species with a process off the lateral face of the trigeminal foramen, directed ventromesially, include *ornata*, *lutrensis*, *garmani*, *analostana*, and *chloristia* (Fig. 64).

The lateral commissure is broad in most species. In *xaenura* and *pyrrhomelas* it is more narrow, especially in the latter. In these two species a shelf is formed posterolateral to the lateral commissure, covering the normally depressed region between the trigeminal foramen and the expanded *bulla acoustica utricularis*.

In all species except *pyrrhomelas* and *xaenura* the anterior margin of the trigeminal foramen is bordered solely by the pterosphenoid. The foramen in these two is bounded anteroventrally by a ventrally directed process of the prootic like most other cyprinids examined.

The lateral strut or process crossing the facial foramen is derived within *Cyprinella* since closest outgroups examined lack this feature. The complete strut is also considered derived over the process since juveniles of these species have only the process. The narrow lateral commissure and posterior shelf in *xaenura* and *pyrrhomelas* are derived. Outgroups typically have a broad commissure like other *Cyprinella*. The posterior shelf is unique to this species pair. Having the trigeminal foramen bounded anteriorly by the pterosphenoid only is considered derived since species of *Luxilus* and *Lythrurus* have the anterior border composed of both the pterosphenoid and prootic, like *xaenura* and *pyrrhomelas*.

Dermopterotic (DPT, Figs. 49–56, 59, 60, 65). The dermopterotics are paired dermal ossifications overlying the endochondral autopterotics. Anteriorly, they have varying degrees of articulation with the sphenotics and

may overlap these bones. Posteriorly, the dermopterotics overlap the epiotics. As discussed previously, they may or may not articulate with the posterolateral margins of the frontals. Medially these paired bones articulate with the parietals and posteriorly they contact the epiotics and the paired posttemporals.

Within *Cyprinella* the dermopterotics may or may not extend over the lateral edge of the autopterotic and autosphenotic. If expanded, they form a small to fairly large roof over the dilator fossa where the *levator operculi* and *adductor operculi* muscles originate. Species with a roofed dilator fossa include members of the *lutrensis* clade, *spiloptera*, *camura*, *analostana*, *galactura*, and *venusta*. All other *Cyprinella* have no bony extension over the dilator fossa. The lack of a bony extension is derived within *Cyprinella*. Outgroups almost always develop this shelf.

The shape and orientation of the dermopterotic is diagnostic within *Cyprinella*. Generally, two basic orientations exist. Either there is a fairly shallow slope of the bone laterally, giving the occipital region a more or less flattened aspect or the dermopterotic slopes laterally at a much greater angle, producing a steep-sided occipital region. The flattened condition is present in most *Cyprinella* and close outgroups. Species with the steeper sided, more highly angled condition include *whipplei*, *analostana*, *chloristia*, *lutrensis*, *garmani*, *lepida*, *formosa*, *bocagrande*, *proserpina*, *panarcys*, *xanthicara* and to a lesser degree *rutila*. *Cyprinella ornata* has the flattened condition. Extremes of both conditions also exist. *Cyprinella gibbsi*, *trichroistia*, and *caerulea* all have a more depressed occipital condition, and *lepida*, *xanthicara*, *proserpina*, and *panarcys* have a more vertical aspect with the most extreme condition being in *panarcys*.

The pattern of articulation of the dermopterotic and the parietals varies somewhat between and within species, but generally two conditions exist. The first condition is to have a fairly straight articulation between the two elements. The second condition and here considered derived, is to have a concave bor-

der to the parietals and a convex border on the dermopterotic, such that the appearance is to have the dermopterotic invading the parietals. Species with this condition but fairly weakly developed include *spiloptera*, *caerulea*, *xaenura*, *pyrrhomelas*, *trichroistia*, *gibbsi*, and *callistaenia*. *Cyprinella nivea*, *leedsi*, *callisma*, and *callistia* show a strong intrusion pattern.

Fused to the dermopterotic is the lateral posttemporal canal. This canal extends longitudinally and connects with the laterally directed supratemporal canal. Together these two canals merge into one posttemporal canal on the posttemporal or dermopterotic bone. The lateral posttemporal canal has a pore at each end and one in the middle. The posttemporal canal has one medial pore and a single pore at either end.

Autopterotic (APT, Fig. 64). Located posterolaterally on the skull, this endochondral ossification fits between the anterior sphenotic and the posteromesial epiotic and exoccipital. Posteriorly it forms the lateral margin of the posttemporal fossa together with the exoccipital and epiotic, and mesially partakes in the posterior hyomandibular socket as well as forming the lateral rim of the subtemporal fossa. The most conspicuous feature of this bone is the spine and mesial shelf from the spine produced from its posterolateral corner. This spine is connected by ligaments to the supracleithrum and posttemporal. Ventrolaterally, the autopterotic contains the lateral semicircular canal. Ventrally the intercalary articulates with the main body of the autopterotic as well as the mesial shelf of the posterolateral spine.

The size of the autopterotic spine and posttemporal fossa vary in *Cyprinella*. All species, except *panarcys*, have a well-developed spine. In this species the spine is reduced to a small process (Fig. 66). The posttemporal fossa is large in all species except the *caerulea* species complex. In these species the epiotic and dermopterotic are compressed ventrally, reducing the size of the fossa (Fig. 66).

The reduced spine and posttemporal fossa

in *Cyprinella* is derived. All species examined outside of this group have a well-developed fossa and all close outgroups develop a long autopterotic spine.

Parietal (PA, Figs. 33, 49–56, 66). The parietals are large paired, dermal bones which cover much of the posterior of the cranium. They are typically rectangular and articulate medially with one another, anteriorly with the frontals, laterally with the dermopterotics, and posteriorly with the epiotics and supraoccipital. These bones overlie portions of the supraoccipital, autosphenotics, autopterotics, and epiotics.

Variation exists in the lateral margins of the parietals as discussed previously in reference to the dermopterotics and in the posterior margins where they meet with the supraoccipital and epiotics. In the *lutrensis* clade a very definite ridge is developed between where the parietals terminate posteriorly and where they meet with the supraoccipital. This ridge also extends onto the dorsal surface of the parietals in an arch generally following the arc pattern of the lateral margins of the supraoccipital crest. In this clade the parietals also extend more posteriorly and cover the dorsal and anterior portion of the supraoccipital crest. This posterior extension is magnified even more in *panarcys*, *proserpina*, *xanthicara*, and *rutilla*. Other species of *Cyprinella* also have this but its development is not as great. These taxa also have their parietals ending before the supraoccipital crest and no shelf is formed over the epiotics; much of the medial supraoccipital and its crest are exposed.

Fused to the posteriormost margin of the parietals and along the rim of the previously mentioned ridge is the supratemporal canal. This canal is variably shaped within and between species of *Cyprinella*.

Exoccipital (EOC, Figs. 33, 49–56, 64–66). These paired, endochondral elements form most of the occipital region of the skull. They articulate ventromesially with the basioccipital. Above the basioccipital a shelf is formed from mesial extensions of both bones. This shelf forms the floor of the posterior neurocranium.

nium and foramen magnum, and the roof of the paired recessi sacculi and the median cavum sinus impar. Dorsally, in addition to the large and tear-shaped foramen magnum, two large lateral occipital foramina are developed, one on each side of the midline. Lateral to these the exoccipital is expanded posteriorly and contains the horizontal semicircular canal. The dorsal margin of the exoccipital abuts against the supraoccipital mesially and epiotic and pterotic laterally. Anteriorly, it forms part of the subtemporal fossa and articulates with the prootic and parasphenoid.

Except for the exoccipitals being elevated mesially in the *lutrensis*, *formosa*, and *lepida* species groups, relative to other *Cyprinella* and outgroups, the morphology of this element is consistent throughout the genus. As discussed above, this modification of the exoccipital is correlated with the elevation of the entire occipital region.

Epiotic (EPO, Figs. 33, 66). Located dorsolaterally above the exoccipitals, these endochondral bones fit between the mesial unpaired supraoccipital and the lateral pterotics. Posteriorly, it is expanded and contains part of the horizontal semicircular canal. The anterior surface forms part of the inner subtemporal fossa and the anterior wall encloses the semicircular canal. Projecting posteriorly from the expanded epiotic enclosing the canal is a bony process for the insertion of epaxial muscles. Laterally, above the posttemporal fossa a second and larger bony process is formed. This process together with the posttemporal and pterotic forms the roof of the posttemporal fossa.

Variation in this element is minimal. Only members of the *caerulea* species complex varied significantly. These species all share a dorsoventrally compressed posterolateral epiotic where this element contributes to the posttemporal fossa (Fig. 66). All other species have epiotics similar to outgroup taxa. Thus, as mentioned above, the compressed posttemporal fossa is derived in this genus.

Supraoccipital (SOC, Figs. 33, 49–56, 65, 66). The supraoccipital is an unpaired bone of

compound origin (Patterson, 1977). It is composed of a large expanded and roughly triangular base and a vertical crest posteriorly. The base is endochondral and the crest is membrane bone. Anteriorly, the supraoccipital articulates with and extends beneath the parietals. Laterally and posterolaterally it broadly articulates with the epiotics and exoccipitals, respectively, and partially roofs the foramen magnum. Dorsomesially it is concave and anteriorly it is convex. Medially, a well-developed ridge is formed from an expansion to accommodate the posterior semicircular canal. Epaxial muscles are attached to the posterior face of the base of the supraoccipital and ligaments from the Weberian apparatus and predorsal bones are attached to the crest. Except for the compressed supraoccipital, typical of all species of *Cyprinella*, no significant interspecific systematic variation occurs in the morphology of the supraoccipital. Within a species a horizontal plate may be formed on the dorsal surface of the crest.

Intercalar (IC). The intercalar is a small, crescentic endochondral ossification ventral to the autopterotic. Generally, it lies under the mesial side of the autopterotic spine and extends up under the posteroventral margin of the same bone. Occasionally, it may even extend over the suture between this bone and the exoccipital. No interspecific variation of systematic significance was noted for this bone in *Cyprinella*.

BASICRANIAL REGION

Two bones comprise the basicranial region, the basioccipital and the parasphenoid (Figs. 59, 60, 64–66). Both bones are unpaired and together span the entire length of the neurocranium ventrally. The basioccipital is a cartilage bone and the parasphenoid is a dermal bone. Both elements serve as attachment areas for dorsal gill arch muscles and form the floor, roof, and some walls of the neurocranium and posterior myodome.

Basioccipital (BO, Figs. 33, 64–66). This bone is located posteroventrally on the cranium and articulates with the parasphenoid

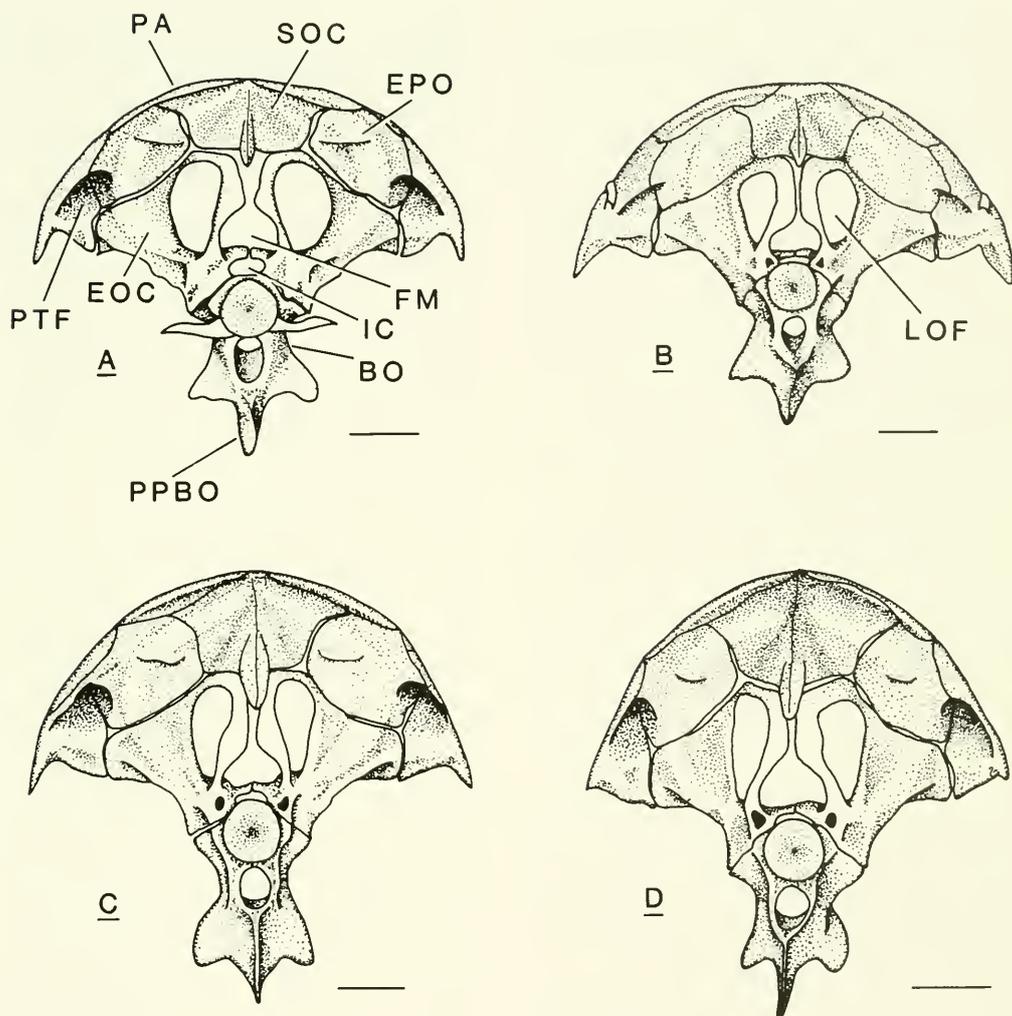


Fig. 66. Posterior view of cranium of species of *Cyprinella*. A) *C. callisema*, 52 mm, KU 8842. B) *C. gibbsi*, 57 mm, KU 18892. C) *C. lutrensis*, 55 mm, KU 19431. D) *C. panarcys*, 44 mm, UMMZ 208212. Horizontal bar equals 1 mm.

and prootic anteriorly, the exoccipital laterally, and via the proatlas, the first vertebral centrum posteriorly. The posterior myodome is partially contained in the basioccipital where it forms much of the posterior walls, roof, and floor. Also contained posteriorly is the *recessus sacculi* which houses the posterolaterally located astericus and the anteromesially located sagitta. The exoccipital forms the roof and most of the lateral surfaces of this cavity. The location of the *recessus sacculi* can be noted by the obvious ventral expansion of the

basioccipital and exoccipital forming a bulge in the cranium, the *bulla acoustica lagenaris*. Mesially, the basioccipital also forms the floor and walls of the *cavum sinus impar*.

Anteriorly, the basioccipital is forked, producing two processes extending above the posterior parasphenoid, and forms the posterior rim of the oval, centrally located opening in the floor of the posterior myodome. Posteroventrally the pharyngeal process of the basioccipital is developed. This large process is laterally compressed posteriorly, forming a

vertical plate with a rounded posterior edge. Anteriorly this vertical plate widens ventrally into a semi-horizontal, concave masticatory plate which opposes the pharyngeal teeth. Dorsal to the plate is a supporting arch and canal formed between the pharyngeal process of the basioccipital and the dorsal portion of the basioccipital, through which passes the dorsal aorta.

The shape of the dorsal portion of the basioccipital is consistent in *Cyprinella*, but the morphology of the pharyngeal process varies systematically between species (Fig. 65). All species have concave ventral surfaces to the masticatory plate, except *lepida*, *garmani*, *pyrrhomelas*, *xaenura*, *caerulea*, *gibbsi*, and *trichroistia*, which have a relatively flat ventral surface. Most species develop a pharyngeal pad with two lateral to posterolateral wings and a pointed posterior margin. In *formosa*, *lepida*, *panarcys*, *proserpina*, *xanthicara*, and *rutila*, however, the pad is oval in shape, lacking the lateral wings.

All species of the *lutrensis* group, except *xanthicara* and *rutila*, have a deep, triangular pharyngeal process (Fig. 65). These two species have a very narrow and elongate process. All other members of the genus except *analostana* and *gibbsi* develop a narrow process like the outgroups. These two species have a deep, spatulate and rounded process.

The deep, triangular pharyngeal process of the *lutrensis* clade is derived since no outgroups have this morphology. The rounded pharyngeal pad is also derived, being found in this group and convergently in some members of the genera *Phoxinus* and *Pimephales*. The deep and rounded pharyngeal process of *analostana* and *gibbsi* is also derived but independent.

Parasphenoid (PS, Figs. 57–59, 64, 65, 67). This elongate dermal ossification extends most of the length of the neurocranium ventrally. Anteriorly it is spatulate and lies above the vomer and below the posterior planum ethmoidale, ventromesial to the lateral ethmoids, and posterior to the mesethmoid. Extending posteriorly mesial to the orbits, its

shaft slopes posteroventrally to the posterior end of the optic foramen. Here it is expanded laterally, is more horizontal, and produces two dorsolateral ascending wings, one per side. These wings articulate with the prootic laterally and form a bridge between the posterolaterally placed carotid foramen (which is bounded by the prootic and parasphenoid) and the mesially located posterior myodome (also bounded by these bones). Posteriorly, the parasphenoid arches dorsally and narrows. At its posterior edge it is forked and ventral to the forked anteroventral surfaces of the basioccipital. The forked ends of these two bones together form the rim of the large, centrally located, and oval opening in the floor of the posterior myodome.

The width of the ascending wings is variable between species (Fig. 67). All species have a broad ascending process, relative to most outgroup taxa, but in some species it is broader than in others. *Cyprinella callistia*, *pyrrhomelas*, *camura*, *whipplei*, *analostana*, and *chloristia* have very broad ascending wings, especially the latter two taxa.

The length of the anterior neck of the parasphenoid, anterior to the ascending wings varies in *Cyprinella* (Fig. 67). At a similar body size, all species of the *lutrensis* clade have shorter necks, as do *camura*, *callistia*, *callisema*, and *leedsi*. The latter two species are somewhat more elongate than others. All other members of this genus have longer necks on the parasphenoid.

Because most close outgroups, exceptions being *coccogenis* and *fumeus* (*Luxilus* and *Lythrurus*, respectively) have a short anterior neck to the parasphenoid the long neck in *Cyprinella* is hypothesized derived. The broad ascending wings are also hypothesized derived. In *Luxilus* and *Lythrurus* and many other outgroups the narrow condition is common.

OPERCULAR REGION

Four dermal bones form the opercular series, the opercle, preopercle, subopercle, and interopercle. All elements are thin and paired.

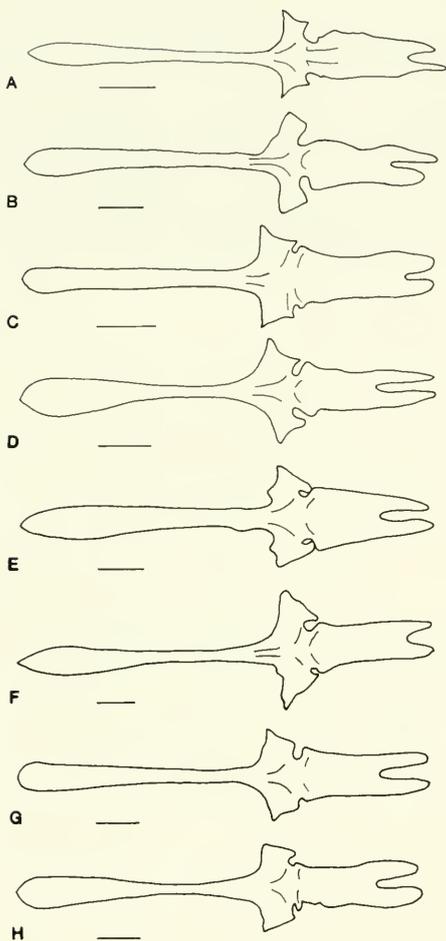


Fig. 67. Ventral view of parasphenoid of species of *Cyprinella* and outgroups. A) *Notropis atherinoides*, 53 mm, KU 18935. B) *Luxilus cornutus*, 60 mm, KU 8686. C) *Cyprinella camura*, 45 mm, KU 15792. D) *C. garmani*, 50 mm, KU 5416. E) *C. chloristia*, 54 mm, KU 8882. F) *C. xaenura*, 76 mm, KU 18994. G) *C. leedsi*, 53 mm, KU 18985. H) *C. callisema*, 52 mm, KU 8842. Horizontal bar equals 1 mm.

Together they cover the branchial chamber posteroventrally and ventrolaterally. They all interarticulate and some articulate with the neurocranium and bones of the hypopalatine region dorsally, ventrally, and anteriorly.

Opercle (OP, Figs. 68, 69). This is the largest bone of the opercular series. In most *Cyprinella* it is a broad bone as in most outgroups. Dorsally and medially it is concave

medially, but is relatively flat ventrally. The dorsal margin varies individually within a species from being straight, concave, and occasionally convex. Dorsoanteriorly a process of variable length is produced for the insertion of the *dilator operculi*. Below this is a variable size notch in the anterior face into which the posterodorsal margin of the hyomandibular inserts anterior to the opercular condyle. The anterior margin is generally straight or slightly sigmoidal. The posterior margin can be sigmoidal or straight. If straight, it is directed posteroventrally at about 45 degrees from the horizontal. Ventrally, the opercle is much wider than the dorsal margin and is variably inclined from the horizontal.

Interspecific variation is most notable in the width of the opercle. Most species of the *lutrensis* clade and *analostana* have a narrow and deep opercle (Figs. 68, 69). *Cyprinella formosa*, *xanthicara*, and *rutilla* are exceptions in the southwestern clade. These species have a broad opercle (Fig. 68). *Cyprinella galactura* is unique among other *Cyprinella* in having a very broad opercle (Fig. 69).

Preopercle (POP, Figs. 68, 69). The preopercle is an elongate, quasi-crescentic dermal ossification. The long anterior arm articulates dorsally with the posterior arm of the quadrate and ventrally with the interopercle. The long ascending arm articulates with the anterior edge of the opercle and the posterior edge of the hyomandibular (Figs. 68, 69). On the lateral surface of this bone is a large portion of the preoperculomandibular canal of the lateralis system.

In all *Cyprinella* this bone is broadened medially and anteriorly more than any outgroups examined. Some interspecific variation exists, however, in the width of the bone and the height of the ascending arm. The broadest condition is found in *camura*, *galactura*, and *venusta* (Fig. 69). A narrowed condition occurs in *rutilla* and *xanthicara* (Fig. 68). In these two species broadening of the preopercle is restricted to the anterior arm only. The ascending arm and the medial portions of this bone in these species are similar to the condition found

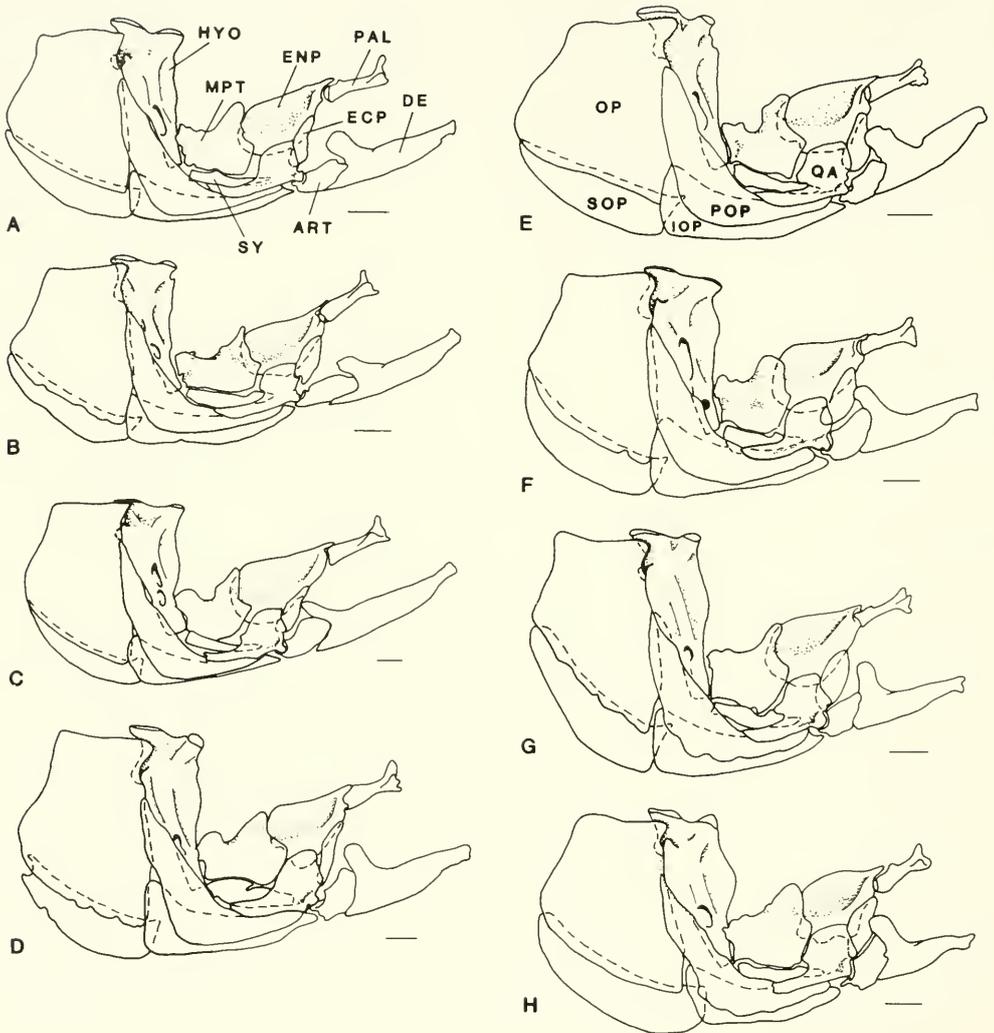


Fig. 68. Lateral view of opercular series and hyopalatine region in some species of *Cyprinella* and outgroups. A) *Notropis atherinoides*, 53 mm, KU 18935. B) *Lythrurus fumeus*, 52 mm, KU 6244. C) *Luxilus coccogenis*, 72 mm, INHS 79254. D) *Cyprinella lutrensis*, 55 mm, KU 19431. E) *C. formosa*, 42 mm, KU 8399. F) *C. lepida*, 44 mm, TU 55189. G) *C. panarcys*, 43 mm, UMMZ 208212. H) *C. rutila*, 55 mm, ASU 5982. All drawn to equal size from anterior endopterygoid to ventral tip of hyomandibular for comparisons. Horizontal bar equals 1 mm.

in outgroups. All other *Cyprinella* are similar in having a broadened condition. Height of the ascending arm varies in two different species groups. *Cyprinella xaenura* and *pyrrhomelas* have tall ascending arms, while *gibbsi*, *trichroistia*, and *caerulea* have reduced ascending arms, compared to other *Cyprinella* and outgroups (Fig. 69).

The margins of the preopercle are generally entire, except for occasional notches and spurs which varied on an individual basis. *Cyprinella rutila*, *proserpina*, and *panarcys* varied from this in having distinctly scalloped posteroventral and ventral margins (Fig. 68), being best developed in the latter two species.

Interopercle (IOP, Figs. 68, 69). This is an

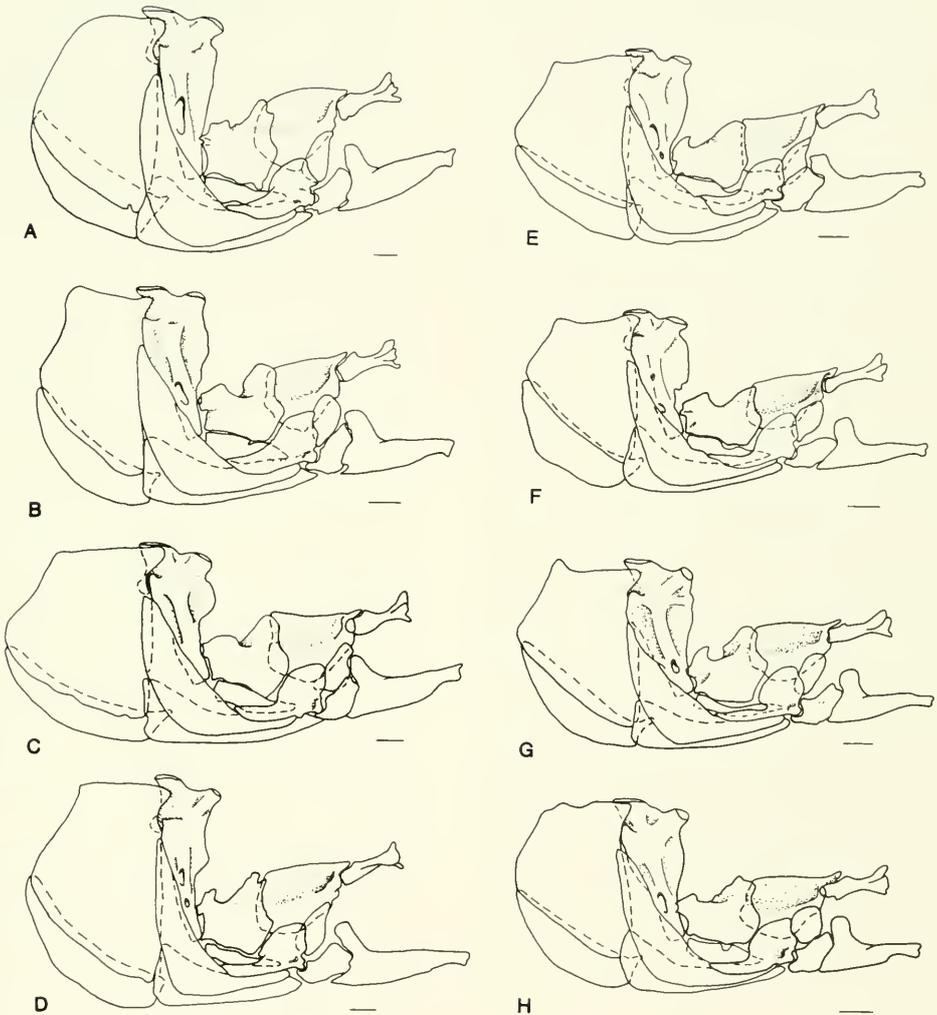


Fig. 69. Lateral view of opercular series and hyopalatine region in species of *Cyprinella*. A) *C. camura*, 73 mm, KU 19715. B) *C. analostana*, 65 mm, INHS 77855. C) *C. galactura*, 60 mm, KU 12029. D) *C. pyrrhomelas*, 70 mm, INHS 76978. E) *C. gibbsi*, 57 mm, KU 18892. F) *C. leedsii*, 60 mm, KU 18985. G) *C. callisema*, 55 mm, KU 8842. H) *C. callitaenia*, 60 mm, TU 92770. All drawn to equal size from anterior endopterygoid to ventral tip of hyomandibular for comparison. See Figure 68 for identification of elements. Horizontal bar equals 1 mm.

elongate dermal bone anterolateral to the subopercle and ventromedial to the preopercle. Mesially it articulates with the posterior ceratohyal and the interhyal. In all species this bone is broadest posteriorly and tapers to about one half that height anteriorly, where it is ligamentously connected to the retroarticular.

Most species of *Cyprinella* have the posterior of this bone expanded more than most other cyprinids examined. The closest outgroups to *Cyprinella* (*Luxilus*, *Lythrurus*, *Notropis* (s.s.), and *Nocomis*) have a narrow interopercle (Fig. 68). *Cyprinella whipplei*, *trichroistia*, *callitaenia*, and *callisema* have narrow interoper-

culi similar to other cyprinids. All other species have some expansion at the posterior margin. The deepest condition is found in *ornata*, *lutrensis*, *formosa*, *bocagrande*, *proserpina*, *panarcys*, *camura*, *analostana*, *leedsii*, *venusta*, *gibbsii*, *pyrrhomelas*, *xaenura*, *nivea*, and *caerulea* (Figs. 68, 69). These species have the interopercle about twice as high as close outgroups. Other species have a broadened interopercle, but less extreme than those listed above. *Cyprinella rutila* is apparently unique in having a short interopercle (Fig. 68).

Subopercle (SOP, Figs. 68, 69). This is the posteroventral bone of the opercular series. Generally, it has a crescentic shape with concave dorsal and ventral margins. Anteriorly it may be rounded or blunt and with or without a dorsoanteriorly directed nipple for articulation with the posteromesial surface of the interopercle. The anterior margin varies intraspecifically. The subopercle articulates for most of its length dorsally with the ventral margin of the opercle. Anteriorly, it is mesial to the interopercle and preopercle. In all *Cyprinella* except *xanthicara* and *galactura*, this bone is broader than many close outgroups examined, except *Luxilus pilsbryi*, which has an equally broad subopercle. Although a correlation has been noted between narrow operculi and deep subopercles (Coburn, 1982) all *Cyprinella*, except where noted in the discussion of the opercle, have noticeably broader operculi.

Orientation of the subopercle varies interspecifically. Most species have an orientation like that found in most outgroups, with the posteriormost tip being considerably elevated above the anterior. In *formosa* and *bocagrande* the subopercle is relatively straight, the posterior tip being only moderately elevated above the dorsalmost point anteriorly. In *caerulea*, *analostana*, *ornata*, *lepida*, *rutila*, *xanthicara*, *panarcys*, and *proserpina* the posterior subopercle tip is extreme, being greatly elevated above the anterior tip, especially in the latter two species.

HYOPALATINE REGION

The seven paired elements comprising the hyopalatine region of the cranium form the supporting structures of the lower and upper jaws, the palate, and the opercular series (Figs. 68, 69). Included is the cartilaginous hyomandibular, symplectic, quadrate, palatine, and metapterygoid, and the dermal endopterygoid and ectopterygoid. The dorsolateral surfaces of the pterygoids form the floor of the orbit.

Hyomandibular (HYO, Figs. 68, 69). This is the largest and heaviest endochondral bone of the hyopalatine region. It is widest dorsally where it articulates with the cranium via two cartilage-tipped condyles. The smaller anterior condyle is ball-like and fits into a facet formed by the prootic, pterosphenoid, and autosphenotic. The posterior articular facet is more elongate, like the condyle, and is formed by the prootic, autosphenotic, and pterotic bones. Below the posterior condyle a knob-like condyle is produced, extending posteriorly and articulating with the operculum via the dorsoanterior articular facet for the hyomandibular. Ventrally the hyomandibular gradually narrows to a slim, yet heavy shaft with a cartilage covered tip. Here it articulates with the symplectic, interhyal, and two points on the metapterygoid. The heavy median strut extends for most of the length of the hyomandibular and contains the variable sized oval foramen for the hyomandibular branch of the vagus nerve. Dorsally, this thickened supporting strut divides into three struts supporting the anterior, posterior, and opercular condyles, and delineates regions for attachment of the *dilatator operculi*, *adductor mandibulae*, and *levator arcus palatini*.

Extending to either side of the median supporting strut is a thin sheet of bone for muscle attachment. The anterior wing begins at the dorsoanterior condyle and terminates at a point between the ventral tip and midlaterally, depending on the species. This wing is the point of insertion of the *levator arcus palatini*. The heavier posterior wing is rarely as broad as the anterior. Dorsally, this posterior wing begins

anterior and ventral to the opercular condyle. It may begin as a semi-horizontal ridge from the point of division of the median strut, or it may be a continuation of a dorsally extending ridge below the posterior condyle. This wing extends ventrally, lateral to the ascending arm of the preopercle for most of its length. It then tapers anteriorly where the broadened preopercle begins to overlap the lower portion of the hyomandibular. The posterior wing acts as a point of origin of the subdivisions of the *adductor mandibulae* (Winterbottom, 1974; Coburn, 1982).

Variation occurs in the size and shape of anterior and posterior wings. The anterior wing of *whipplei*, *chloristia*, *analostana*, *camura*, *lutrensis*, *garmani*, *proserpina*, *panarcys*, *lepida*, *formosa*, and *pyrrhomelas* is small like that found in the genera *Notropis*, *Lythrurus*, *Pteronotropis*, and the closely related genus *Luxilus* (Figs. 68, 69). Other *Cyprinella* have a more expanded anterior wing (Figs. 68, 69). The shape of the anterior wing also varies interspecifically. All species with the small wing have a smooth edge except *rutila* and *xanthicara* which have a median oval expansion anteriorly, and *ornata* and *pyrrhomelas* which have a prominent notch midway along the hyomandibular (Figs. 68, 69). The notched morphology is common to the remaining species with the broadened anterior wing, except *callisema*, *gibbsi*, and *trichroistia*. In these species the anterior notch is lacking and the wing is broad, but has a rounded and gradually sloping anterior margin which extends most of the length of the median strut.

Separation of the "notched" and "smooth" morphologies is not always complete for some species. Occasionally one or two specimens vary from the most frequently observed condition for that species. These variants were sometimes due to obvious developmental abnormalities.

The posterior adductor wing also varies in size and contour. The wing is expanded posteriorly to cover the opercular condyle partially or entirely in all species of *Cyprinella* except *ornata*, *lutrensis*, *garmani*, *formosa*,

bocagrande, *proserpina*, *panarcys*, *lepida*, *camura*, and *pyrrhomelas*. Generally in these species only a small wing extending from the median strut of the hyomandibular is present and it only occasionally overlaps the preopercle. In *trichroistia*, *gibbsi*, and *callisema* the wing extends farther ventrally than in other species, to near the ventral tip of the median strut (Fig. 69). Contour of the posterior adductor wing varies between species from flat to highly curled. All species have a flat wing except *whipplei*, *analostana*, *chloristia*, *callistia*, *trichroistia*, *gibbsi*, and *caerulea* which develop a distinctly concave wing.

Polarity of these characters varying in *Cyprinella* are as follows. The notched or smooth morphology is discussed by Coburn (1982). He considered the smoothed edge to be derived, based on comparisons to other genera which commonly have an anterior wing producing a distinct angle or notched morphology. My observations are in agreement, that the smooth condition may represent a derived condition, but it has obviously reversed at least two times, once in *Cyprinella* and at least once in some species of *Notropis*. This is probable since it occurs not only in the *whipplei* clade, but also in species of a large clade of *Notropis* related to the subgenus *Notropis* and other species of uncertain affinities.

Since species of *Luxilus* and most other species possessing the derived condition of having an opening in the posterior myodome have a narrow hyomandibular with a smooth and reduced anterior wing, the broadened hyomandibular and the notched anterior wing present in some *Cyprinella* is derived. The curled adductor wing found in two groups of *Cyprinella* is also derived since all *Luxilus* have a flat posterior wing and the curled condition is rarely encountered elsewhere.

Palatine (PAL, Figs. 68–70). These paired endochondral ossifications articulate posteriorly with the endopterygoid and anteriorly with the supraethmoid, vomer, maxillary, kinethmoid, and lacrymal. The posterior articulation involves a simple socket, formed by the endopterygoid. Generally, there are two

ventral ligaments on the posterior palatine. One connects to the anteromedial face of the endopterygoid, the other connects the dorsoanterior endopterygoid to the dorsal surface of the palatine (Fig. 70A). These points of connection on the palatine are generally well marked by one or two small ligamental scars or ridges ventrally and a single scar dorsally.

The anterior end of the palatine is considerably more complex than the posterior, consisting of three processes, a maxillary (MP), vomer (VP), and supraethmoid (SEP) (Fig. 70A,C). The maxillary process is not well defined in *Cyprinella*. This process is lateral and is connected via ligaments to the lacrymal, kinethmoid, and maxilla. The two medial processes, one dorsal and one ventral, form an articular socket, like other cyprinids, with which the preethmoid articulates. The dorsal process is connected to the supraethmoid and the ventral with the vomer. Both connections are ligamentous.

In general, the gross shape of the palatine when viewed dorsally (Fig. 70) does not differ greatly in *Cyprinella*. Most species have heavy palatines that are typically triangular, with the broadest aspect anteriorly, and are without a well defined maxillary process. This shape is derived and also typical of species of the genera *Luxilus* and *Lythrurus* (Fig. 29).

The following characters vary between species. The palatines of *nivea*, *leedsii*, *callisema*, and *callitaenia* are more elongate than other species of *Cyprinella* and outgroups at a similar body size (Fig. 70L–O). These four species and *rutila*, *xanthicara*, *proserpina*, and *panarcys* have a well-developed maxillary process on the palatine which is directed anteriorly (Fig. 70L–O,S,T). The dorsal supraethmoid process of most species is similar, rising above the horizontal 70–80° and terminating in a small point. *Cyprinella callitaenia* differs in having a broad dorsal process (Fig. 70 O) and in *ornata*, *panarcys*, and *lepida* the angle of the dorsal process is considerably less (Fig. 70P–Q). The ventral process is well-developed in all species except *leedsii*, *callisema*, and *callitaenia*. These species have a

small dorsal process (Fig. 70M–O).

All species except *trichroistia*, *gibbsii*, *xaenura*, and *callistia* have a well-developed, deep, and contained anteromesial socket for the articulation of the preethmoid (Fig. 70). In *trichroistia* and *gibbsii* the socket is smaller and more restricted anteriorly (Fig. 70J). In *callistia* and *xaenura* the socket is less restricted posterodorsally and a weak channel is formed (Fig. 70H,K).

Interspecific variation is observed in the number of ventral ligamentous scars from the endo- and ectopterygoids. In all species of *Cyprinella* except *trichroistia*, *gibbsii*, *caerulea*, *xaenura*, *pyrrhomelas*, and *callistia* two scars occur ventrally as in all other cyprinids examined. In these species, only a single ventral ridge is developed. This observation is related to the development of the number of connecting ligaments. In all but the above mentioned species there are two branches of the ligament connecting the posteroventral palatine to the endo- and ectopterygoid. Species with a single scar develop only one large ligament (Fig. 70).

The elongate and more delicate palatines of *nivea*, *leedsii*, *callisema*, and *callitaenia* represent a derived morphology relative to the heavy and short condition in other *Cyprinella* and near outgroups. Further, within this group the reduced ventromedial vomerine process of the latter three species is derived and supports their close relationship. The well-developed anteriorly directed maxillary process of *rutila*, *xanthicara*, *proserpina*, and *panarcys* as well as *nivea*, *leedsii*, *callisema*, and *callitaenia* (Fig. 70) supports the monophyly of these groups, although independent evolution of this morphology is hypothesized. The reduced anterior preethmoid socket of the palatine in *pyrrhomelas*, *callistia*, *trichroistia*, and *gibbsii* represents a derived condition and supports their monophyly. *Cyprinella xaenura*, another member of this group, is apomorphic in having a very long and modified socket. In *trichroistia* and *gibbsii* the socket is even more reduced and represents a further modification relating these two species.

The number of ligaments connecting the

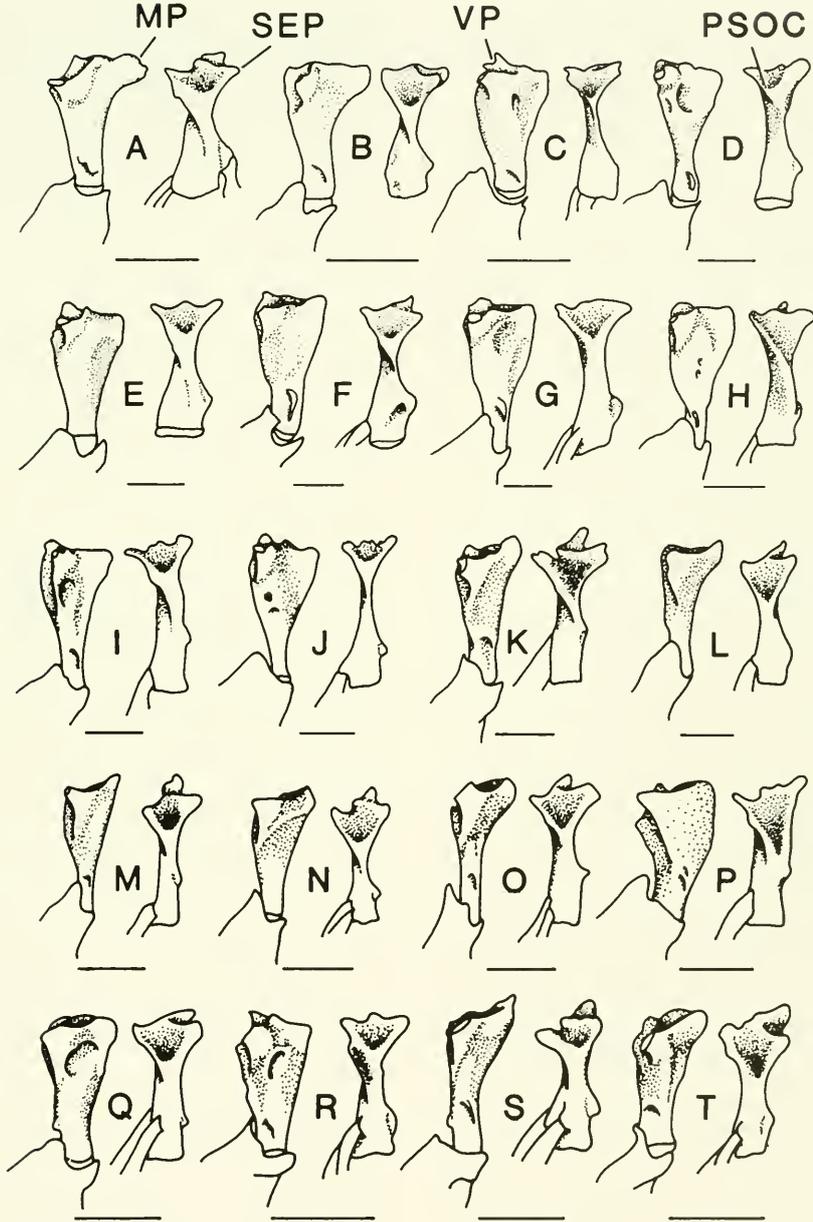


Fig. 70. Dorsal (left) and medial (right) view of palatines of species of *Cyprinella* and outgroups. A) *Notemigonus crysoleucas*, 63 mm, KU 1357. B) *Phoxinus erythrogaster*, 52 mm, KU 13198. C) *Lythrurus fumeus*, 52 mm, KU 6244. D) *Luxilus zonistius*, 72 mm, KU 18995. E) *L. chrysocephalus*, 78 mm, KU 12654. F) *Cyprinella spiloptera*, 69 mm, KU 17776. G) *C. venusta*, 83 mm, KU 8810. H) *C. xaenura*, 72 mm, KU 18994. I) *C. pyrromelas*, 73 mm, INHS 76978. J) *C. trichroistia*, 72 mm, KU 18853. K) *C. callistia*, 74 mm, KU 18848. L) *C. nivea*, 60 mm, KU 18987. M) *C. leedsi*, 52 mm, KU 18985. N) *C. callisema*, 52 mm, KU 8842. O) *C. callitaenia*, 58 mm, TU 92770. P) *C. ornata*, 56 mm, KU 8405. Q) *C. lepida*, 46 mm, TU 55189. R) *C. formosa*, 47 mm, KU 8399. S) *C. proserpina*, 50 mm, TNHC 3262. T) *C. xanthicara*, 41 mm, ASU 3642. Horizontal bar equals 1 mm.

ventral palatine to the ecto- and endopterygoids is also phylogenetically informative within *Cyprinella*. The derived condition of having a single ligament instead of two is found in the group composed of *xaenura*, *pyrrhomelas*, *trichroistia*, *gibbsi*, *caerulea*, and *callistia*. All other *Cyprinella* and outgroups examined have two ligaments.

Ectopterygoid (ECP, Figs. 68, 69). These paired, dermal ossifications lie anterior to the quadrate and endopterygoid and posteroventral to the palatine. They articulate ventrally with the medial face of the anterior portion of the quadrate and dorsally with the lateral face of the endopterygoid. In some instances these bones may be partially fused and their outlines obliterated. Generally, this bone is oval or pear shaped with the dorsoanterior tip being constricted and oriented slightly anterior (Figs. 68, 69).

In *nivea*, *leedsi*, *callisema*, and *callitaenia* the bone is short and broad (Fig. 69). *Cyprinella callitaenia* is most extreme with the bone approaching a circular aspect. Species of the *lutrensis* clade, except *xanthicara*, have an elongate and narrow ectopterygoid (Fig. 68). *Cyprinella xanthicara* has a broad and short condition, similar to that present in species of the *nivea* group.

Most outgroups examined have an oval or pear shaped ectopterygoid as is found in *spiloptera*, and the *whipplei*, *venusta*, and *pyrrhomelas* species groups. Therefore, conditions present in the *lutrensis* clade and in the *nivea* species group are derived.

Endopterygoid (ENP, Figs. 68, 69). The endopterygoid is a paired, dermal ossification which articulates posteromesially with the metapterygoid, ventromesially with the quadrate and ectopterygoid, and anteriorly with the palatine. Like most species with an open posterior myodome the lateral surface of the endopterygoid is concave. Anteriorly, a socket is formed for the articulation with the posterior palatine. Mesial to the socket an anterior process is formed for support of the palatine. This process glides along the ventral surface of the lateral ethmoids.

Similar to species of *Luxilus*, in most members of *Cyprinella* the endopterygoid is not the largest bone of the pterygoid series and is equal in size to the metapterygoid. *Cyprinella xanthicara* is unique in having a larger endopterygoid. In most outgroups examined the endopterygoid is larger than the metapterygoid and represents the largest ossification of the pterygoid series. Coburn (1982) noted that *Notropis volucellus*, *N. maculatus*, *N. emiliae*, and *N. heterolepis* also have equally sized meta- and endopterygoids. *Notropis ozarcanus* and *N. spectrunculus* also have similarly sized elements. Other *Notropis*, *Phenacobius*, *Hybopsis*, *Nocomis*, and *Rhinichthys* generally have longer endopterygoids. Thus, having roughly equally sized endo- and metapterygoids is derived.

Quadrate (QA, Figs. 68, 69). This long and heavy endochondral bone lies ventral to, but articulates with the pterygoid series. Anteriorly, the quadrate is compressed laterally into a broad fan which is closely associated with the ventral ecto- and endopterygoid and loosely associated with the anteroventral margin of the metapterygoid. Anteroventrally it slopes laterally from the expanded fan into a broad semi-horizontal shelf (typical of all *Cyprinella*). Anteriorly it bears a condyle for articulation with a notch in the posterior articular. Posterior to the fan is produced a long, heavy recurved process lateral to the symplectic. This process is a continuation of the broad shelf posterior to the condyle. The process curves upward posteriorly, approaching the ascending arm of the preopercle and ventrolateral to the posterior margin of the symplectic.

In most species the posterior process of the quadrate is heavy with its dorsal margin joining the expanded fan at its posteriormost edge (Figs. 68, 69). The posterior process is heavy and deep in *analostana*, *chloristia*, *gibbsi*, *lutrensis*, and *proserpina* (Figs. 68, 69). In *ornata*, *rutila*, *proserpina*, *panarcys*, and *formosa* the posterior process joins the fan at a point midway along its posterior margin such that the union is anteroventral to the posterior edge.

Among outgroups, connection of the posterior arm to the fan occurs at the edge of the fan and in no case is the quadrate as heavy and deep as that observed in the species mentioned above.

Symplectic (SY, Figs. 68, 69). Anteriorly this elongate and paired cartilage bone lies mesial to a thin sheet of bone connecting the anterior and posterior portions of the quadrate. Along the remainder of its length posteriorly it fits into a channel along the dorsal surface of the posterior extension of the quadrate. At its posteriormost extent the symplectic is generally more expanded and participates in a four-part articulation including the descending ramus of the hyomandibular, the posteroventral arms of the metapterygoid, and the interhyal.

In all but a few species of *Cyprinella* the symplectic is a very broad and flat bone. Exceptions to this include *whipplei*, *caerulea*, *xaenura*, *callisema*, and *rutila*. Outgroups are variable with respect to the size of the symplectic, but comparisons with closest outgroups *Luxilus*, *Lythrurus*, and *Notropis* (s.s.) indicate that the elongate and narrow morphology is primitive. Thus, the broad condition of most *Cyprinella* is derived.

Metapterygoid (MPT, Figs. 68, 69). In lateral aspect this is a broad, but thin bone with a flat to slightly concave ventral portion. Dorsally there are two ascending processes, one posterior and one anterior, separated by a prominent middorsal notch. Anteroventrally, it broadly articulates with the quadrate via a cartilage interface and anterodorsally it is closely applied to the lateral surface of the posterior endopterygoid. Posteriorly, there are two heavy struts, one oriented horizontally and articulating with the hyomandibular and one oriented ventroposterior and opposing the interhyal.

The anterior ascending arm of the dorsal surface is well developed in all *Cyprinella*, and as a continuation of the endopterygoid, is strongly concave. The posterodorsal process shows some interspecific variation. Most species have a broad and high posterior process.

However, it is narrow and low in *camura*, *galactura*, *whipplei*, *trichroistia*, *callitaenia*, *callistia*, *garmani*, *rutila*, *formosa*, and *xanthicara*. In most species the ventral margin of the metapterygoid is relatively straight, following the dorsal margin of the symplectic. *Cyprinella proserpina* and *panarcys* have an anteroventral process extending into a region normally occupied by the symplectic.

The size of the posteroventral point of articulation of the metapterygoid with the interhyal varies between species. In all *Cyprinella* except *whipplei*, *caerulea*, *nivea*, *leedsi*, *callisema*, and *xanthicara* this process is very small and almost pinpoint in appearance. In these species the articulation is broad. Species of the *lutrensis* clade are most extreme in this character in having a very small articular connection. Outgroups examined have a broad articular connection with the interhyal, a smooth ventral edge, and a low posterodorsal process.

UPPER JAW

Premaxilla (PMX, Fig. 71). The premaxillaries are thin and elongate dermal ossifications which in most species are semi-L-shaped. Anteriorly, they develop a roughly triangular-shaped ascending process which slides between the premaxillary and rostral processes of the maxilla. The paired premaxillaries articulate with each other anteriorly along the mesial edge of the ascending process and dorsally with the kinethmoid via a ligament. Posteriorly, these bones become constricted to a narrow shaft which may be rounded or flattened. Over most of the length the bone is thin with the lateral surface slightly convex.

Considerable interspecific variation exists in the morphology of the premaxilla in *Cyprinella*. Orientation of the long posterior ramus varies from straight to strongly decurved. Species with a straight process include *bocagrande*, *lepida*, *whipplei*, *camura*, *spiloptera*, *pyrrhomelas*, and *trichroistia*. The remaining species have some degree of curvature but *proserpina*, *panarcys*, *rutila*, *analostana*, *chloristia*, and *gibbsi* are most

extreme in having strongly decurved processes. *Cyprinella nivea*, *leedsi*, *callisema*, and *callitaenia* also have a decurved posterior ramus, especially *nivea*, but in these taxa the change from horizontal is more abrupt and not as gradual as in other species. The posterior process of all species is restricted posteriorly. In *trichroistia*, *gibbsi*, and *caerulea* it is extreme. In these species it is rounded and tapered into a very thin shaft.

The dorsal margin of the premaxilla is smooth in all species except *nivea*, *leedsi*, *callisema*, and *callitaenia*. These species differ in having a serrated posterodorsal margin. The margins of the premaxilla of *callitaenia*, and to a certain degree *leedsi*, are only slightly serrated.

In all species the extension of the thick posterior process anteriorly produces a slightly thick dorsal margin to the premaxilla. In *proserpina* and *panarcys* this shaft is heavier than other members of the genus. These two species, together with *xanthicara* and *rutila*, also differ from other *Cyprinella* in having a very deep anterior premaxilla.

The ascending process of the premaxilla in most species is triangular, narrowest dorsally where it articulates with the kinethmoid. Some members vary, however, in having a more elongate and taller process. This includes *rutila*, *xanthicara*, *analostana*, *chloristia*, *callisema*, *callitaenia*, *nivea*, *callistia*, and *gibbsi*.

Maxilla (MX, Fig. 72). Together with the premaxillaries these paired dermal ossifications comprise the protrusible upper jaws. The complex mechanics are possible only with the rotational and gliding actions between the maxilla, premaxilla, and surrounding articular surfaces. Anteriorly the maxilla bears two processes, a mesial fingerlike rostral process (RPM) directed anteroventrally and a broad lateral premaxillary process (MXM). Between these two the ascending ramus of the premaxilla is contained and glides when the mouth is opened. The rostral process is joined to its opposite at the midline by a ligament. Above the rostral and premaxillary processes are two robust and larger protuberances for articula-

tion with the lateral process of the palatine and preethmoid. The anteriormost tubercle articulates with the preethmoid. The lateral palatine process is joined at the posteriormost tubercle of the maxilla and is also ligamentously joined to the lateral face of the maxilla slightly posterior to the premaxillary process. Medially the maxilla is deeply notched dorsally, creating the isthmus. Posterior to the isthmus is a large and broad ascending ramus and an elongate posteroventral shaft. The shaft is expanded and curved posteriorly where the posterior arm of the premaxilla is connected and articulates.

The lateral face of the maxilla is slightly convex and smooth, except anteriorly where two small, laterally directed tubercles are developed. The anteriormost tubercle is for the insertion of the palatine-maxillary ligament and is at the base of the premaxillary process. The second process is for the insertion of the *adductor mandibulae* A1 and is slightly posterior to the first, located along the ventral edge of the maxilla, directly below the large dorsal articulation surface for the palatine.

Significant systematic variation in maxilla morphology includes location of the *adductor mandibulae* A1 insertion, depth of the isthmus and premaxillary process, and the orientation of the rostral process. In all species except *venusta* and *proserpina* the *adductor mandibulae* A1 tubercle is placed far forward relative to other cyprinids examined. In members with the more anteriorly placed process two groups are recognizable. All species, except *caerulea*, *gibbsi*, *trichroistia*, and *xaenura* have the process placed below the posterior margin of the dorsal palatine-maxillary articular surface. In these four species the process is intermediate between that found in *venusta* and *proserpina* and species with the extreme anterior process.

Some *Cyprinella* have a deep isthmus, thus a shallow dorsal notch, and a deep premaxillary process as compared to other species and outgroup taxa. Species with a deep isthmus include *nivea*, *leedsi*, *callisema*, *callitaenia*, *proserpina*, *ornata*, *camura*, *chloristia*, and

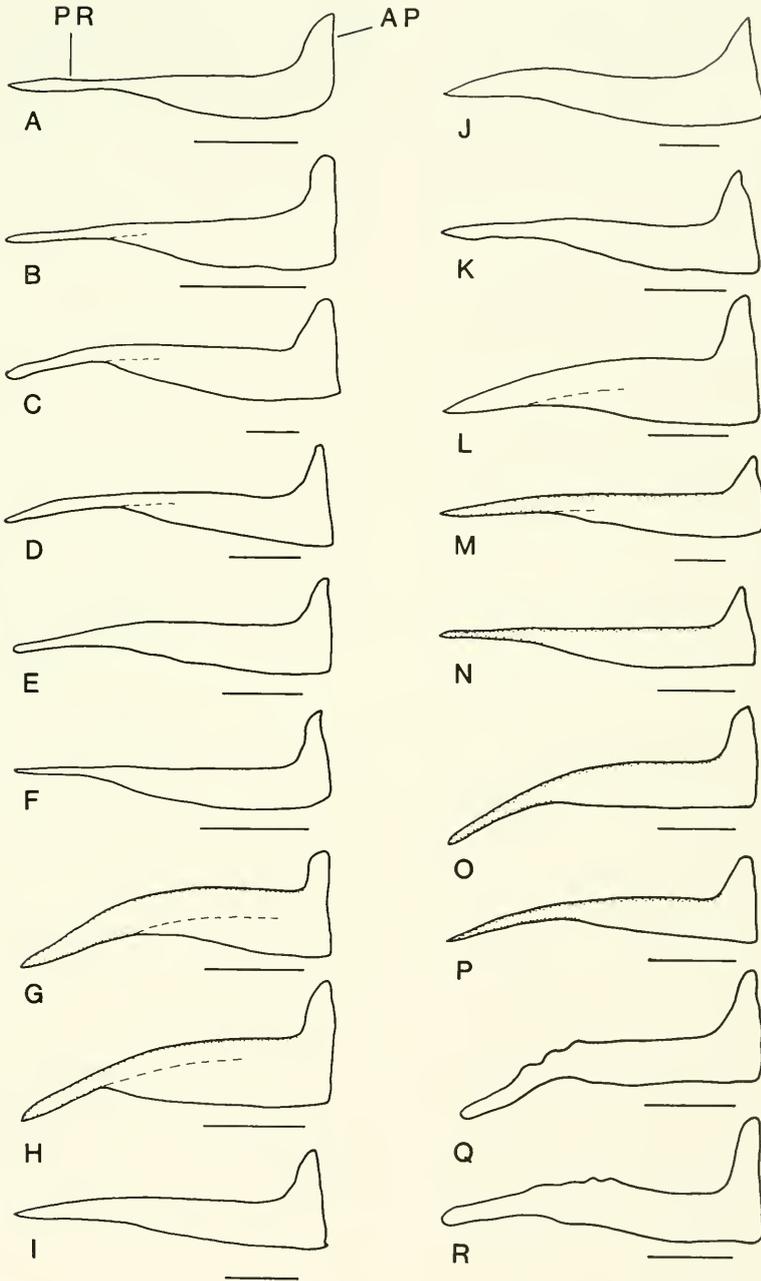


Fig. 71. Premaxilla of species of *Cyprinella* and outgroups. A) *Notropis atherinoides*, 50 mm, KU 18935. B) *Lythrurus lirus*, 45 mm, KU 18933. C) *Luxilus cardinalis*, 65 mm, KU 15281. D) *L. cornutus*, 60 mm, KU 8686. E) *Cyprinella lutrensis*, 55 mm, KU 19431. F) *C. bocagrande*, 32 mm, KU 20399. G) *C. proserpina*, 58 mm, TNHC 3262. H) *C. rutila*, 57 mm, ASU 5982. I) *C. spiloptera*, 56 mm, KU 17776. J) *C. camura*, 45 mm, KU 15782. K) *C. whipplei*, 55 mm, KU 14211. L) *C. analostana*, 61 mm, INHS 77855. M) *C. pyrrhomelas*, 70 mm, INHS 76978. N) *C. trichroistia*, 60 mm, KU 18853. O) *C. gibbsi*, 57 mm, KU 18892. P) *C. caerulea*, 60 mm, KU 18978. Q) *C. nivea*, 59 m, KU 18987. R) *C. callisema*, 52 mm, KU 8842. Horizontal bar equals 1 mm.

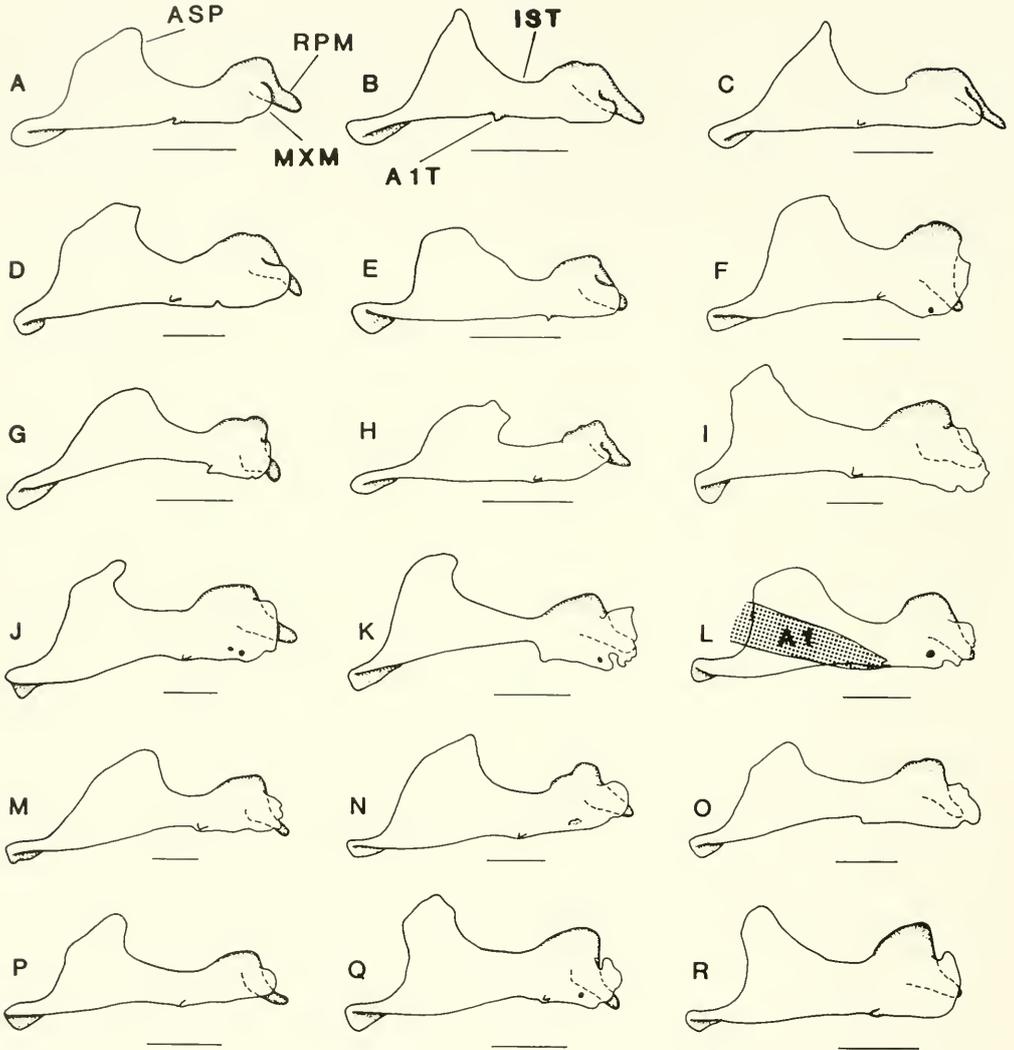


Fig. 72. Maxilla of species of *Cyprinella* and outgroups. A) *Notropis atherinoides*, 53 mm, KU 18935. B) *Lythrus lirus*, 47 mm, KU 18933. C) *L. bellus*, 46 mm, KU 14511. D) *Luxilus cornutus*, 62 mm, KU 8686. E) *Cyprinella garmani*, 50 mm, KU 5416. F) *C. proserpina*, 58 mm, TNHC 3262. G) *C. panarcys*, 42 mm, UMMZ 208212. H) *C. bocagrande*, 32 mm, KU 20399. I) *C. venusta*, 83 mm, KU 8810. J) *C. camura*, 76 mm, KU 15792. K) *C. whipplei*, 64 mm, KU 14211. L) *C. analostana*, 59 mm, INHS 77855. M) *C. pyrrhomelas*, 73 mm, INHS 76978. N) *C. xanura*, 71 mm, KU 18994. O) *C. gibbsi*, 65 mm, KU 18892. P) *C. caerulea*, 58 mm, KU 18978. Q) *C. nivea*, 60 mm, KU 18987. R) *C. callitaenia*, 59 mm, TU 92770. Horizontal bar equals 1 mm.

analostana. Other species have a very narrow isthmus. Included here are *gibbsi*, *trichroistia*, *caerulea*, *whipplei*, *panarcys*, and *bocagrande*. Other *Cyprinella* have an isthmus of intermediate depth, like outgroups.

The premaxillary process of the maxilla is relatively short, about half the height of the

maxilla anteriorly, in members of the *lutrensis* clade, except *proserpina*, *chloristia*, *galactura*, and *caerulea*. All other species have a tall and relatively broad process, especially *nivea*, *callisema*, *callitaenia*, and *leedsii*.

The rostral process of the maxilla is a heavy, fingerlike projection, generally directed an-

terovertrally. In some species, however, it may be quite heavy and then L-shaped, first directed ventrally and then bending mesially. Species with the L-shaped process are those with the most inferior mouths, *nivea*, *leedsii*, *callisema*, *callitaenia*, and *rutila*, *xanthicara*, *panarcys*, and *proserpina*. The latter four species also have a more robust rostral process than other *Cyprinella*.

LOWER JAW

The lower jaw is composed of eight elements (Figs. 73, 74). Two are endochondral ossifications, the retroarticular and mentomeckelian, two are dermal, the dentary and sesamoid articular, and one is a compound bone, the anguloarticular. This element is composed of the dermal angular, endochondral articular, and ossified portion of Meckel's cartilage, which extends from the mentomeckelian to the anguloarticular on the mesial surface of the dentary.

Dentary (DE, Figs. 68, 69, 73, 74). This paired element is the stoutest of all lower jaw ossifications and is most obviously curved mesially, especially anteriorly, where it articulates via a symphyseal joint to its complement. Posteriorly, it is broad and develops the coronoid process (CP), a dorsal extension of the gnathic ramus. The posterior margin of the gnathic ramus is broad and sloped posteriorly, articulating with the anguloarticular and retroarticular. Typically, the coronoid process in these species is directed dorsally. Laterally, the surface is smooth and rounded with a mesially sloping ventral surface. Fused to the lateral face of the gnathic ramus is the anterior element of the mandibular canal. Dorsally, anterior to the coronoid process, there may be a lateral shelf formed and a slight depression ventrally.

Mesially, the dentary is largely concave, especially ventrally. Dorsally there may be a weak to strongly developed shelf. Anteriorly it is expanded at the joint with its complement and curves mesially. Posterior to this joint the mentomeckelian is visible as a thin rod pointed anteriorly and truncating posteriorly where it

is continued by Meckel's cartilage.

Systematic variation in the morphology of the dentary includes depth and thickness of the gnathic ramus, orientation of the coronoid process, curvature of the anterior gnathic ramus, and the development of a dorsal shelf. Most species of *Cyprinella* have a short, dorsally directed, and relatively broad coronoid process. *Cyprinella trichroistia*, *gibbsii*, *pyrrhomelas*, and *xaenura* differ in having a more posteriorly directed process. *Cyprinella lepida*, *proserpina*, *panarcys*, and *xanthicara* are divergent in that the process is thin and more elongate, less so in the last species. The posterior margin of the gnathic ramus is broad in *Cyprinella*, but is even more so in *ornata*, *lutrensis*, and *garmani*. These species have a very deep and heavy posterior aspect of the dentary.

All species have some development of a dorsolateral shelf anterior to the coronoid process, but in some the shelf is more strongly developed than in others. In the species pair *chloristia* and *analostana* and all members of the *lutrensis* clade the shelf is well developed and wide. Within this latter clade, *lutrensis* has the least development and in *ornata*, *rutila*, *xanthicara*, *panarcys*, and *proserpina* the shelf is very strongly developed. The anterior curvature and thickness of the gnathic ramus is diagnostic for some members of the genus. In most species the orientation of the gnathic ramus is nearly vertical, except *callistia*, *leedsii*, *nivea*, *callitaenia*, *callisema*, *rutila*, and *xanthicara*. In these taxa the anterior tip is curved mesovertrally, producing a more horizontal orientation. In species of the *lutrensis* clade the anterior gnathic ramus is deep and thick, more so than in other members of the genus.

Anguloarticular (ART, Figs. 73, 74). This ossification is the second largest of the lower jaw elements. Posteriorly, it is stout, generally deep, and articulates with the quadrate. Anteriorly the shaft gradually narrows to a point and is located between the mesial surface of the dentary and lateral surface of Meckelian cartilage. Articulation with the quadrate is possible through a partially contained socket formed by

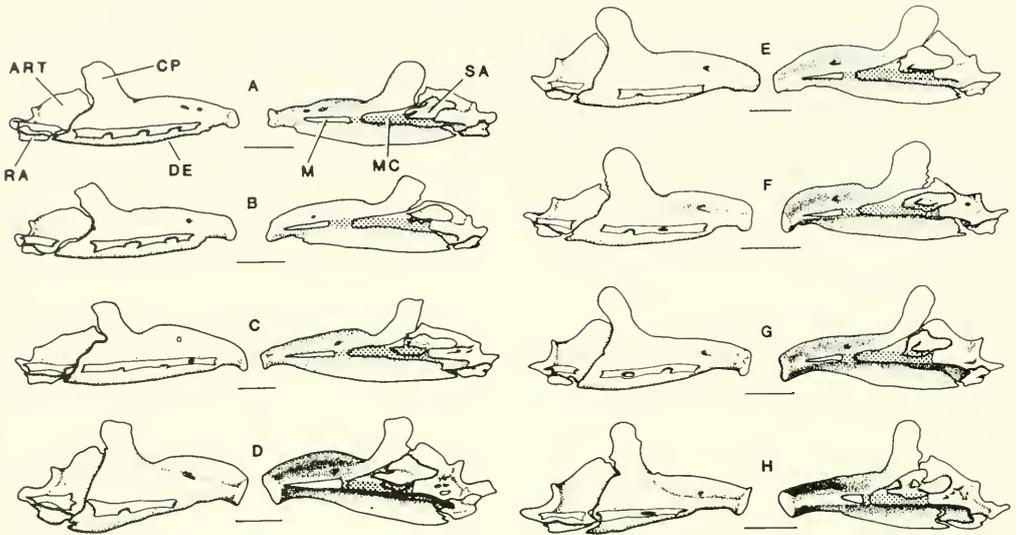


Fig. 73. Lower jaws of species of *Cyprinella* and outgroups. A) *Notropis atherinoides*, 55 mm, KU 18935. B) *Lythrurus fumeus*, 55 mm, KU 6244. C) *Luxilus cardinalis*, 60 mm, KU 15281. D) *Cyprinella ornata*, 55 mm, KU 8405. E) *C. lutrensis*, 55 mm, KU 19431. F) *C. formosa*, 47 mm, KU 8399. G) *C. lepida*, 50 mm, TU 55189. H) *C. proserpina*, 58 mm, TNHC 3262. Left is lateral view and right is mesial view. Horizontal bar equals 1 mm.

a posterior broadening of the bone and the development of a posteriorly directed process ventrally, into which fits the anteriorly directed and heavy process of the quadrate. Fused to the ventrolateral surface of the anguloarticular is a short portion of the mandibular canal.

In most species the dorsal surface of the anguloarticular is expanded, oblique, and directed dorsally. Here it articulates with the coronoid process as well as the posterior gnathic ramus. In *panarcys*, *formosa*, *leedsii*, *whipplei*, and to a certain degree *xaenura*, this crest is absent and the dorsal surface is nearly horizontal.

Retroarticular (RA, Figs. 73, 74). The retroarticular is generally short and robust and located ventral to the anguloarticular and posteroventral to the dentary. Posteriorly, it articulates via a quasi-ball and socket joint with the anguloarticular and anteriorly with the dentary by a ligament. It is connected to the anterior tip of the interopercle and posterior ceratohyal by ligaments.

The shape of the retroarticular varies from being relatively short to elongate and straight

or oval to L-shaped. In all species the bone is short and oval except *panarcys*, *proserpina*, and *venusta* in which it is long and slender. In these taxa, plus *lepida*, *xanthicara*, *rutila*, and *galactura* it is roughly L-shaped.

Sesamoid articular (SA, Figs. 73, 74). This ornate and thin bone is complex and lies partially above and partially lateral to Meckel's cartilage and mesial to the anguloarticular. A posterior process is developed above the ossified Meckelian portion of the anguloarticular and may partially overlap it mesially. Anteriorly, at least two, sometimes three, pointed processes are developed. Centrally a more mesial process is developed for the insertion of the *adductor mandibulae* A3. In all species, except *panarcys* and *proserpina*, this central process is directed anteriorly and elongate. These two species share a very reduced and dorsally directed central process.

Mentomeckelian (M, Figs. 73, 74). This ossification represents the anterior extent of Meckel's cartilage and is fused to the mesial surface of the anterior gnathic ramus of the dentary. In *leedsii*, *callitaenia*, *callisema*, *pyrrhomelas*, *camura*, *analostana*, *chloristia*,

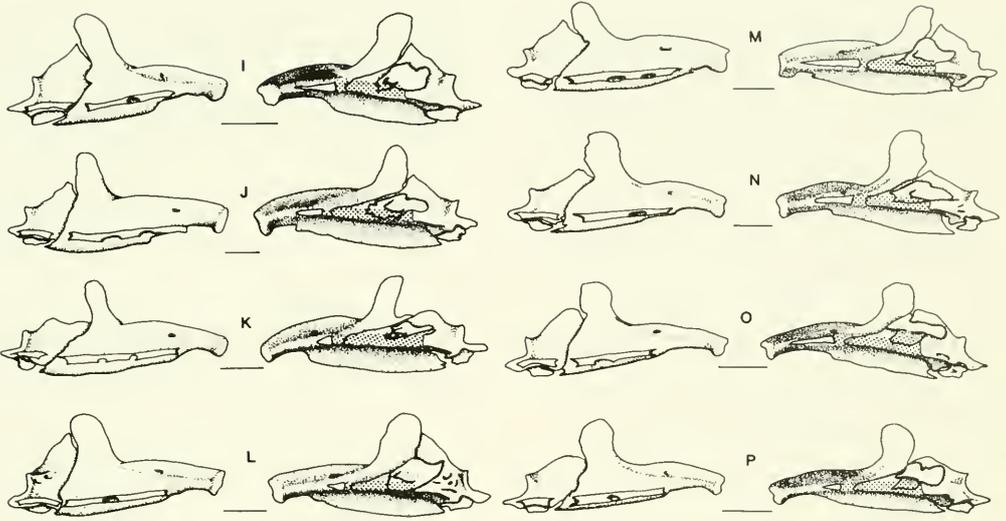


Fig. 74. Lower jaws of some species of *Cyprinella*. I) *C. rutila*, 57 mm, ASU 5982. J) *C. camura*, 45 mm, KU 15792. K) *C. whipplei*, 55 mm, KU 14211. L) *C. analostana*, 61 mm, INHS 77855. M) *C. gibbsi*, 57 mm, KU 18892. N) *C. callistia*, 60 mm, KU 18848. O) *C. nivea*, 59 mm, KU 18987. P) *C. leedsi*, 55 mm, KU 18985. Left is lateral view and right is mesial view. Horizontal bar equals 1 mm.

proserpina, *panarcys*, *xanthicara*, and *boca-grande* the mentomeckelian is very short, represented only by a small cone. In other *Cyprinella* it is elongate and thin.

HYOID REGION

Ten bones form the hyoid region. Included are the paired interhyals, anterior and posterior ceratohyals, dorsal and ventral hypohyals, the three branchiostegals, and the unpaired urohyal and basihyal. All elements are cartilage, except the urohyal. The urohyal has a complex origin. Following Patterson (1977) it may represent a compound bone, the median vertical plate being membrane and the horizontal ventral plate being dermal. These elements help to support and form part of the branchial chamber.

Interhyal (IH, Fig. 75). This endochondral element articulates with the posterior ceratohyal, where it fits into a notch located posterodorsally. Dorsally it is included in the three element hyomandibular-symplectic joint. All *Cyprinella* have a short, stout interhyal.

Ceratohyal (CH, Figs. 75, 76). The ceratohyals are paired, endochondral elements

located on either side of the hyoid region. The posterior ceratohyal (PCH) is deep anteriorly and narrows posteriorly to a point where it articulates with the interhyal. The anterior ceratohyal (ACH) is the larger of the two; deepest posteriorly where it articulates with the posterior element and narrows anteromedially where it twists and forks into two stout processes, one directed dorsomesially and one directed ventrolaterally. The dorsal and ventral processes of the ceratohyal articulate with the dorsal and ventral hypohyals, respectively.

Both the anterior and posterior ceratohyals contain foramina. The posterior ceratohyal contains two, generally located along the dorsal surface, through which passes the hyoideal artery. The anterior ceratohyal, together with the hypohyals, forms the hypohyal foramen. This foramen is generally bounded by all three elements. In some species, *leedsi*, *callisema*, and *callitaenia*, a second foramen may exist in the anterior ceratohyal ventrally just before the forked neck.

Within *Cyprinella* systematic variation in ceratohyal morphology is expressed in depth of elements, location of the posterior cera-

tohyal foramina, location and size of the hypohyal foramen, and neck size of the anterior ceratohyal. Most species have relatively slender ceratohyals. *Cyprinella garmani*, *lutrensis*, *lepida*, *proserpina*, *panarcys*, *rutila*,

analostana, *chloristia*, *whipplei*, and *spiloptera* have very deep elements (especially those of the *lutrensis* clade and *analostana*). Most species have relatively similar sized ceratohyals at a similar body size. *Cyprinella boca-*

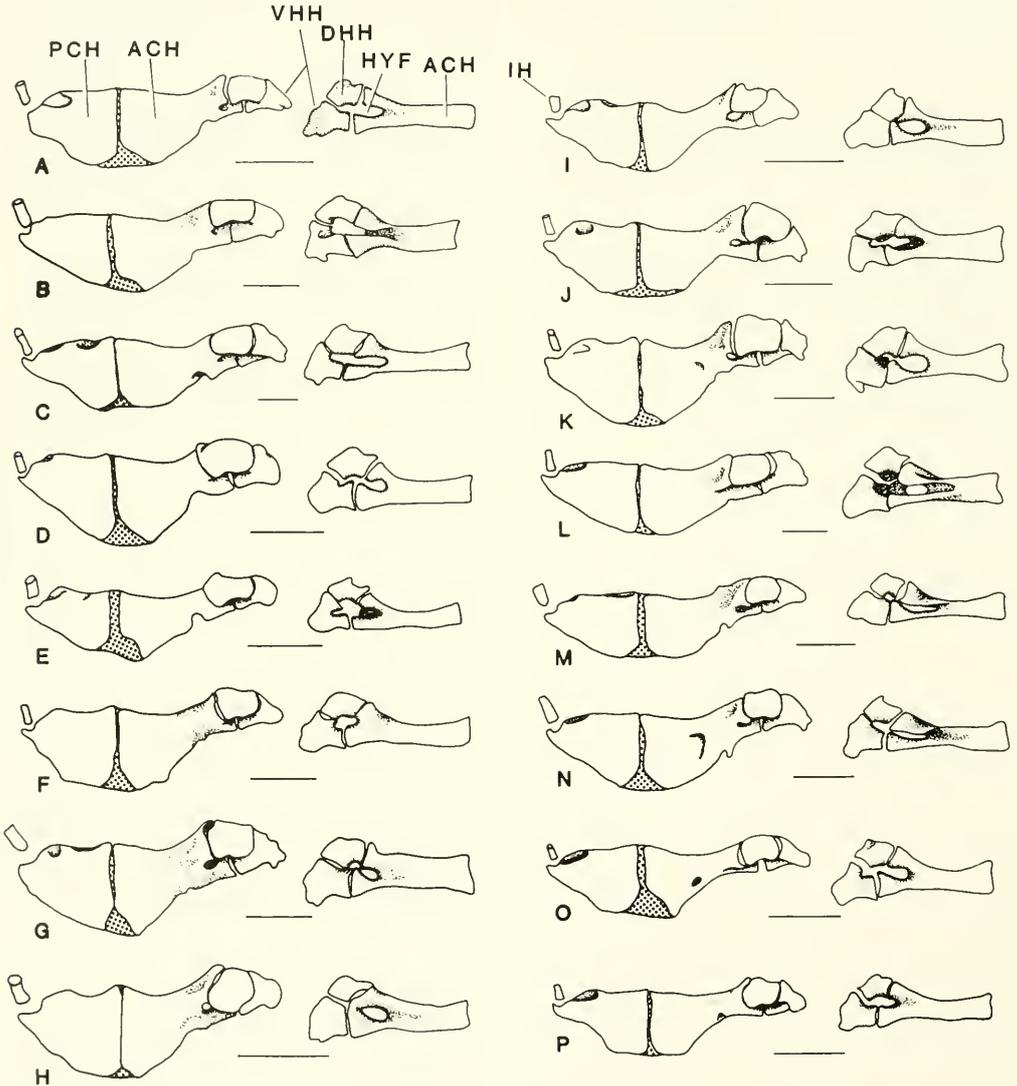


Fig. 75. Interhyals, ceratohyals, and hypohyals of species of *Cyprinella* and close relatives. A) *Notropis atherinoides*, 53 mm, KU 18935. B) *Lythrurus umbratilis*, 59 mm, KU 15521. C) *Luxilus cardinalis*, 82 mm, KU 15281. D) *Cyprinella garmani*, 50 mm, KU 5416. E) *C. bocagrande*, 32 mm, KU 20399. F) *C. lepida*, 50 mm, TU 55189. G) *C. proserpina*, 58 mm, TNHC 3262. H) *C. rutila*, 50 mm, ASU 5982. I) *C. xanthicara*, 43 mm, ASU 3642. J) *C. chloristia*, 55 mm, KU 8882. K) *C. analostana*, 56 mm, INHS 77855. L) *C. venusta*, 78 mm, KU 8810. M) *C. trichroistia*, 60 mm, KU 18853. N) *C. gibbsi*, 58 mm, KU 18892. O) *C. callisema*, 53 mm, KU 8842. P) *C. callitaenia*, 58 mm, TU 92770. Horizontal bar equals 1 mm.

grande is an exception and has a more elongate ceratohyal, correlated with its enlarged head (a 32 mm SL specimen of this species has ceratohyals equal in length to a 43 mm *formosa*). Most species have thick and relatively strong necks on the anterior ceratohyal. *Cyprinella panarcys*, *proserpina*, and *rutila* have a broad neck. *Cyprinella callisema*, *callitaenia*, *leedsi*, and *xanthicara* all have very narrow anterior necks on the anterior ceratohyal.

Most *Cyprinella* have the foramina on the posterior ceratohyal located dorsally, along the top of the thickened dorsal margin as found in outgroups. Some species, however, have the posterior foramen located mesially and one species, *ornata*, has a lateral anterior foramen. Species with a mesoposterior foramen include *ornata*, *analostana*, *chloristia*, *spiloptera*, and *leedsi*.

Location and size of the hypohyal foramen varies interspecifically. Some species have the foramen confined to the anterior ceratohyal, while in others it is equally bounded by the anterior ceratohyal and both hypohyals. Adults of *xanthicara*, *rutila*, *proserpina*, *panarcys*, and *venusta* have the hypohyal foramen restricted to the anterior ceratohyal. In these taxa the foramen is restricted by the expansion and condition of the dorsal and ventral processes anteromedially or as a result of the foramen passing through the shaft of the bone (e.g. *xanthicara*). In some individuals of *rutila* the foramen is also bounded by both hypohyals. The hypohyal foramen is quite large in most species. In the *caerulea* species complex the foramen is a narrow slit and in *galactura*, *lutrensis*, and *ornata*, it is very small and generally confined anteriorly.

Hypohyal (HH, Figs. 75, 76). These paired cartilage bones articulate with one another and each with the anterior ceratohyals. The dorsal hypohyal (DHH) also articulates with the basihyal posteriorly via a ligamentous connection. The ventral hypohyal (VHH) is more ornate, developing tubercle scars from ligaments connecting the right and left elements, and connecting each element to the anterior urohyal and basihyal. In most members of the

genus and in the outgroups the dorsal and ventral elements are subequal in size. In *rutila* and *xanthicara* and species in the *pyrrhomelas* and *nivea* species groups the dorsal element is smaller than the ventral.

Basihyal (BHY, Figs. 77, 78). In most *Cyprinella* the basihyal is a relatively long bone. It lies at the anterior end of the branchial region and extends forward to near the tip of the mouth. Posterodorsally the basihyal is connected to the anterior end of the first basibranchial. Posteroventrally a ligament extends from the center of the basihyal to the anteroventral edge of the first basibranchial (Fig. 77).

As viewed dorsally, the basihyal is generally rodlike to weakly triangular, with the widest aspect anteriorly and narrowing gradually to near its posterior extent where it is then more expanded (Fig. 78). The shape of this bone is variable. Within the same species the shape of the basihyal may range from narrow and cylindrical to a more triangular shape. Laterally, the basihyal is straight to slightly-arched upward (Fig. 77). Contrary to observations by Coburn (1982), most *Cyprinella* develop a process posteroventrally on the basihyal where there is ligamentous attachment to the first basibranchial (Fig. 77). In most species and individuals there are two concavities midlaterally (one per side) for the attachment of the ligament extending to the ventral hypohyal. These cavities are generally fairly small except in *lutrensis*, *garmani*, *whipplei*, *chloristia*, and *analostana* where they are large (Fig. 77). Additional variation includes the relative depth of the basihyal. All species have basihyals with a similar narrow depth except for *whipplei*, *lutrensis*, *garmani*, *lepida*, and *formosa* that have noticeably deeper basihyals (Fig. 77). In the former three the increased depth is attained by enlarging the centrally located keel. In *formosa* the entire basihyal is more robust (Fig. 77).

The deep basihyal morphology in *whipplei*, *lutrensis*, *garmani*, *lepida*, and *formosa* is considered derived because outgroups typically have the narrow development like other

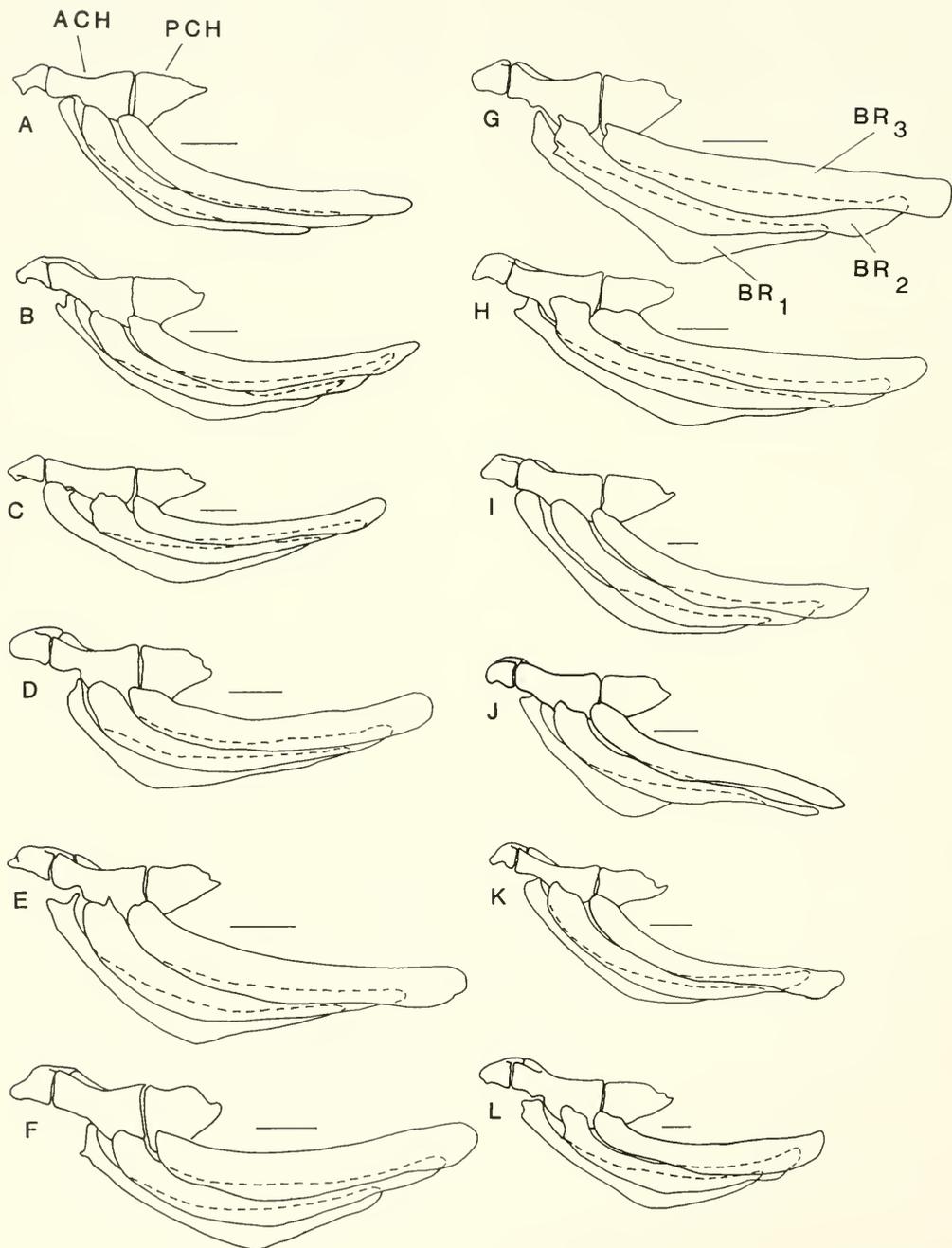


Fig. 76. Branchiostegal rays of species of *Cyprinella* and outgroups. A) *Notopis atherinoides*, 53 mm, KU 18935. B) *Lythrurus fumeus*, 57 mm, KU 6244. C) *Luxilus cardinalis*, 82 mm, KU 15281. D) *C. garmani*, 50 mm, KU 5416. E) *C. formosa*, 43 mm, KU 8399. F) *C. proserpina*, 58 mm, TNHC 3262. G) *C. rutila*, 50 mm, ASU 5982. H) *C. whipplei*, 63 mm, KU 14211. I) *C. venusta*, 78 mm, KU 8810. J) *C. trichroistia*, 60 mm, KU 18853. K) *C. caerulea*, 58 mm, KU 18978. L) *C. pyrromelas*, 73 mm, INHS 76978. Horizontal bar equals 1 mm.

members of the genus. Because the increased depth in these species appears to be due to different factors, the homologies of this character are uncertain. Further, because only juveniles of *bocagrande*, the presumed closest relative of *formosa*, are available, it is uncertain as to whether this species would develop a deep basihyal morphology. The develop-

ment of greatly enlarged midlateral cavities on the ventral surface of the basihyal is derived. Outgroups examined typically lack these cavities or, if present, they are small.

Urohyal (UO, Figs. 77, 79). Posteriorly this single median dermal bone is composed largely of a vertical plate medially and a horizontal plate ventrally. Anteriorly these thin

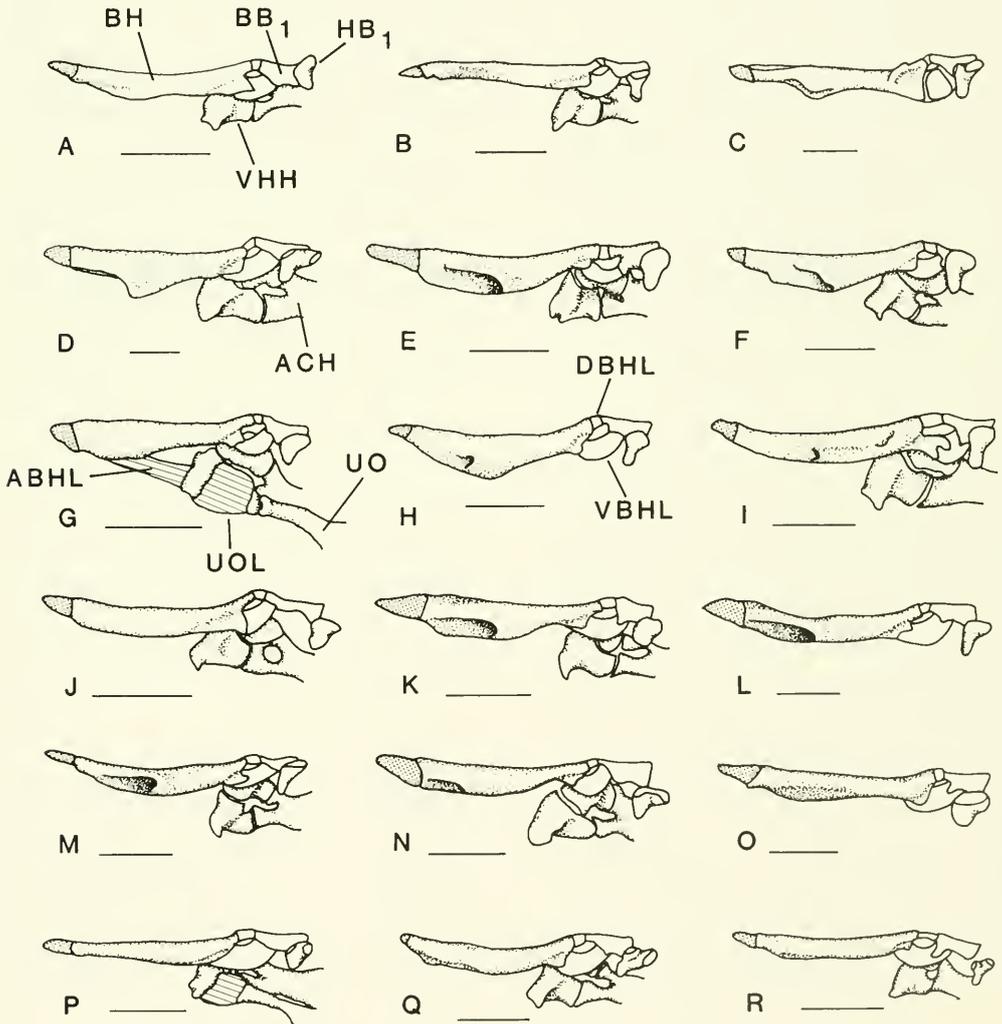


Fig. 77. Basihyals of some species of *Cyprinella* and close relatives. A) *Lythrurus lirus*, 45 mm, KU 18933. B) *L. fumeus*, 55 mm, KU 6244. C) *Luxilus zonistius*, 66 mm, KU 18995. D) *L. zonatus*, 85 mm, KU 12648. E) *Cyprinella garmani*, 50 mm, KU 5416. F) *C. lutrensis*, 53 mm, KU 19431. G) *C. formosa*, 43 mm, KU 8399. H) *C. lepida*, 49 mm, TU 55189. I) *C. proserpina*, 58 mm, TNHC 3262. J) *C. xanthicara*, 43 mm, ASU 3642. K) *C. whipplei*, 55 mm, KU 14211. L) *C. analostana*, 60 mm, INHS 77855. M) *C. chloristia*, 55 mm, KU 8882. N) *C. galactura*, 68 mm, KU 12029. O) *C. xaenura*, 71 mm, KU 18994. P) *C. nivea*, 50 mm, KU 18987. Q) *C. callisema*, 56 mm, KU 8842. R) *C. callitaenia*, 58 mm, TU 92770. Horizontal bar equals 1 mm.

plates merge into a heavy rounded neck which bifurcates into two anteriorly directed processes, separated from each other by a well-developed notch. The anterior face of each process is variably enlarged and serves as a point of attachment for the ligament extending from this bone to the ventral hypohyals (Fig. 77). The posterior margin of the ventral horizontal plate serves as a point of insertion for the *sternohyoïdes* muscle.

Variation in urohyal morphology includes width of horizontal plate, height of vertical plate, depth of anterior notch, and posterior margin of horizontal plate. Species with a broadly developed horizontal plate include *lutrensis*, *garmani*, *lepida*, *proserpina*, *panarcys*, some *rutila* (ASU 5982), *whipplei*, and *callistia*. All other *Cyprinella* have a narrowly developed ventral plate (Fig. 79). The vertical plate is deep in *callistia* and all species of the *lutrensis* clade, with the possible exception of *xanthicara* which has a slightly more narrow condition (Fig. 77). In all other species the vertical plate has a low profile (Fig. 77).

The posterior margin of the horizontal plate shows interspecific but little intraspecific variation. All species, except *ornata*, have either a forked or relatively straight posterior margin to the horizontal plate (Fig. 77). In *ornata* the posterior margin is ovoid (Fig. 77). Most species of *Cyprinella* have a shallowly developed notch with moderately developed posterolateral processes extending beyond the posterior extent of the vertically oriented plate for insertion of the *sternohyoïdes*. *Cyprinella formosa* and *bocagrande* have strongly developed posterolateral processes. *Cyprinella xaenura*, *pyrrhomelas*, *gibbsi*, *trichroistia*, *caerulea*, and species of the *nivea* group (except *callistia*) have reduced posterolateral projections and an almost straight posterior margin of the urohyal (Fig. 77). *Cyprinella callistia* has a deep notch and large projections.

Two conditions of the anterior notch separating the stout anterior arms of the urohyal exist in *Cyprinella*. Most species have a shallow notch. *Cyprinella xaenura*, *pyrrhomelas*, *trichroistia*, *gibbsi*, *caerulea*, *nivea*, *leedsii*,

callisema, and *callitaenia* have a notch that is deeply incised (Fig. 77).

Within *Cyprinella*, the narrowly developed ventral horizontal plate is derived. Species of *Luxilus* and *Lythrurus* have broad horizontal plates like *callistia* and species of the *lutrensis* clade (*xanthicara* and *rutila* are exceptions). Thus, the narrow ventral plate supports the monophyly of the *whipplei* clade and the *rutila* species pair. Independent reversals have apparently occurred in *whipplei*, *gibbsi*, and *callistia*. The reversed conditions in these species is not considered homologous since their structures are quite different (Fig. 77). *Cyprinella whipplei* and *callistia* have urohyals like outgroups and *gibbsi* has a uniquely shaped urohyal.

The deep vertical plate of the urohyal is derived in *Cyprinella*. Outgroups, *Luxilus* and *Lythrurus*, have the narrowly developed vertical plate like all other members of *Cyprinella*. Thus, the deep morphology supports the monophyly of the *lutrensis* clade and is apomorphic for *callistia*.

The presence of a shallow and concave posterior notch in the horizontal plate of the urohyal is primitive within *Cyprinella*. Two independent modifications of this condition have occurred. First, *ornata* has an ovoid urohyal and thus a convex posterior margin. This condition is apomorphic for this species. Second, species of the *nivea* and *pyrrhomelas* species groups have an almost straight posterior margin. This morphology is also derived and supports the sister relationship of these two species groups, if one considers the condition in *callistia* to be a reversal. The *pyrrhomelas* species group is also derived in lacking well-developed posteriorly directed processes for the attachment of the *sternohyoïdes*. In *formosa* and *bocagrande*, the posterior processes for *sternohyoïdes* attachment are enlarged and derived.

Development of a deeply incised anterior notch separating the stout anterior arms of the urohyal in the *pyrrhomelas* and *nivea* species groups is derived within the genus. Outgroups have a shallow notch like other *Cyprinella*.

Branchiostegals (BS, Fig. 76). These three

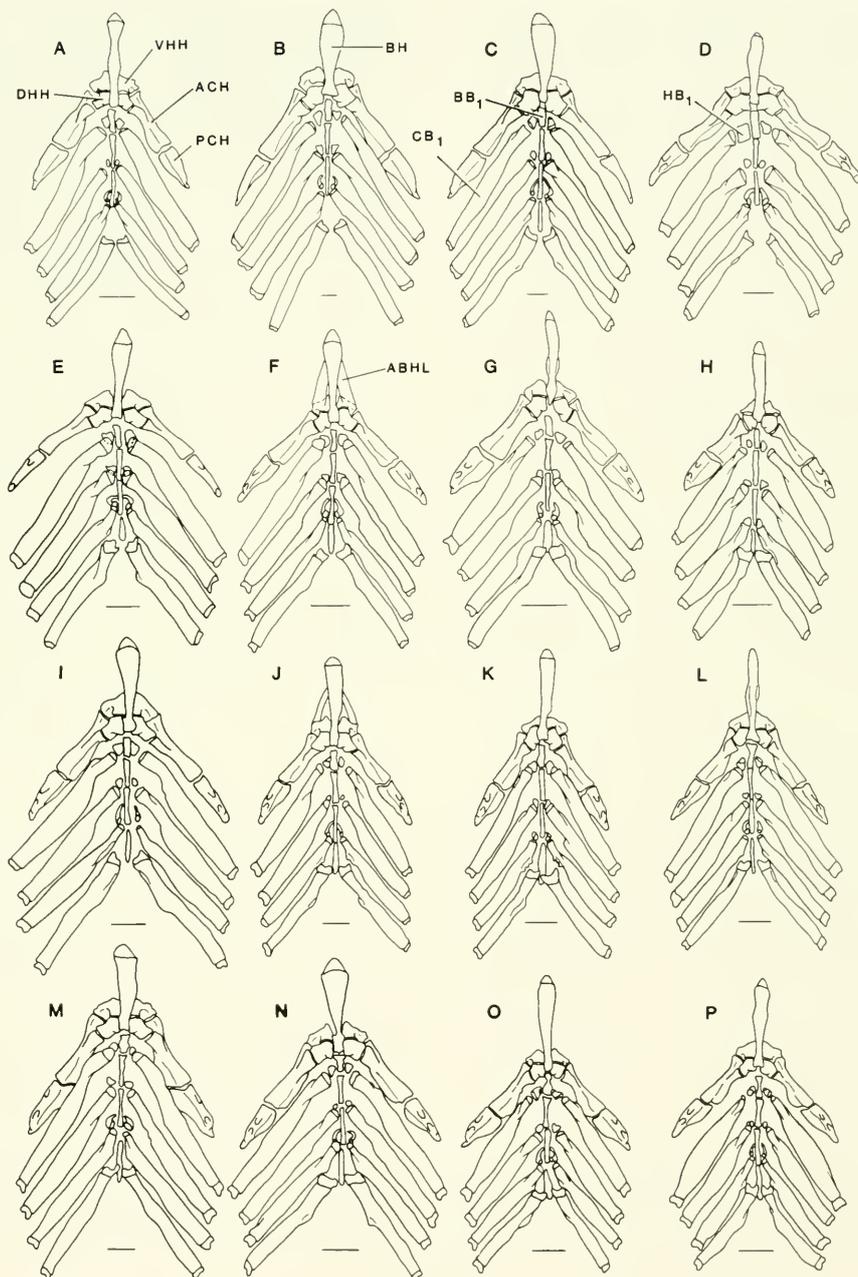


Fig. 78. Dorsal view of ventral portions of gill arches of some species of *Cyprinella* and close relatives. A) *Lythrurus fumeus*, 56 mm, KU 6244. B) *Luxilus cornutus*, 125 mm, KU 8686. C) *L. zonatus*, 88 mm, KU 12648. D) *Cyprinella ornata*, 34 mm, KU 8405. E) *C. lutrensis*, 54 mm, KU 19431. F) *C. lepida*, 54 mm, TU 55189. G) *C. proserpina*, 47 mm, TNHC 3262. H) *C. ruifila*, 50 mm, ASU 5982. I) *C. camura*, 61 mm, KU 19715. J) *C. spiloptera*, 68 mm, KU 11356. K) *C. analostana*, 56 mm, INHS 77855. L) *C. venusta*, 56 mm, KU 8810. M) *C. pyrhomelas*, 73 mm, INHS 76978. N) *C. gibbsi*, 58 mm, KU 18892. O) *C. nivea*, 60 mm, KU 18987. P) *C. callitaenia*, 58 mm, TU 92770. Horizontal bar equals 1 mm.

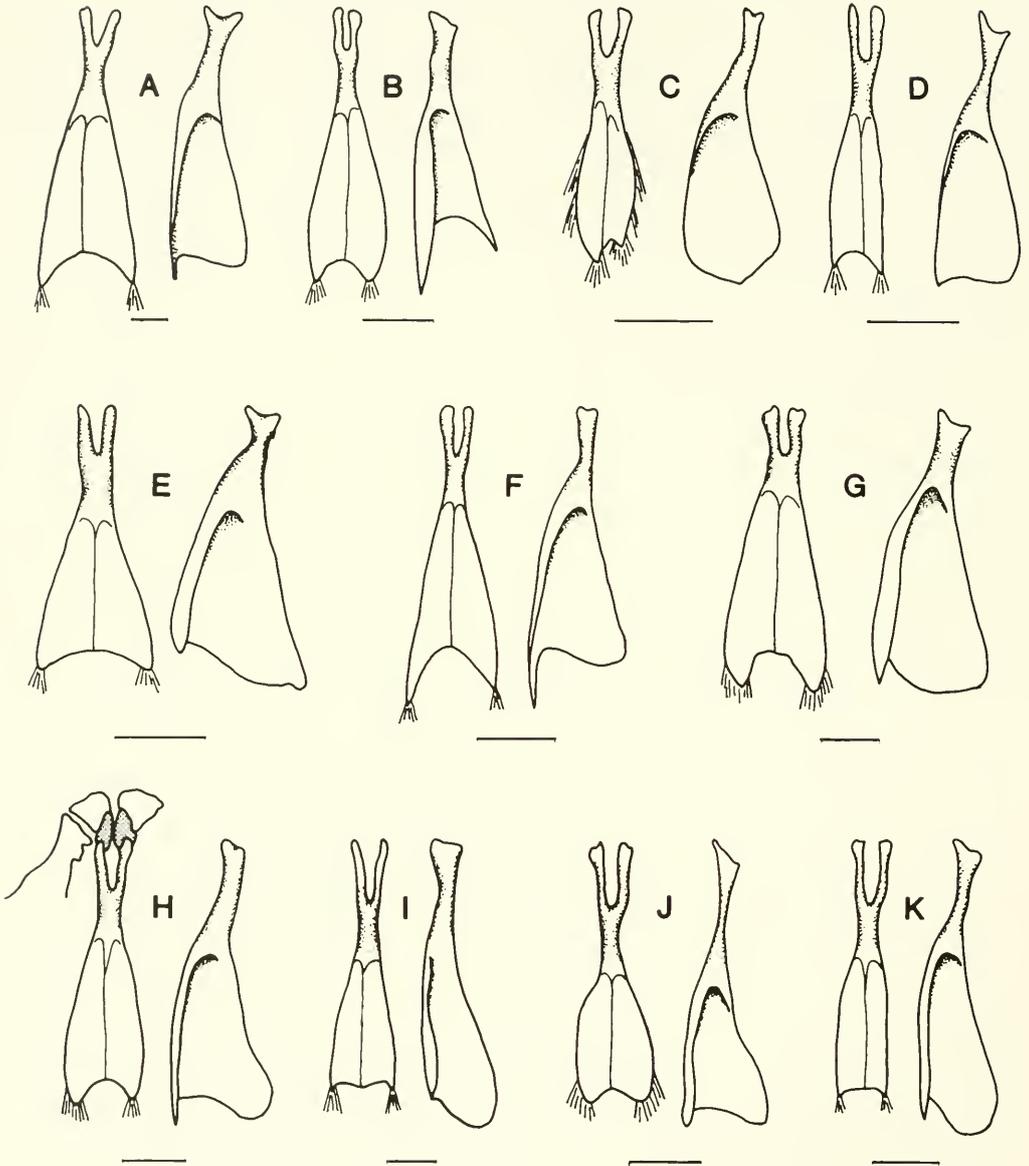


Fig. 79. Ventral (left) and lateral (right) view of urohyals for species of *Cyprinella* and outgroups. A) *Luxilus chrysocephalus*, 80 mm, KU 12654. B) *Lythrurus fumeus*, 56 mm, KU 6244. C) *Cyprinella ornata*, 34 mm, KU 8405. D) *C. xanthicara*, 43 mm, ASU 3642. E) *C. garmani*, 50 mm, KU 5416. F) *C. formosa*, 43 mm, KU 8399. G) *C. callistia*, 78 mm, KU 18848. H) *C. chloristia*, 55 mm, KU 8882. I) *C. xaenura*, 71 mm, KU 18994. J) *C. gibbsi*, 58 mm, KU 18892. K) *C. callisema*, 56 mm, KU 8842. Horizontal bar equals 1 mm.

flattened dermal bones articulate anteriorly with the ceratohyals. The first two are attached to the anterior ceratohyal. Branchiostegal 1 is attached by an anterior process, fitting into a small notch in the lateral face of the anterior ven-

tral edge of the ceratohyal. The second is pressed against the lateral surface. The third is connected to the lateral surface, between the anterior and posterior ceratohyals. All three are similar in shape, most often lunate. The

first is the narrowest and is strongly bent in adults, producing a mesially directed, right angle process. The second and third are less sharply bent, being moderately curved.

Very little variation occurs in *Cyprinella*. Most species have branchiostegals of similar length. *Cyprinella pyrrhomelas* and *xaenura* have short branchiostegals. Branchiostegals 2 and 3 are expanded and broad in the *lutrensis* clade (except *xanthicara*), while narrow in other taxa. The anterior neck of the first element is narrow and pointed in *panarcys*, *proserpina*, *rutila*, and *xanthicara*, and broad and expanded anteriorly in other species. *Cyprinella trichroistia* has an unusually thin first element, reduced posteriorly and pointed.

The short, broad, and narrow neck conditions of the branchiostegals are derived in *Cyprinella*. Species of *Luxilus*, *Lythrurus*, and most *Notropis* have narrow branchiostegals with a broad anterior neck where they articulate with the ceratohyals. Most of these taxa also have long branchiostegals like most *Cyprinella*.

BRANCHIAL REGION

The bones of the branchial series form the gill arches. Included are the pharyngobranchials, epibranchials, ceratobranchials, hypobranchials, and basibranchials (Figs. 78, 80). All of the elements are cartilage and paired, except the basibranchials, which are ventral, medial, and unpaired. The dorsal gill arch elements (epibranchials and pharyngobranchials) are suspended from the ventral neurocranium and are connected to the ventral gill arch elements (ceratobranchials) laterally. Gill rakers are of dermal origin and are associated with all paired elements.

Pharyngobranchials (PBR1–4, Fig. 80). These paired, robust endochondral bones articulate end to end with each other medially and laterally with all epibranchials. Only the first three are ossified, the fourth remaining cartilage, and the second and third become fused (Hubendick, 1942). Thus, as adults there are two ossified anterior elements and one posterior cartilage element. The first is robust

and semi-oval to tear-shaped, lying partially beneath and articulating posteriorly with the fused second and third compound element. Laterally, the first articulates with the mesial end of the first epibranchial and articulates via a cartilage cap. Epibranchial 2 also has a cartilage connection with the posterolateral face of pharyngobranchial 2. The fused second and third pharyngobranchial is more elongate and lunate in shape. This element articulates laterally with the mesial ends of epibranchials 2 and 3. The cartilaginous fourth element articulates with the posterior margin of pharyngobranchial 2 and 3 and the medial cartilage tip of epibranchial 4.

Variation of the pharyngobranchials was minimal and restricted to minor shape differences. Most *Cyprinella* have pharyngobranchials like closest outgroup relatives *Luxilus* and *Lythrurus*. The first element is typically tear-shaped with a broad and rounded anterior end that narrows posteriorly (Fig. 80). Dorsally, the posterior half of pharyngobranchial 1 has an obvious recessed region where the fused second element seats. In *analostana* and *chloristia* the anterior margin does not make a smooth curve, but has a laterally directed anterior tip, giving the bone a more sinuous profile (Fig. 80). *Cyprinella leedsi* and *nivea* both differ from other species in having a more elongate and narrow first element (Fig. 80).

Pharyngobranchial 2 is a more elongate element and shows more interspecific variation. In most species, like outgroups, the bone is lunate with narrow posterior and anterior tips and a broad medial region. The dorsal surface of all species except members of the *nivea* group differs from species of *Luxilus* and *Lythrurus* in having considerably more topographic differentiation. Members of the *nivea* species group as well as the above mentioned outgroups, except *Luxilus pilsbryi*, have relatively smooth dorsal surfaces on the fused pharyngobranchial 2 and 3 (Fig. 80). Species of the *nivea* group also vary from other members in having more elongate elements (Fig. 80). In *bocagrande* and *formosa* pharyngobranchial 2 is more narrow and straightened

(Fig. 80). In *panarcys*, *proserpina*, *rutila*, and *xanthicara* the lateral edge of this element is expanded into a well-developed shelf (Fig. 80). *Cyprinella lepida* also develops a shelf laterally, but in this species it is not as extensive as in other members of the *lepida* species group (Fig. 80)

Epibranchials (EB1–4, Fig. 80). All four epibranchials articulate with their respective ceratobranchials laterally and with the two pharyngobranchials medially. Epibranchials 1–3 are approximately the same size, but are relatively thin and grooved dorsally for the branchial arteries as in the ceratobranchials. Mesially where they articulate with the pharyngobranchials they are thickened and robust. The anterior margin of the first epibranchial is slightly angled in most species with the highest point mesially to slightly anteromesially. Posteriorly, its margin is relatively straight lateral to the uncinat process. Mesial to the uncinat process it is restricted medially and develops a thickened neck. Epibranchials 2 and 3 are more flattened relative to the first and slightly wider, but are like the first except for a broader neck and wider head. The posteriorly directed uncinat processes of the second and third elements are also more strongly developed, the third being the largest of the three. Epibranchial 4 is the most distinctive of the four. The shaft of this element is more slender and heavier than others, the uncinat process is heavier and more laterally placed, and a dorsally directed process is developed mesial to the attachment point of the uncinat process of epibranchial 3.

Variation of epibranchials is expressed mainly in overall shape. At a given body size, however, the overall size of epibranchials is similar. The first element varied with respect to shape of the anterior margin, orientation of the mesial neck, and connection of the flattened posterolateral plate to the thickened mesial neck. In all *Cyprinella* except *bocagrande* and *formosa*, as well as outgroups, the posterior plate connects and is continuous with the mesial neck ventrally (Fig. 80). In these two species, connection of the plate is more dorsally placed,

forming a ridge posteriorly on the neck (Fig. 80) and creating a shelf. The anterior margin of the first element is moderately straight in *ornata*, has a high anteriorly directed ridge in *bocagrande*, *formosa*, *camura*, *spiloptera*, *whipplei*, *analostana*, *chloristia*, *galactura*, and *venusta*, or has a medial ridge as in all other species.

Like all outgroups, except for *Luxilus pilsbryi*, *L. cardinalis*, and *L. zonatus*, the mesial neck of epibranchial 1 in most *Cyprinella* is straight. Species of the *lutrensis* clade, except for *xanthicara* and some *rutila* (ASU 5982), *chloristia*, *venusta*, *trichroistia*, and *gibbsi* all have a posteriorly directed neck. In *xanthicara* and some *rutila* the neck is directed anteriorly. Generally, the expanded mesial neck and the lateral body are oriented in the same plane. In *analostana* and *chloristia*, however, the head is rotated about 45 degrees from the plane.

In overall shape the second epibranchial is similar to the first. Generally, the uncinat process is larger and the mesial neck is less pronounced. In some species the neck is straight like all close outgroups except *fumeus*, and in others it is directed anteriorly. Species with the anteriorly directed mesial neck includes *panarcys*, *proserpina*, *xanthicara*, *chloristia*, *analostana*, *pyrrhomelas*, *xaenura*, *galactura*, *trichroistia*, *gibbsi*, *caerulea*, *nivea*, *callisema*, and *callitaenia* (Fig. 80). In *trichroisia*, *gibbsi*, *xaenura*, *pyrrhomelas*, *nivea*, and *callisema* the neck is more pronounced, having a well-developed posterior notch mesial to the uncinat process (Fig. 80).

Other variants of epibranchial 2 include the location of the connection of the ligament between the uncinat process of epibranchial 1 and the anterior margin of epibranchial 2. In most *Cyprinella* and all outgroups the connection to the second element is anterior to the uncinat process of the same bone. In *nivea* and *leedsi* the connection is lateral to this point (Fig. 80).

Little variation of systematic importance was noted in epibranchial 3. *Cyprinella proserpina*, *rutila*, and *xanthicara* have an

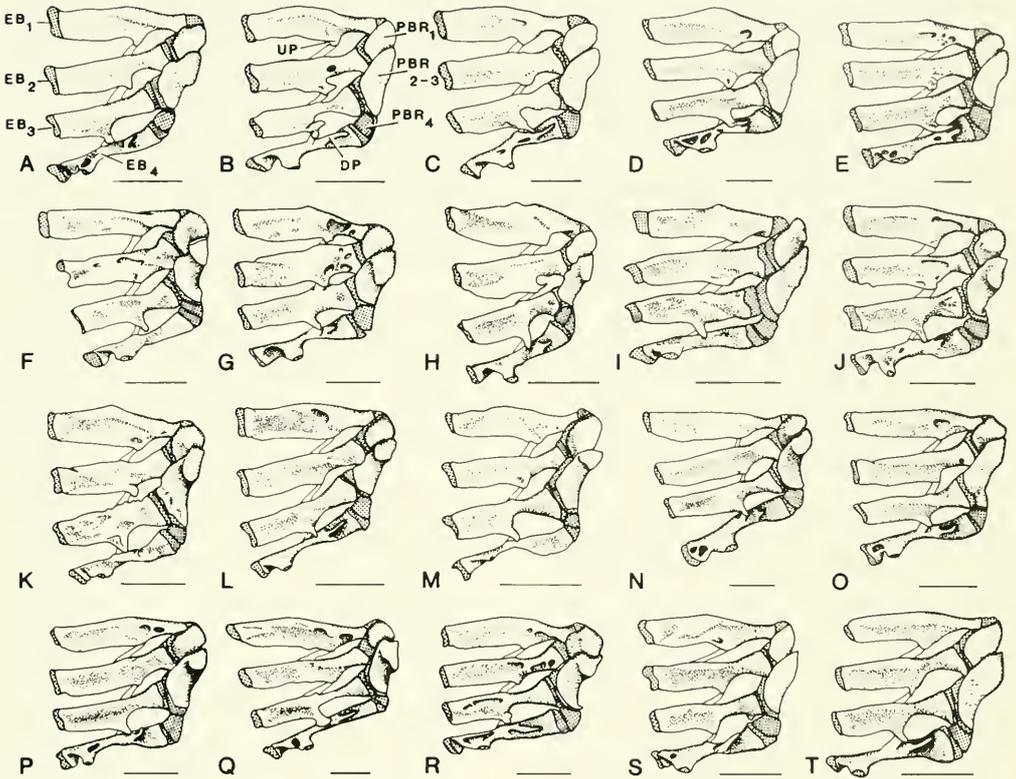


Fig. 80. Epibranchials and pharyngobranchials of species of *Cyprinella* and close relatives. A) *Notropis atherinoides*, 53 mm, KU 18935. B) *Lythrurus fumeus*, 56 mm, KU 6244. C) *L. ardens*, 72 mm, KU 4136. D) *Luxilus zonatus*, 67 mm, KU 12648. E) *L. chrysocephalus*, 80 mm, KU 12654. F) *Cyprinella ornata*, 44 mm, KU 8405. G) *C. lutrensis*, 55 mm, KU 19431. H) *C. formosa*, 43 mm, KU 8399. I) *C. bocagrande*, 32 mm, KU 20399. J) *C. lepida*, 48 mm, TU 55189. K) *C. panarcys*, 42 mm, UMMZ 208212. L) *C. ruilla*, 52 mm, ASU 30264. M) *C. xanthicara*, 42 mm, ASU 3642. N) *C. camura*, 61 mm, KU 19715. O) *C. analostana*, 60 mm, INHS 77855. P) *C. chloristia*, 55 mm, KU 8882. Q) *C. pyrrhomelas*, 73 mm, INHS 76978. R) *C. gibbsi*, 58 mm, KU 18892. S) *C. nivea*, 62 mm, KU 18987. T) *C. callisema*, 53 mm, KU 8842. Stippled regions represent cartilage. Horizontal bar equals 1 mm.

anteriorly directed mesial neck, like the second epibranchial of other *Cyprinella* (Fig. 80). Most species have a moderately restricted neck like other cyprinids examined. In *lutrensis*, *bocagrande*, *lepida*, *panarcys*, *callistia*, and *callitaenia* the neck is more broadly developed and in *xanthicara*, *xaenura*, *pyrrhomelas*, *trichroistia*, and *gibbsi* the neck is narrow (Fig. 80).

Variation in the fourth epibranchial includes width of the element, the degree of development of the dorsally directed mesial fingerlike process, and the length of the bone mesial to the uncinatous process. The width of this bone is

similar in all species, like most other cyprinids, except in *xaenura* and *pyrrhomelas*. These species have a very narrow condition (Fig. 80). The dorsally directed process posterior to the uncinatous process of the third epibranchial is consistently developed in all species except members of the *lutrensis* clade (Fig. 80). In this group, development of this process is very spotty, some individuals have no process and others have the process developed only on one side. Further, if present in this group, it is almost always small.

Mesial to the uncinatous process of epibranchial 4 the body of this bone is generally

elongate. The species *ornata*, *lutrensis*, *garmani*, *formosa*, *trichroistia*, and *callistia* all differ in having a shorter mesial portion to this element (Fig. 80).

The dorsal connection of the posterior plate of epibranchial 1 to the mesial neck is derived in *Cyprinella*. In all other species and outgroups the connection is ventral and no shelf is formed. Having a straight neck on epibranchial 1 in *Cyprinella* is primitive for the group since all outgroups, except *Luxilus zonatus*, *L. cardinalis*, and *L. pilsbryi*, have a straight neck. Thus, the posteriorly directed neck is derived for the *lutrensis*, *formosa*, and *lepida* species groups, *chloristia*, *venusta*, and the *gibbsi-trichroistia* species pair. The anteriorly directed tip of the neck in some *rutilla* and *xanthicara* is considered a further derivation from the straight or posteriorly directed condition.

Polarity of the ridge along the anterior margin of epibranchial 1 is difficult to determine. The conditions present in outgroups varies from having a medial to anterior ridge. All species of *Lythrurus* have a medial ridge, except *umbratilis*, which has the anterior ridge. Within *Luxilus*, *pilsbryi*, *cardinalis* and *zonatus* have a medial ridge and others develop the ridge anteriorly. The ridge in *Notropis atherinoides* and other *Notropis* (s.s.) is anterior. Thus, one interpretation of the evolution of this characteristic is for an anterior condition to be primitive in the ancestor of *Cyprinella* and a medial condition developed in the ancestor of *Lythrurus* and in the *pilsbryi-zonatus* species group of *Luxilus*. Within *Cyprinella*, the medial morphology is derived for the *pyrrhomelas* and *nivea* species groups, as well as in some species of the *lutrensis* clade. Other species have retained the primitive anterior condition.

The anteriorly directed and restricted neck of the second epibranchial is derived for *Cyprinella*. Outgroups, except *Lythrurus fumeus*, have a straight neck. The distribution of the anteriorly projected neck of epibranchial 2 is spotty, however, and requires several changes in the evolution of this character. The laterally

placed insertion of the ligament on the anterior face of epibranchial 2 is also derived within this genus. Close outgroups such as *Luxilus* and *Lythrurus* have a more mesially placed ligament.

The narrow epibranchial 4 is derived in *Cyprinella*. In close outgroups this element is similar to species with the broad morphology. The weakly and variably developed dorsal process of epibranchial 4 is unusual, but is considered derived for the *lutrensis* clade. Generally, every individual of other taxa consistently develop this process.

Ceratobranchials (CBR1–5, Fig. 78). The first four of the five ceratobranchials are thin and ventrally concave. The first three articulate mesially with hypobranchials 1–3, while the fourth articulates with the unossified copula extending from the posterior end of basibranchial 3 to the anterior arm of ceratobranchial 5. Each of these bones is tipped mesially with an ovoid or rounded cartilage and laterally with a forked cartilaginous element. Laterally the profile of these first four bones from their lateral articulation with epibranchials to mesial hypobranchial articulation is slightly concave, the lowest aspect being medially. The fifth pair of ceratobranchials represents the heavy pharyngeal arches.

Variation in morphology of ceratobranchials 1–4 is primarily with respect to shape. Some species also vary in relative lengths of these bones. At similar body sizes *lutrensis*, *camura*, *chloristia*, *pyrrhomelas*, *xaenura*, *trichroistia*, and *gibbsi* had longer ceratobranchials than remaining members of the genus (Fig. 78). The elongate nature of these bones in these species was not correlated with overall width. *Cyprinella camura* and *lutrensis* have broader ceratobranchials like other members of the genus, while the remaining species with the elongate morphology have narrow ceratobranchials.

The shape of the first ceratobranchial is roughly rectangular, although typically widest medially, primarily from the expansion of the posterior margin. In some taxa a restricted anteroventral neck is present before articula-

tion with the first hypobranchial. In most species the anterior end is straight. The restricted neck is present in *rutila*, *xanthicara*, *spiloptera*, and species of the *nivea* species group (Fig. 78). In *xaenura*, *pyrrhomelas*, *trichroistia*, *gibbsi*, *lutrensis*, and *camura*, however, the anterior tip is bent mesially towards the first hypobranchial approximately 30–45° from the primary axis. In members of the *nivea* group and *rutila* the anterior margin of the first ceratobranchial is expanded anteriorly, producing a wider medial region than in other species (Fig. 78).

Morphology of the second ceratobranchial is similar to the first except that all species excluding *ornata* (Fig. 78) have a narrowing of the anterior end into a neck. In most taxa the narrowed neck is short, but in *lepida*, *panarcys*, *proserpina*, *rutila*, *xanthicara*, *camura*, and *trichroistia* it represents up to one-half the total length.

In most species ceratobranchial 3 is a relatively straight bone with a small restricted anterior neck. *Cyprinella xanthicara* and *rutila* are distinctive in having a rounded and expanded anterolateral margin (Fig. 78), compared to a straight margin as is found in other members of the genus. These species plus *proserpina* and *panarcys* also have a more elongate anterior neck (Fig. 78). The posterior margin of ceratobranchial 3 in most *Cyprinella* is smooth and straight except for a small posteriorly directed process near the posterior end of the anterior neck. In *analostana* and *chloristia* this process is serrated (Fig. 78).

Unlike the first three, the fourth ceratobranchial articulates with the unossified copula, has an expanded anterior end, and is the shortest of the series of four. The typical morphology of this bone is to have the posterior two thirds being relatively straight and the anteriormost third bent anteriorly. Similar to ceratobranchial 3, many species have a smooth process on the posterior margin near the anterior end. *Cyprinella pyrrhomelas*, *xaenura*, *trichroistia*, *gibbsi*, *caerulea*, *callistia*, *nivea*, *leedsi*, *callitaenia*, and *callisema* have a very reduced process or none at all.

Determining the polarity of the variation in the length of ceratobranchials 1–4 in species of *Cyprinella* is difficult. All species, except *lutrensis*, *camura*, *chloristia*, *pyrrhomelas*, *xaenura*, *trichroistia*, and *gibbsi* have short ceratobranchials. Species of *Luxilus* and some members of *Lythrurus* have long ceratobranchials. One may interpret the short condition of most *Cyprinella* to represent a derived condition for the genus and reversed to elongate elements in the above species and species groups. This is a possibility since *lutrensis* and *camura* both have elongate ceratobranchials for their size, but they are also broad like other *Cyprinella*. Other taxa with the elongate condition have narrow ceratobranchials, different from *lutrensis* and *camura*.

The restricted neck of ceratobranchial 1 appears to be derived for *Cyprinella*, but appears to have been derived several times within the genus. The restricted neck is evidence for the monophyly of the species pair *rutila* and *xanthicara* and for the *nivea* species group. It also represents an autapomorphic condition for *spiloptera*.

The bent anterior neck of the first ceratobranchial is derived in *Cyprinella*. Species of *Luxilus* and *Lythrurus* all have a straight neck and thus the bent neck supports the monophyly of the *pyrrhomelas* species group and is apomorphic for *camura* and *lutrensis*. Having an expanded anterior margin on the first ceratobranchial is also a derived condition. Species of close outgroups all have straight anterior margins on ceratobranchial 1. Thus, this morphology supports the monophyly of the *nivea* species group and is apomorphic for *rutila* independently.

An elongate and narrow anterior neck on ceratobranchial 2 has been derived three times. Close outgroups have a short, poorly developed and reduced neck like many members of *Cyprinella*. Thus, the long and slender neck of the second ceratobranchial is evidence for the monophyly of the *lepida* species group and is apomorphic in *trichroistia* and *camura*.

The rounded anterior margin of the third ceratobranchial in *rutila* and *xanthicara* and

the elongate neck in these species and *panarcys* and *proserpina* is derived within *Cyprinella*. Outgroups and other species of *Cyprinella* typically have straight anterior margins and weakly developed necks or no necks at all.

A posterior process on ceratobranchial 3 is common in *Cyprinella* and outgroups, but having a serrated edge is derived. This morphology supports the monophyly of the *analostana-chloristia* species pair.

Hypobranchials (HB1–3, Figs. 77, 78). These three paired ossifications are lateral to the basibranchials and at the anteromesial ends of the first three ceratobranchials. The first and second are heaviest and rounded or oblong when viewed dorsally (Fig. 78) and both are more elongate dorsoventrally. The third is the smallest dorsally and develops a thin, elongate ventral process which curves anteromesially. In most species a single, dorsal cartilage head is developed on all three pairs in juveniles and adults. In some species, however, the first hypobranchials have the single dorsal cartilage head divided by a median ossification producing two heads, one anteriorly and one posteriorly. Species with this development include *callisema*, *callistia*, *callitaenia*, *leedsii*, and *nivea* (Fig. 78). The dorsal cartilage head of hypobranchials 2 and 3 is single in all species.

Development of a double cartilage head on hypobranchial 1 is derived within *Cyprinella*. Outgroups, except for *Luxilus zonistus*, *L. coccogenis*, *L. pilsbryi*, *L. cardinalis*, and *L. zonatus* have a continuous dorsal cartilage head.

Basibranchials (BB1–3, Figs. 77, 78). These three small, quasi rod-shaped perichondral ossifications form the medial axis of the gill arch. They articulate end to end and anteriorly with the posterior tip of the basihyal (Fig. 78). The first is always the smallest of the three and in dorsal profile is cylindrical or hourglass shaped. As viewed laterally, it is deepest posteriorly and narrows anteriorly with an occasional ventral process developed where it receives a ligament from the posteroventral margin of the basihyal (Fig. 77). The second

and third are generally equal in length, but longer than the first, and are cylindrical. The third is connected posteriorly to a slender unossified copula that bifurcates posteroventrally and articulates with the anteroventral arms of the fifth ceratobranchials. All three basibranchials articulate laterally with the hypobranchials.

Variation in basibranchial morphology is minimal. In *venusta* and *analostana* the first basibranchial is typically longer than in other species (Fig. 78). In some species the first basibranchial is hourglass in shape when viewed dorsally, with the anterior and posterior ends being broadest and the smallest diameter located medially. The constriction of basibranchial 1 is best developed in species of the *nivea* group (except *callisema*), but was apparent in *trichroistia*, *gibbsii*, *callistia*, *caerulea*, *xaenura*, and *pyrrhomelas* (Fig. 78). A more weakly developed hourglass shape occurs in *whipplei*, *analostana*, *chloristia*, *spiloptera*, *galactura*, and *venusta* (Fig. 78). In other species the first basibranchial has a uniform diameter and appeared cylindrical (Fig. 78).

The increasing development of an hourglass-shaped first basibranchial is derived within *Cyprinella*. *Cyprinella whipplei*, *analostana*, *chloristia*, *spiloptera*, *galactura*, and *venusta* have the derived condition, but the constriction is slight. Species of the *nivea* species group represent the extreme in development of this morphology. Outgroups all have the cylindrical basibranchial 1 with no constriction.

WEBERIAN APPARATUS

This osteological complex is probably the most complicated series of bones in the cyprinid skeleton (Fig. 33). Composed of the pars auditum and par sustenaculum, the apparatus is an otophysic connection between the anterior air bladder chamber and the inner ear. The par auditum is the series of four small ossicles interconnected by the interosseus ligament. These elements are used to transmit sound from the gas bladder to the ear. The pars

sustenaculum includes the gas bladder and first four modified vertebrae and arches which act as support for the ossicles. Variation in *Cyprinella* and other cyprinids examined was essentially nonexistent.

Pars sustenaculum. The first vertebra of the pars sustenaculum is thin and articulates anteriorly with the proatlas of the basioccipital. A short and stout transverse process is produced laterally and is connected to the supracleithrum by a ligament. Because the ligament may become ossified, the length of the transverse process is somewhat variable intraspecifically. The movable scaphia and claustra are located dorsolaterally and dorsally on this centrum, respectively (Fig. 33).

The second, third, and fourth centra are increasingly larger than the first and are more amphicoelous. Arising ventrolaterally from the second centrum are two large and stout transverse processes, one per side. Dorsally the large, platelike second neural arch is separate from the centrum by the anterior extension of the third neural arch. The intercalaria ossicles articulate laterally and dorsolaterally on this centrum.

The third centrum is large and articulates with an enlarged neural arch which supports most of the dorsal neural complex. Laterally, this centrum has a channel on each side for the articulation of the large tripus. The neural arch to this element is broad at the base, constricted medially, and expanded anteriorly near the dorsum. The anterior expansion separates the second neural arch and centrum.

Centrum four supports an enlarged neural arch and elongate spine dorsally. Ventrolaterally it supports the enlarged os suspensoria and enlarged parapophyses. The enlarged parapophyses extend laterally and slightly anteriorly from the centrum. The os suspensorium extends posteriorly and lies against the tunica externa of the swimbladder. This structure represents an independent ossification of the third centrum that migrates posteriorly and becomes fused to the parapophyses of centrum four (Niazi, 1964; Coburn, 1982).

The neural complex is located above the

third neural arch. This complex is posterior to the neural arch of centrum 2 and anterior to the neural arch and spine of centrum 4. It has an expanded and arched base which narrows dorsally to a neck of variable width. Dorsally, a divided V-shaped crest is formed and is larger than the base and median neck. Only occasionally will the anteriormost predorsal bone extend between the walls of this crest. Large ligaments extend between the neural complex and the supraoccipital crest and exoccipital.

The neural crest, together with the neural spine of centrum 4, are the only systematically variable structures noted in *Cyprinella* and outgroups. Relative to close outgroups, all species of *Cyprinella* have an elevated neural complex and fourth neural spine. These structures are extremely tall in most species of the *lutrensis* clade (Fig. 33). The height of the neural complex and fourth neural spine in *rutila* and *xanthicara* is like species of the *whipplei* clade, representing a reversed and derived condition for these two species. All other members of the *lutrensis* clade, however, are derived in having a very tall neural complex (Fig. 33).

Pars auditum. Included here are the Weberian ossicles, including the claustrum, scaphium, intercalarium, and tripus. These four elements are modifications of the first four vertebral elements and are ligamentously joined to transmit sound received by the gas bladder to the inner ear. None of these elements vary in *Cyprinella*.

The claustrum (CLA, Fig. 33) is above centrum 1 and covers the atrium sinus impar ventromedially. Dorsally it is roughly triangular and ligamentously joined posteriorly to the neural arch of centrum 2 and anteriorly to the exoccipital above the foramen magnum.

The scaphium (SCA, Fig. 33) is a small, ornate and complex bone. It articulates laterally on centrum 2, covers part of centrum 1, and forms the lateral walls covering the atrium sinus impar. As described by Coburn (1982), it may be divided into four parts, a large and mesially convex cup, a posterodorsally di-

rected spine (ascending process), a ventromedial articulating process, and a small, blunt tubercle posteriorly off the lateral surface of the cup for attachment to the interosseus ligament. Ligaments connect the dorsal spine to the second and third neural arches.

The intercalarium (ICA, Fig. 33) is the smallest ossicle and is roughly T-shaped. It is elongate and lies anteriorly on the lateral surface of the second centrum, oriented anteroventral to posterodorsal. Anteroventrally, the tip of this bone is expanded into a knob and is joined to the interosseus ligament. The articular process with centrum 2 is small and is opposite the dorsoposterior ascending process. The ascending process is joined by a ligament to the third neural arch.

The large, roughly triangularly shaped tripus (TRP, Fig. 33) is of compound origin, from a parapophysis and pleural rib. The most obvious features of this bone are the broad mesial articular surface and an anterior and posterior ramus. The parapophysis forms the medial triangular portion of the bone and the articular process; the pleural rib forms the large posterior process and a portion of the body and anterior ramus. The lateral margin of the posterior process is closely associated with the peritoneal tunic of the anterior chamber of the gas bladder. From the main body, this bone is curved mesially between the lateral process of the fourth rib and the os suspensorium. Distally, it tapers to a thin shaft and is attached to the tunic externa and to the posterodorsal surface of the os suspensorium via ligaments. The anterior ramus is elongate and connected anteriorly to the interosseus ligament.

VERTEBRAE

Posterior to the Weberian apparatus the vertebrae are separated into caudal and precaudal elements (Figs. 16, 33). Caudal vertebrae develop haemal spines and arches, and lack parapophyses. Generally, there are two transitional vertebrae. These elements have an incomplete haemal arch fused to the centrum and small, free ribs. On these vertebrae the haemal postzygapophyses are well developed

and the prezygapophyses are absent or weakly developed. The total number of vertebrae, inclusive of the first four Weberian elements, and the number of precaudal and caudal elements are given for each species in the species accounts section.

The precaudal vertebrae are monomorphic. Each has a well-developed neural spine directed posterodorsally and a prezygapophysis directed anterodorsally. The prezygapophyses are best developed anteriorly, extending almost to the neural spine of the preceding element and decrease in size posteriorly. Vertebra 5 has weakly developed prezygapophyses. Posterior to the neural spine are the small postzygapophyses. These processes are directed dorsally or posterodorsally and have a moderately large foramen at the base. Ventrolaterally, the ribs articulate with the parapophyses.

Between each of the neural arches and between the first neural arch and the neural complex are the predorsal bones. These elements are thin and platelike ventrally. In some they may be thickened dorsally and have a ventrally directed, medially thickened shaft. In the *whipplei* clade and all close outgroups, except for very large individuals of *Luxilus*, these bones are relatively small, largest anteriorly and decreasing in size posteriorly to the dorsal fin pterygiophores. Generally, they are absent or very small just before the dorsal fin. In the *lutrensis* clade, however, these bones are very large and sometimes ornate, and extend between the neural crest and the dorsal fin.

Caudal vertebrae are also generally monomorphic. All processes of the precaudal vertebrae are present, but both the pre- and postzygapophyses are smaller. All caudal vertebrae have an enclosed haemal arch and spine. The first element may have the arch weakly developed. Each element has small haemal pre- and postzygapophyses, although weakly developed anteriorly. Posteriorly, close to the caudal fin, the haemal and neural spines become increasingly bent posteriorly.

The only variable characteristic of the vertebral elements and associated processes in

Cyprinella is the length of the neural spines. Species of the *lurensis* clade all have more elongate neural spines than members of the *whipplei* clade and most close outgroups. Large adults of species of the *cornutus* species group of *Luxilus* also have tall neural arches, but these species are over 100 mm SL. Individuals of equal or larger size than members of the *lurensis* clade have smaller arches.

CAUDAL SKELETON AND FIN SUPPORTS

The caudal skeleton and first few preural centra of *Cyprinella* and other cyprinids examined (Fig. 16) represents one of the most conservative complexes analyzed. In basic structure the caudal skeleton of *Cyprinella* is similar to that described by Buhan (1972) for many North American minnows.

Articulating posteroventrally with the compound centrum is the fused parhypural and the first hypural element. The caudal vein and artery passes between these two elements and ventral to this opening is the hypurapophysis (Fig. 16). Posteriorly, the compound centrum is fused with the second hypural. Dorsally it is fused with the first and second uroneurals, which form a compound uroneural commonly referred to as the first uroneural. Dorsal to the fused hypural 2 are hypurals 3–6. Between 2 and 3 marks the division of the upper and lower caudal lobes. Anterodorsally to the sixth hypural and lateral to the fused first and second uroneurals, lies the paired uroneural 3. Anterior to this structure and directly above the compound centrum is the single epural. Directly anterior to the compound centrum is preural centrum 1.

My observations of the cyprinid caudal morphology reflect minimal variation of systematic interest. Generally, only minor inter- as well as intraspecific variation occurs in the caudal skeletons. Some characteristics, however, seem to be consistent within and between species and of relevance to the evolution of *Cyprinella*.

Within and outside *Cyprinella* intraspecific variation includes fusion or loss of hypural

bones, number of neural and haemal spines on precaudal vertebrae, and the degree of ornamentation in the form of median plates on the spines. All *Cyprinella* and most other cyprinids examined have a low frequency of individuals with double or at least bifurcated neural and haemal arches (Fig. 16). Occasionally a single individual may have one to two double haemal and neural arches.

Except for *ornata*, the loss of a hypural is variable in each species examined. *Cyprinella ornata* is unique among all species in consistently lacking the sixth hypural. As noted by Buhan (1972) for *Luxilus chrysocephalus*, *Notropis photogenis*, and *Rhinichthys atratulus*, when a hypural element is missing it is invariably the sixth bone of the series that is absent. *Exoglossum laurae*, *Cyprinella panarcys*, *C. proserpina*, and *C. whipplei* each had a single individual with the sixth hypural absent.

Fusion of hypurals is not very common, but when present, it is variable with respect to which elements are involved. *Cyprinella xanthicara* and *venusta* each have a single case of fusion between hypurals 5 and 6, one *venusta* has hypurals 4 and 5 fused and one individual of *C. caerulea* and *Lythrurus fumeus* has hypural 1 and the parhypural fused.

Neural and Haemal Arches and Spines (NS, HS, NA, HA, Fig. 16). Ornamentation of neural and haemal arches varies in a species with age. Generally, younger specimens possess simple arches and spines with no processes, except for small neural and haemal pre- and postzygapophyses. With increasing size, arches develop more elaborate median plates. This is not without exception as similar size adults of a single species may have differing amounts of ossification of these plates. No relevant systematic data could be gained in this study from shape or size of these median plates.

Epural (EP, Fig. 16). Variation of the epural follows a similar pattern as that shown by the preural vertebral arches and their associated median plates. Generally, young-of-the-year have a thin rodlike epural extending from

the tip of the fused uroneural 1 and 2 to and closely associated with neural arch of preural centrum 1. Increasing body size is accompanied with a thickening of the shaft. The anteroventral tip becomes expanded into a spatula or a single-barbed, harpoon-shape, with the tip shape being somewhat variable in a species. Species of the *lutrensis* clade, however, generally develop a heavier epural, relative to other *Cyprinella* and outgroups.

Length of the third uroneural, referred to as urodermal by Buhan (1972), varies systematically within *Cyprinella* (Fig. 16D–F). As detailed by Patterson (1968) urodermals are dermal scale derivatives and are present in only a few primitive teleosts. Uroneural is the correct nomenclature for these elements because they are derived from ural neural arches. Using hypurals 4–6 as a reference for extent of anterior development, all *Cyprinella* show development of the third uroneural to a point between the anterior extent of hypurals 5 and 6 or less. *Cyprinella rutila*, *proserpina*, and *panarcys* have their third uroneurals extending only to the anterior end of hypural 6 (Fig. 16D). Although variable, 60% of the individuals of *lepida* adults have the reduced condition. *Cyprinella rutila* from Río Salado de los Nadadores (ASU 63-0264) and *xanthicara* have uroneural 3 extending anteroventrally to between hypurals 5 and 6. *Cyprinella gibbsi*, *trichroistia*, and *caerulea* also have a reduced third uroneural condition. In these species the maximum size of their third uroneural is smaller than hypural 6 (Fig. 16F). In most cases outgroups have the third uroneural extending to hypural 5. *Luxilus pilsbryi*, *L. cardinalis*, *L. zonatus*, *L. zonisti*, *Phenacobius catostomus*, *P. teretulus*, and *Hybopsis zanema* have the element extending to between hypurals 5 and 6. The reduced condition of all *Cyprinella* may be considered derived for this group, with further independent reduction of this condition in the *lepida* species group and *caerulea* species complex. The hypothesis of independent reduction in these two clades seems reasonable since species most closely related to each of these groups have the typical *Cyp-*

rinella condition. Development of a long uroneural 3 may be a derived condition of a larger group of eastern North American cyprinids, inclusive of *Cyprinella*.

Additional variation in the caudal skeleton includes the overall shape of the caudal fin and associated supporting elements and preural vertebrae. Species of *Cyprinella*, with the exception of *venusta*, *galactura*, *callitaenia*, *callisema*, *leedsii*, and *nivea*, have a caudal fin shape different from all other cyprinids examined. In this genus the overall shape of the fin supports and neural and haemal arches is deeper and more erect, giving the fin a broader fan shape. The exceptions mentioned above have a slightly more narrow caudal skeleton, similar to outgroups. Changes in the overall shape of the caudal skeleton are not restricted to *Cyprinella*. *Erimystax dissimilis*, *E. insignis*, *E. cahni*, *E. monacha*, *Phenacobius catostomus*, *P. teretulus*, and *P. uranops* all have a much compressed caudal and precaudal skeleton, relative to any *Cyprinella* and other cyprinids surveyed. This condition as well as the broadened morphology of *Cyprinella* is considered derived from the primitive condition found in most other cyprinids and are indicative of monophyly of each group.

PECTORAL GIRDLE

Posttemporal (PTT, Fig. 81). This thin, spatulate dermal bone overlaps the supraclithrum ventrally and is strongly connected to the epiotic and dermopterotic dorsally. Dorsally, the lateral surface contains part of the posttemporal head canal after the fusion of the posttemporal and supratemporal canals. Ventrally, the posttemporal forms much of the roof and lateral face of the posttemporal fossa.

The shape of the posttemporal varies between species of *Cyprinella*. Generally, two conditions exist. Species of the *lutrensis* clade have a teardrop-shaped posttemporal. In *ornata* and the *formosa* and *lepida* species groups it is broad and rounded ventrally and narrows dorsally to a long, narrow, and pointed shaft. The shaft on *ornata* is broader and more blunt. The posttemporal of *lutrensis* and *garmani* is

less extreme. In species of the *whipplei* clade the posttemporal resembles the primitive morphology present in other genera examined.

Cleithrum (CL, Figs. 31, 82). The cleithrum is dermal and the largest of the pectoral girdle elements and forms most of the lateral face of the girdle. It is roughly L-shaped with a large ascending process and a slightly smaller horizontal branch directed anteriorly. Mesially, the ascending limb is flat posteriorly where the dorsally flattened supracleithrum is attached. Ventrally, the ascending limb is attached to a flattened and broad posterior process of the scapula. Anteriorly, there is a mesial ridge extending from the scapula, dorsally to the tip where the ascending limb terminates in a blunt spine. Slightly above the scapula the mesocoracoid is connected to the mesial ridge.

The horizontal process of the cleithrum is connected to its complement anteriorly. At the symphysis the two form a roughly straight margin in *Cyprinella* and not a shallow V as in other genera. The lateral face of the cleithrum is narrowest anteriorly and very broad posteriorly. Mesial to the lateral face a ridge is devel-

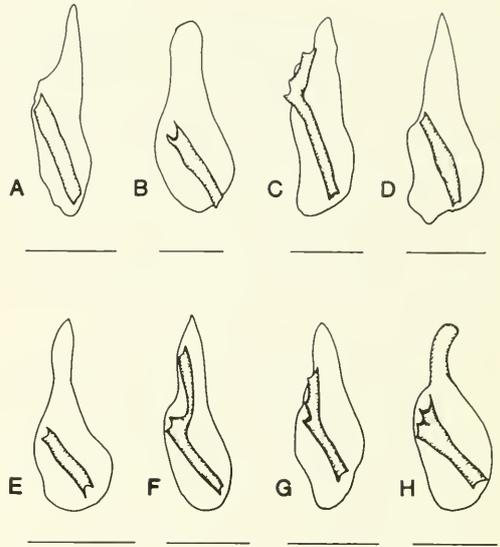


Fig. 81. Posttemporal bone in species of *Cyprinella*. A) *C. camura*, 45 mm, KU 15792. B) *C. ornata*, 56 mm, KU 8405. C) *C. lutrensis*, 55 mm, KU 19431. D) *C. formosa*, 47 mm, KU 8399. E) *C. bocagrande*, 32 mm, KU 20399. F) *C. lepida*, 50 mm, TU 55189. G) *C. rutila*, 57 mm, ASU 5982. H) *C. panarcys*, 44 mm, UMMZ 208212. Horizontal bar equals 1 mm.

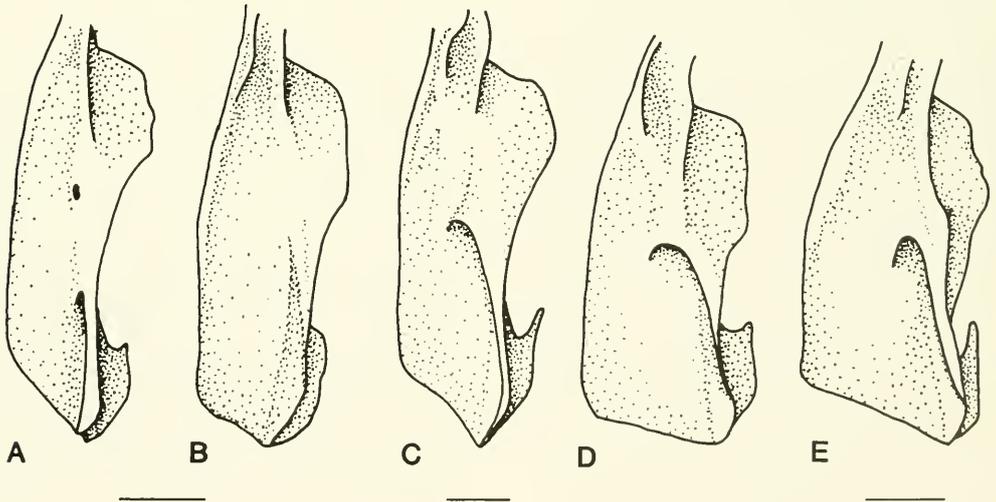


Fig. 82. Dorsal view of cleithrum of some species of *Cyprinella* and outgroups. A) *Notropis telescopus*, 67 mm, KU 15231. B) *Lythrurus umbratilis*, 56 mm, KU 15521. C) *Luxilus cardinalis*, 79 mm, KU 15281. D) *C. analostana*, 58 mm, INHS 74347. E) *C. callistia*, 78 mm, KU 18848. Horizontal bar below *N. telescopus* for all species except *L. cardinalis*. Horizontal bar equals 2 mm.

oped that extends posteriorly up the ascending limb. Mesial to the ridge the cleithrum is connected to the coracoid. Articulation with the coracoid is divided into anterior and posterior segments, divided by a large foramen. The posterior connection is higher than the anterior connection, forming a shelf over and posterior to the latter. Other than the anterior margin of the cleithrum, apparently no consistent systematic variation in the morphology of the cleithrum occurs in the genus.

Supracleithrum (SCL, Fig. 83). Connected to the posttemporal dorsally and cleithrum ventrally, this dermal element contains part of the continuation of the sensory canal leading from the posttemporal to the lateral line. It is flat and broadest medially and ventrally where the margin forms a broad point ventrally. Dorsally it narrows and may produce a hooked point. The morphology of the supracleithrum of these species is very similar. *Cyprinella proserpina* differs in having a very broad supracleithrum.

Coracoid (COR, Fig. 31). As described under the cleithrum, these elements share a broad articular surface anterior and posterior to the large interosseus foramen. Mesially, the coracoid is slightly convex and slopes ventrally. Posteriorly, it is elevated and forms a base, along with the scapula, for the attachment of the mesocoracoid. Lateral to the mesocoracoid-coracoid articulation, the coracoid articulates broadly with the scapula. Posteriorly, the four radials are attached ligamentously. The morphology of the coracoid is similar for all species of *Cyprinella*.

Mesocoracoid (MCO, Fig. 31). This element is a slender spine, broadest ventrally where it articulates with the scapula and coracoid. It extends dorsally from this base as a pointed process and is attached to the mesial ridge of the ascending arm of the cleithrum. Species of *Cyprinella* are essentially monomorphic morphologically for this bone.

Scapula (SCA, Fig. 82). This endochondral element articulates with the cleithrum laterally, coracoid mesially, and the first two radials and first pectoral fin ray posteriorly.

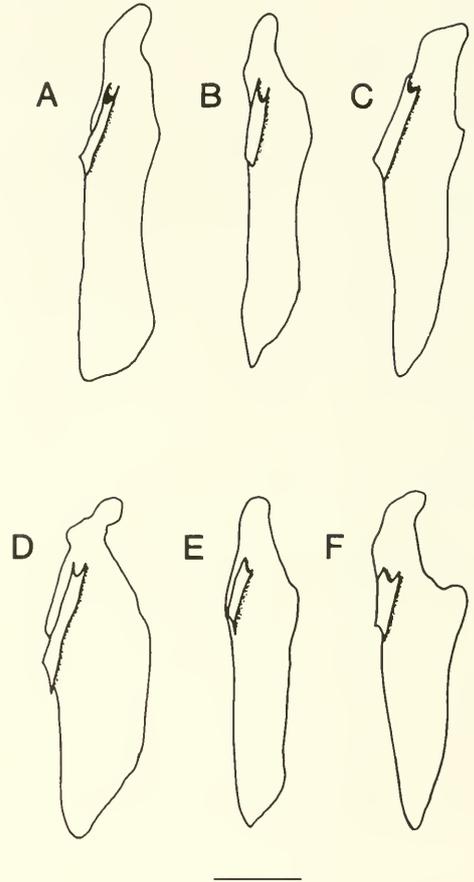


Fig. 83. Supracleithrum bone in some species of *Cyprinella*. A) *C. analostana*, 61 mm, INHS 77855. B) *C. galactura*, 57 mm, KU 12029. C) *C. callisema*, 52 mm, KU 8842. D) *C. proserpina*, 58 mm, TNHC 3262. E) *C. garmani*, 50 mm, KU 5416. F) *C. formosa*, 47 mm, KU 8399. Horizontal bar equals 1 mm.

The anterior and mesial margins are rounded; posteriorly and laterally it is flattened. Contained within the scapula is the scapular foramen. The scapula may be expanded posterodorsally into a small, flat plate which is pressed against the mesial surface of the cleithrum.

Species of *Cyprinella* vary from most other cyprinids examined in the morphology of the scapula. In all close outgroups, except the genus *Luxilus*, a thin, flat, posterodorsal flange is produced from the scapula which is attached to the mesial surface of the cleithrum. *Cyprinella analostana*, *chloristia*, *leedsii*, *nivea*,

callitaenia, *callisema*, *trichroistia*, and *gibbsi* all have a very small process off the scapula, much smaller than in other cyprinids. All other species of the genus lack any type of process. The absence of the scapular process in *Cyprinella* and *Luxilus* is derived and supports the monophyly of these two groups.

Postcleithrum (PCL, Fig. 31). This bone is roughly S-shaped and weakly attached to the mesial surface of the cleithrum posteriorly. It is generally flattened dorsally and may or may not be expanded. Ventrally, it is pointed and generally not flattened. No variation occurs between species in the shape or size of the postcleithrum.

PELVIC GIRDLE

The pelvic girdle is simple and essentially monomorphic in *Cyprinella* (Fig. 84). Each girdle consists of a large, expanded basipterygium (BPT) which is concave dorsally. Anteriorly, it is forked and produces two pointed processes. Posteriorly, the radials (RAD) are attached laterally. Medially, a hooked ischiac process (ISC) is developed. Between the ischiac process and the lateral margin, three radials articulate along the posterior edge. The

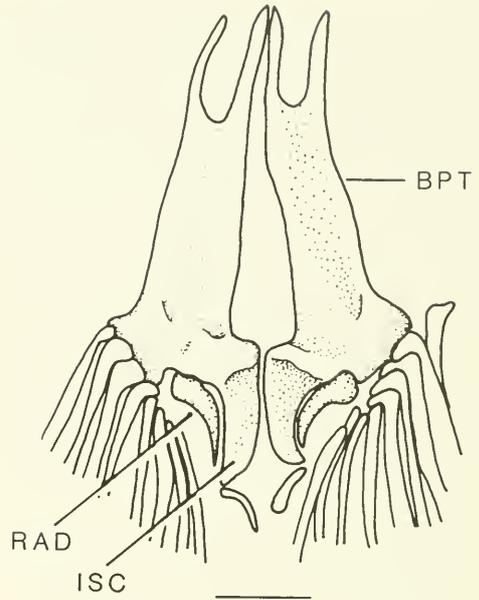


Fig. 84. Pelvic girdle of *Cyprinella lutrensis* (55 mm, KU 19431). Horizontal bar equals 1 mm.

mesial radial is elongate and slightly hooked. The lateral two radials are rounded. Coburn (1982) discusses muscle attachments on the pelvic girdle.

PHYLOGENETIC RELATIONSHIPS

The evidence for monophyly of the genus *Cyprinella* is discussed above and will not be repeated here. Below is a sequential listing of characters which support species relationships illustrated in Fig. 85. For each stem the supporting suite of characters is listed, followed by a discussion of nonosteological synapomorphies. For osteological characters appropriate arguments for determination of character polarity within *Cyprinella* are provided in the osteology section of this paper.

Statements of species relationships within *Cyprinella* are few. The most comprehensive works on this group have been by Gibbs (1955, 1957a), Contreras-Balderas (1975), and Lytle (1972). Gibbs evaluated species relationships within the *whipplei* clade (as used here), and Contreras-Balderas concentrated on Mexican

representatives of the *lutrensis* clade. Lytle examined species relationships in the *lepida* species group. Only Gibbs presented any sort of formal phylogeny of the species studied. Contreras-Balderas and Lytle did not illustrate a phylogeny, but discussed relationships within the *lutrensis* clade as it was then comprised.

Results of the present study based on 206 osteological, meristic, coloration, and tuberculation character transformations suggest species relationships within *Cyprinella* that are at variance with some conclusions of these authors. Some parts of the phylogeny are, however, very similar to the phylogeny presented by Gibbs. Two major clades are recognizable in the genus, the primarily southwestern *lutrensis* clade and the eastern *whipplei* clade (Fig. 85). Within the *lutrensis* clade, *ornata* is

the sister of all other members, which fall into three monophyletic species groups: the *lutrensis* species group, the *formosa* species group, and the *lepida* species group. The *lutrensis* group includes *lutrensis* and *garmani* and is the sister to a clade composed of the *formosa* and *lepida* species groups. Included in the *formosa* group are *formosa* and *bocagrande*. In the *lepida* group *lepida* is the sister to *proserpina* plus *panarcys* and *rutila* plus *xanthicara*. In the *whipplei* clade, *spiloptera* is the sister to the remaining members, which form four monophyletic groups. The *whipplei* species group includes *camura*, *whipplei*, *analostana*, and *chloristia* and is the sister group to remaining members. The *venusta* species group includes *venusta* and *galactura* and is the sister group to a clade composed of the *pyrrhomelas* and *nivea* species groups. The *pyrrhomelas* species group includes two monophyletic groups. The first is the *pyrrhomelas* species pair, inclusive of *pyrrhomelas* and *xaenura*, and the second is the *caerulea* species complex, including this species, *gibbsi*, and *tricholastia*. The *nivea* species group forms the sister group to the *pyrrhomelas* group and includes *callistia*, *nivea*, *leedsi*, *callisema*, and *callitaenia*.

Justifications for these phylogenetic statements are presented below and discussed in the osteology section.

***Cyprinella lutrensis* clade (Suite 2).** The monophyly of this group is supported by 29 shared derived characters. Characters indicative of a common origin in this group include: 1) a short second infraorbital bone, 2) facial foramen with an internal jugular process on lateral rim, 3) ectopterygoid extremely elongate and thin, 4) posterior process of quadrate joins vertical plate well below edge, 5) operculum narrow and deep, 6) anterior margin of frontals with mesial extensions over supraethmoid, 7) frontals widely broadened laterally, 8) supraethmoid extremely short, 9) metapterygoid-interhyal connection extremely narrow, 10) posterior tip of subopercle greatly elevated, 11) vertical plate of urohyal deep, 12) optic foramen bordered largely by pterosphenoid, 13) lacrymal curled, 14) branchiostegals broad, 15) occipital region extremely compressed and vertical, 16) ridge between parietals and supraoccipital present, 17) dorsal process of epibranchial 4 rarely developed and, when present, small, 18) parietals forming small shelf over supraoccipital region, 19) posterior margin of gnathic ramus of dentary

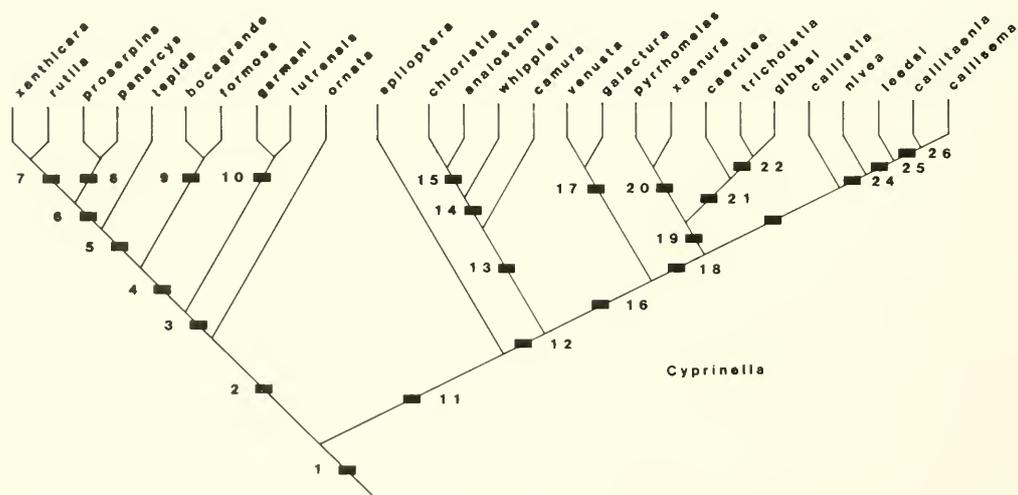


Fig. 85. Hypothesized phylogenetic relationships of species in the genus *Cyprinella*. Numbered character suites are discussed in the text.

very tall, 20) dorsolateral shelf of dentary present, 21) gnathic ramus of dentary deep anteriorly, 22) neck of epibranchial 1 bent posteriorly, 23) neural complex and fourth neural spine extremely tall, 24) predorsal bones large and continuing to dorsal fin origin, 25) neural spines tall, 26) epural heavy, 27) posttemporal bone tear shaped, 28) no pharyngeal teeth in secondary row, and 29) mandibular tubercles absent.

The reduction to no teeth in the secondary tooth row is derived, since other members of *Cyprinella* and species in the genera *Luxilus* and *Lythrurus* all have a secondary tooth row. Since close relatives and most other members of the genus have mandibular tubercles, the absence of these organs in most species of the *lutrensis* clade is interpreted here as a derived condition.

***Cyprinella lutrensis-formosa-lepida* species groups** (Suite 3). The monophyletic origin of these three species groups combined is supported by nine derived characters, including: 1) smooth anterior hyomandibular wing, 2) horizontal plate of urohyal broad, 3) lateral slope of dermopterotic steep, 4) exoccipitals tall, 5) ceratohyals very broad, 6) gular bar very dark, 7) preorbital tubercles few and reduced in distribution to the anterior lacrymal area, 8) central tubercles of caudal-peduncle scales enlarged relative to submarginal and edge tubercles, and 9) tuberculation on caudal peduncle greatest below lateral line, forming tubercle pad from anal fin origin to base of caudal fin.

The dark gular stripe is unique to this group of *Cyprinella* and represents a further derivation of the lightly pigmented gular bar unique to the genus. The restriction of preorbital tubercles to the anterior lacrymal is derived for this group since *ornata*, other *Cyprinella* (where applicable), and close relatives of *Cyprinella* have tubercles dispersed over the lacrymal area. Some species of the *whipplei* clade also have a reduced tubercle pattern in the preorbital region, but in these species the tubercles are found along the dorsal margin of the lacrymal. Thus, these two conditions of

reduced tuberculation are considered convergent.

The enlarged central tubercles of the caudal-peduncle scales and the dense mat of tubercles on the lower caudal peduncle are derived for this group of species since no other *Cyprinella* have this pattern and in no close relatives do these conditions exist. If outgroups have central tubercles on the caudal-peduncle scales they are equal in size to marginal and edge tubercles. The only other cyprinid examined with a similar mat of tubercles on the lower caudal peduncle is the Mexican *Dionda dichroma* (pers. obs.).

***Cyprinella formosa-lepida* species groups** (Suite 4). Four osteological characters support the monophyly of these seven species. Shared derived characters include: 1) facial foramen with internal jugular strut, 2) pharyngeal pad of basioccipital oval, 3) posterior margin of gnathic ramus of dentary tall, and 4) mentomeckelian short and cone-shaped.

***Cyprinella lepida* species group** (Suite 5). The monophyly of this clade of five species is supported by 11 osteological characters and a single derived condition of breeding colors. These include: 1) frontals slightly broadened, 2) junction of sphenotic and frontals moved anteriorly, 3) ceratobranchial 2 with a long and thin neck, 4) vomer extends beyond posterior edge of lateral ethmoids, 5) infraorbitals 2 and 3 broken into 2–3 smaller segments, 6) lateral slope of dermopterotics nearly vertical, 7) coronoid process of dentary narrow and elongate, 8) retroarticular L-shaped, 9) retroarticular long, 10) lateral margin of pharyngobranchial 2–3 expanded into small shelf, 11) uroneural 3 short, and 12) breeding colors of males purplish yellow.

The distinctive purple-yellow breeding coloration of males of these species is described in their respective species accounts. This condition is unique to this subgroup of *Cyprinella*, and is not presently known to occur outside the genus.

***Cyprinella rutila-proserpina* species pairs** (Suite 6). This clade is one of the most distinctive groups of the genus, supported by 23

shared derived characters. These include the following: 1) narrow fourth infraorbital, 2) posteroventral and ventral margins of preopercle scalloped, 3) frontals narrow, 4) position of epiphyseal bar anteriorly placed due to a change in frontal morphology, 5) neck of ceratohyal broad, 6) neck of ceratobranchial 3 elongate, 7) anterior body of premaxilla deep, 8) rostral process of maxilla heavy, 9) hypohyal foramen enclosed by anterior ceratohyal only, 10) neck of branchiostegal 1 narrow, 11) anterior notch of vomer very deep, 12) supraorbitals broad anteriorly, 13) overlap between supraorbital and lateral ethmoid great, 14) parietals form large shelf over anterior margin of supraoccipital, 15) anterolateral edge of palatine expanded anteriorly into elongate process, 16) rostral process of maxilla bent into L-shaped rod, 17) dorsolateral shelf of dentary strongly developed, 18) broad shelf formed from lateral margin of pharyngobranchial 2-3, 19) neck on epibranchial 2 bent anteriorly, 20) neck on epibranchial 3 bent anteriorly, 21) gular bar dark and extending from symphysis to isthmus of branchiostegals, 22) caudal-peduncle tubercles absent on dorsalmost scale row, and 23) tubercle pad on lower caudal peduncle reduced to 1-1½ scale rows above midventral scale row.

The long gular bar is unique to this group and represents a derived condition over the short gular bar unique to *Cyprinella*. The reduced caudal-peduncle tuberculation of these species, lack of tubercles on dorsalmost scale row of caudal peduncle, and narrow mat of tubercles on the lower caudal peduncle is derived. Outside this group, the tubercle mat is deep, extending up to the lateral line, and when caudal peduncle tubercles are present, they are almost always on the dorsal scale row.

Cyprinella rutila species pair (Suite 7). Fourteen osteological characters support the monophyly of these two species. Both species share the following: 1) a narrow preopercle, 2) anterior wing of hyomandibular with a median bulge, 3) posterior wing of hyomandibular wide, 4) operculum broad, 5) supraorbital canal simple, without many canaliculi, 6) anterior

neck of ceratobranchial 1 restricted, 7) anterior margin of ceratobranchial 3 expanded and rounded, 8) posterior process of vomer narrow, 9) pharyngeal process of basioccipital elongate and narrow, 10) ascending process of premaxilla elongate and narrow, 11) anterior gnathic ramus deep, 12) mesial neck of epibranchial 1 bent anteriorly, 13) dorsal hypohyal small, and 14) neural complex and fourth neural spine short.

Cyprinella proserpina species pair (Suite 8). These two species share 11 derived osteological and tubercle characters. These include the following: 1) ventral and posteroventral margins of preopercle deeply scalloped, 2) ventral margin of metapterygoid with irregular processes extending anteriorly into region normally occupied by symplectic, 3) posterior tip of subopercle extremely elevated above anterior tip, 4) anteroventral margin of lateral ethmoid straight, 5) dorsal margin of premaxilla thick, posterior ramus continues forward, 6) central process of sesamoid articular short and directed dorsally, 7) retroarticular L-shaped, 8) retroarticular long, 9) postorbital tubercles smaller than anterior tubercles on dorsum of head, 10) preorbital tubercles distributed over entire lacrymal area, and 11) no hiatus between dorsal head tubercles and snout tubercles.

The reduced size of postorbital tubercles is unique to these two species and *ornata* of all cyprinids examined. The occurrence of this derived condition in these two groups must be convergent when other characters are considered with parsimony. Further, with reference to other characters, having preorbital tubercles distributed over the entire lacrymal region in these two species is considered a reversal to the primitive state for the genus. As noted above, other members of the *lutrensis* clade have preorbital tubercles restricted to the anterior edge of the lacrymal region. The absence of a distinct hiatus between the snout and dorsal head tubercles in these two species also represents a reversal to the primitive morphology for the genera *Luxilus* and *Cyprinella*.

Cyprinella formosa species group (Suite

9). Ten derived characters support the monophyly of this species pair. These species share the following synapomorphies: 1) broad operculum, 2) sternohyoides processes of urohyal very long, 3) subopercle nearly horizontal, 4) pharyngobranchial 2-3 narrow and straight, 5) posterior plate of epibranchial 1 joins mesial neck dorsally, 6) anterior process of epibranchial 1 located mesoanteriorly, 7) ceratohyals moderately deep, 8) dorsal head tubercles erect, 9) supraorbital tubercle scattered, and 10) caudal-peduncle tubercles below lateral line very thick, forming shagreen.

Antrorse tubercles on the dorsum of the head are derived for the genus *Cyprinella*, but reversed in this species pair to the more primitive morphology of erect tubercles, as in outgroups. The condition of numerous and scattered supraorbital tubercles is derived for these two species since close outgroups typically have a single row of tubercles above the orbit. The shagreen tubercle pattern on the lower caudal peduncle is distinctive for these two species and represents a further modification of the mat of tubercles diagnostic for the *lutrensis* clade.

***Cyprinella lutrensis* species group** (Suite 10). The monophyletic origin of these two species is supported by nine derived characters. Both members share the following: 1) posterior process of quadrate joins the vertical plate at edge, 2) epiphyseal bar placed anteriorly with no modifications of frontals, 3) posterior tip of subopercle only slightly elevated above anterior tip, 4) basihyal deep, 5) mid-lateral cavities of basihyal large, 6) neck on vomer absent, 7) epibranchial 4 with short mesial to dorsal process, 8) posttemporal bone not strongly tear shaped, and 9) scapular bar pigmentation strongly developed.

The very dark scapular bar of these two species is derived. It is interpreted as a further modification of the less intense scapular bar diagnostic for the genus.

***Cyprinella whipplei* clade** (Suite 11). The monophyly of this clade of 17 species is evidenced by their sharing 21 derived features. Although some of these characteristics are

reversed in some members, this group shares the following: 1) anterior hyomandibular wing broad, 2) posterior hyomandibular wing broad, 3) supraethmoid very broad and with no emarginate edges, 4) supraethmoid elongate, 5) basibranchial 1 with slight median constriction, 6) ventral surface of lateral ethmoid completely ossified in adults, 7) lacrymal elongate, 8) pharyngeal process of basioccipital elongate and narrow, 9) anterior neck of parasphenoid long, 10) posterior ramus of premaxilla straight, 11) premaxillary process of maxilla tall, 12) anterior margin of epibranchial 1 with anteromesial process, 13) seventh to ninth dorsal fin membranes with melanophores heavily concentrated, 14) dorsal head tubercles strongly antrorse, 15) preorbital tubercles antrorse, 16) tubercle connection between supraorbital and preorbital regions composed of two rows, 17) snout tubercles erect anteriorly and retrorse posteriorly, 18) supraorbital tubercles antrorse, 19) flank scales above lateral line with several scattered tubercles located centrally, 20) flank scales below lateral line with several scattered tubercles located centrally, and 21) dorsal fin with dark interradiial membranes posteriorly in breeding males only.

The darkened posterior membranes of the dorsal fin of all of these species is unique and derived for this group of cyprinids. A similar condition is found in *Hybopsis labrosa* and *H. zanema*, but in these species all membranes are dark. These two species may be related to other *Hybopsis* (s.s.). Thus, this condition is considered independent in both groups. This clade of *Cyprinella* is further defined by the presence of dark interradiial membranes in breeding males only.

All members of this clade have antrorse tubercles that are much more strongly developed than in members of the *lutrensis* clade. Thus, this condition is considered to be a further modification of the antrorse structure ancestral to the genus. The antrorse preorbital and supraorbital tubercles found in this group are very rare outside *Cyprinella* and are considered derived for this clade. The condition of

having multiple rows of tubercles connecting the supraorbital and preorbital regions is considered derived for this clade since close outgroups and members of the *lutrensis* clade have a single row connection. The presence of erect tubercles anteriorly and antrorse tubercles posteriorly on the snout is unique to this clade. Close outgroups and species of the *lutrensis* clade have erect tubercles over the entire snout region. In close outgroups and members of the *lutrensis* clade, centrally located tubercles on flank scales both above and below the lateral line are rare. Thus, the consistent development of central tubercles on flank scales is considered derived for this clade.

Cyprinella whipplei-venusta-pyrromelas-nivea species groups (Suite 12). The monophyly of this large eastern clade of *Cyprinella* is diagnosed by the presence of five derived features: 1) nasal canal with 2 pores, 2) optic and hypophyseal foramina divided by small processes off of pterosphenoid, 3) tubercle connection between supraorbital and preorbital regions wide, composed of 3–4 rows of tubercles, 4) dorsal fin of both males and females with dark membranes posteriorly, and 5) dorsal fin expanded in breeding males.

The increased number of tubercle rows connecting the supraorbital and preorbital regions is derived for this clade and represents a further modification of the two rows present in the ancestor of the *whipplei* clade. This group of *Cyprinella* is further derived over the ancestor of the *whipplei* clade in that both males and females develop the darkened posterior membranes of the dorsal fin. In *spilotera* only males develop this color pattern and it is absent in the *lutrensis* clade and outgroups. The expanded dorsal fin of these species is derived, but not unique to this group. A similar condition is found in *Notropis hubbsi* and *Pteronotropis welaka* and was mentioned by Bailey and Robison (1978) as possible evidence to relate these species to *Cyprinella*. Based on my observations and those of Dimmick (1987), these species may not be closely related to each other, and are not intimately related to the genus *Cyprinella*.

Cyprinella whipplei species group (Suite 13). This clade of four species is diagnosed on the basis of seven derived features. These include: 1) anterior hyomandibular wing narrow, 2) anterior hyomandibular wing smooth, 3) supraethmoid short, 4) no overlap present between lateral ethmoid and supraorbital, 5) isthmus of maxilla deep, 6) mentomeckelian short and cone shaped, and 7) supraorbital tubercles scattered.

The scattered arrangement of supraorbital tubercles of this group is derived from the single row pattern found in most members of the *lutrensis* clade and close outgroups. The occurrence of scattered tubercles on the supraorbital region in the *formosa* species group of *Cyprinella* is considered independent of the condition found in these four species.

Cyprinella whipplei-analostana-chloristia species group (Suite 14). The close relationship of these three species has been suggested for many years (Gibbs, 1957a). My study supports this hypothesis. These three species share the following six derived osteological characters: 1) posterior hyomandibular wing curled, 2) anterior margin of frontals with mesial extensions over supraethmoid, 3) midlateral cavities of basihyal large, 4) supraorbital bones broad anteriorly, 5) dermopterotics not extending over dilator fossa, and 6) ascending wings of parasphenoid very broad.

Cyprinella analostana-chloristia species pair (Suite 15). The sister relationship of these two species is supported by 16 derived characters: 1) facial foramen with internal jugular process on lateral rim, 2) posterior process of quadrate deep and heavy, 3) posteriorly directed process of ceratobranchial 3 serrate, 4) dentary with dorsolateral shelf, 5) anterior margin of pharyngobranchial 1 with lateral process, 6) neck on epibranchial 1 twisted, 7) vomer with long neck, 8) nasal canal with single pore, 9) lateral slope of dermopterotics steep, 10) posterior ramus of premaxilla strongly curved downward, 11) ascending process of premaxilla elongate and narrow, 12) mesial neck of epibranchial 2 bent anteriorly, 13) posterior hyoideal foramen of cera-

tohyal located mesially, 14) scapula with small, dorsoposterior process, 15) mandibular tubercles scattered, and 16) tubercle connection between supraorbital and preorbital regions narrow, consisting of single row.

The scattered pattern of mandibular tubercles is not unique to this group of *Cyprinella*, but based on other characters, the most parsimonious explanation for its presence in these species represents convergent evolution. The single row of tubercles connecting the supraorbital and preorbital regions found in these species is primitive for *Cyprinella*, but represents a reversal to the primitive condition in their common ancestor. Thus, this character is indicative of their monophyly.

***Cyprinella venusta-pyrrhomelas-nivea* species groups** (Suite 16). The monophyletic origin of these three clades is supported by nine derived features. These include: 1) junction of sphenotic and frontal bones moved posteriorly, 2) anteroventral margin of lateral ethmoid slightly concave, 3) ventromesial margin of lateral ethmoid truncated, 4) loss of a connection between the frontals and dermopterotics, 5) optic and hypophyseal foramina nearly divided by mesial processes of pterosphenoids, 6) posterior ramus of premaxilla with uniform ventral curve, 7) mesial neck of epibranchial 2 bent anteriorly, 8) ceratohyals slender, and 9) caudal base with distinct oval spot.

Although variable among species (see species accounts section), the dark and oval caudal spot is derived for this clade of *Cyprinella*, being absent in all other species of the genus and close outgroups.

***Cyprinella venusta* species group** (Suite 17). These two species, *venusta* and *galactura*, have not previously been associated. However, they share nine derived characters relative to other members of the genus and outgroups: 1) preopercle very wide over entire length, 2) posterior process of vomer narrow, 3) anterodorsal margin of lacrymal elevated, 4) retroarticular L-shaped, 5) retroarticular long, 6) caudal skeleton narrow, 7) pigmentation on scales above lateral line in strongly

acute pattern, 8) pigmentation on scales below lateral line in strongly acute pattern, and 9) supraorbital tubercles scattered.

The strongly acute diamond-shaped pattern on lateral body scales of these two species is considered a further derivation of the cross-hatched pattern developed in the ancestor of *Cyprinella*. In these two species the pigment pattern on the scales is very well defined and sharply pointed posteriorly on each scale. As in the *analostana-chloristia* species pair and the *formosa* species group, the presence of scattered supraorbital tubercles in these two species is considered derived and convergent.

***Cyprinella pyrrhomelas-nivea* species groups** (Suite 18). Based primarily on tubercle development, this distinctive clade of *Cyprinella* was considered by Gibbs (1957a) to be primitive in the genus. Members of this clade share 20 derived characteristics: 1) supraethmoid broadened and with slightly emarginate edges, 2) basibranchial 1 with a strong medial constriction, 3) posterior margin of horizontal urohyal plate moderately notched, 4) deep anterior notch of urohyal separating heavy struts, 5) anteroventral margins of lateral ethmoid straight and oblique, 6) supraorbital bones broad anteriorly, 7) dilator fossa not roofed by dermopterotic, 8) dermopterotics invade parietals, 9) epibranchial 1 with anterior process located medially, 10) ceratobranchial 4 without a posterior process, 11) dorsal hypohyal smaller than ventral hypohyal, 12) caudal-peduncle tubercles absent from dorsal-most scale row, 13) caudal-peduncle tubercles absent from ventralmost scale row, 14) first membrane of dorsal fin heavily pigmented with melanophores, appearing black, 15) fourth membrane of dorsal fin uniformly pigmented except for a clear window posteriorly, 16) fifth membrane of dorsal fin with depigmented window posteriorly, 17) sixth membrane of dorsal fin with depigmented window posteriorly, 18) tubercle pattern on dorsum of head linear throughout development, 19) predorsal scales each with a single large tubercle, and 20) caudal-peduncle scales below lateral line each with a single

large antrorse tubercle.

The presence of extremely large, antrorse tubercles on predorsal and caudal-peduncle scales is unique to this clade of cyprinids, with the exception of *Hybopsis labrosa* and *H. zanema*. Tubercles in these two species are very similar to those of this clade of *Cyprinella*, but since these taxa can be related to other *Hybopsis*, and since the tubercles are not generally located centrally on a scale and number more than one, the presence of large tubercles on the caudal peduncle is considered independent in the two groups. The absence of tubercles on the dorsal and ventral scale rows of the caudal peduncle is also found in the *proserpina* and *rutila* species pairs. This condition is considered independent in these two clades since in the *proserpina-rutila* clade the tubercles are absent from the dorsal scale row only.

The linear tubercle pattern on the dorsum of the head throughout development of breeding males is derived for this clade. Because *Cyprinella* begin development with a linear pattern, Gibbs (1957a) considered the linear pattern of adults to be primitive within *Cyprinella* and not indicative of monophyly of the group. The presence of a linear pattern in these species is here interpreted as a case of neotenic development of secondary sexual features. In this clade the linear pattern in early development is retained in the peak breeding season. This seems likely since these species all produce larger dorsal head tubercles and not additional tubercles over the head to disrupt the linear pattern.

Four characteristics of the dorsal fin appear to be derived for species of this group. All have a darkened first membrane, not found in any other *Cyprinella* and absent from close outgroups. All species, except *pyrrhomelas* and *xaenura*, also develop large depigmented windows in the darkened fourth, fifth, and sixth membranes of the dorsal fin. This pigment pattern is not observed outside this group.

***Cyprinella pyrrhomelas* species group** (Suite 19). Twelve derived osteological and tubercle features are shared by members of

this group. These species share the following: 1) first ceratobranchial with neck bent medially, 2) olfactory foramen bounded by laterally directed shelf of mesethmoid and lateral ethmoid, 3) anterior notch of vomer very shallow, 4) posterior process of vomer terminates before posterior edge of lateral ethmoid, 5) lacrymal short, 6) pharyngeal pad on basioccipital flat, 7) preethmoid socket of palatine shallow, 8) a single ligament connecting the palatine to the ecto- and endopterygoids, 9) *adductor mandibulae* A1 insertion on maxilla very far forward, anterior to isthmus, 10) coronoid process of dentary posteriorly directed, 11) flank scales above lateral line without central tubercles, and 12) flank scales below lateral line without central tubercles.

Members of this clade lack central tubercles on flank scales. This condition is a reversal to a primitive state found in the *lutrensis* clade and close outgroups, but on the basis of other characters, this is considered to be evidence of monophyly of this group.

***Cyprinella pyrrhomelas* species pair** (Suite 20). The monophyly of this species pair is supported by 21 derived characters. Both species share the following characters: 1) lateral commissure narrow, 2) trigeminal foramen bordered anteroventrally by a ventral process of prootic, 3) prootic depression posterior to lateral commissure covered by a shelf, 4) branchiostegals short, 5) ascending arm of preopercle tall, 6) epibranchial 4 narrow, 7) supraethmoid very broad and without emarginate edges, 8) supraethmoid extremely short, 9) nasal canal with one pore, 10) supraorbital bones short, 11) fourth membrane of dorsal fin with pigment uniformly distributed, 12) fifth membrane of dorsal fin with pigment uniformly distributed, 13) sixth membrane of dorsal fin with pigment uniformly distributed, 14) dorsal head tubercles very large, 15) predorsal tubercles very large and with irregular bases, 16) tubercle connection between supraorbital and preorbital region narrow, 17) tubercle hiatus between snout and dorsum of head absent, 18) anterior body scales above lateral line without tubercles, 19) anterior body

scales below lateral line without tubercles, 20) enlarged tubercles found both above and below lateral line on caudal peduncle, and 21) caudal-peduncle tubercles below lateral line very large and with irregularly formed bases.

The pigment pattern on the fourth, fifth, and sixth dorsal fin membranes is derived for these species, representing a reversed condition to the primitive uniform color pattern, typical of species in the *lutrensis* clade and outgroups. The enlarged tubercles with irregularly formed bases on the predorsal and caudal-peduncle scales is derived since no other members of the genus have tubercles this large, and the irregular base morphology has never been observed outside this group. The enlarged dorsal head tubercles of these species represents a further enlargement of head tubercles in *Cyprinella*. No other species develop tubercles as large as these. The presence of enlarged central tubercles both above and below the lateral line on the caudal peduncle is unique to this species pair. The absence of tubercles on flank scales both above and below the lateral line is also unique to these species. The reversed condition of having a single tubercle row connecting the tubercles of the supraorbital and preorbital regions, and absence of a hiatus between dorsal head tubercles and snout tubercles is more parsimoniously considered derived for this clade if the distributions of other characters are considered.

Cyprinella caerulea species complex (Suite 21). This species group is supported by 12 shared derived characters: 1) ascending arm of preopercle very short, 2) location of sphenotic-frontal articulation strongly displaced posteriorly, 3) anterior notch of vomer shallow, 4) lateral slope of dermopterotics flattened and nearly horizontal, 5) posttemporal fossa small and compressed, 6) posterior ramus of premaxilla very narrow and pointed, 7) hypohyal foramen narrow and slidlike, 8) isthmus of maxilla very narrow, 9) uroneural 3 short, 10) first membrane of dorsal fin with pigment uniformly distributed, 11) centrally located tubercles of predorsal scales numbering 2–3 per scale, and 12) supraorbital tu-

bercles scattered.

As in the *formosa* group, the scattered tubercle pattern above the orbit is derived. In reference to other derived characters, this condition is best interpreted as convergent in these groups. These species also share the primitive condition within *Cyprinella* of having melanophores uniformly distributed over the first membrane of the dorsal fin and scattered central tubercles. Both of these conditions represent reversals to a primitive state within *Cyprinella*. However, with reference to other derived characters, these conditions should not be considered homologous with the conditions found in the *lutrensis* clade and outgroups. Thus, they represent independent evolutionary events in this clade, indicative of monophyly of this species complex.

Cyprinella trichroistia-gibbsi species pair (Suite 22). The monophyly of these two species is supported by 16 derived features: 1) anterior wing of hyomandibular smooth, 2) posterior wing of hyomandibular terminating near ventral tip, 3) position of epiphyseal bar displaced posteriorly, 4) supraorbital bones long, 5) lacrymal canal smoothly arched, 6) preethmoid socket of palatine very shallow, 7) neck of epibranchial 1 bent posteriorly, 8) scapula with small dorsoposterior process, 9) diamond-shaped pigmentation pattern on scales above lateral line diffuse, 10) second membrane of dorsal fin depigmented distally and dark basally, 11) third membrane of dorsal fin depigmented distally and dark basally, 12) fifth membrane of dorsal fin with large depigmented window posteriorly and darkly pigmented dorsally, 13) sixth membrane of dorsal fin with large depigmented window posteriorly and darkly pigmented dorsally, 14) seventh to ninth membranes of dorsal fin darkly pigmented distally, 15) scales above the lateral line along flank with scattered central tubercles, and 16) scales below the lateral line along flank with scattered central tubercles.

The diffuse diamond-shaped pattern is a secondary loss of the sharp pattern. Young of both species have the typical diamond-shape pattern on flank scales. The five features of the

dorsal fin membranes are unique to this clade and thus considered derived. The scattered tubercle pattern of flank scales above and below the lateral line is considered derived for the *whipplei* clade, being absent in the *lutrensis* clade and outgroups.

***Cyprinella nivea* species group** (Suite 23). The monophyly of this distinctive clade of five species is supported by their sharing 16 derived features of their osteology, coloration, and tuberculation. These include the following: 1) epiphyseal bar displaced posteriorly, 2) neck on ceratobranchial 1 restricted, 3) hypobranchial 1 with a double cartilage head, 4) vomer with a long neck, 5) lacrymal extremely long, 6) lacrymal canal L-shaped, 7) parietals strongly invaded by dermopterotics, 8) mandibular pores 3, 9) mouth inferior, 10) ascending process of premaxilla narrow and elongate, 11) gnathic ramus of dentary curved ventrally and mesially, 12) fused pharyngobranchial 2-3 with a smooth dorsal surface, 13) scapular bar pigment weakly developed, if present, 14) second membrane of dorsal fin uniformly pigmented and with clear window posteriorly, 15) third membrane of dorsal fin uniformly pigmented and with clear window posteriorly, and 16) preorbital tubercles on dorsal half of lacrymal only.

The scapular bar pigment typical of the genus is reduced and sometimes absent in members of this group. This is considered a secondary modification as a reduction in pigmentation. In these species the unique condition of having large, clear, posterior windows on the second and third membranes of the dorsal fin is derived since no other species in *Cyprinella* or outgroups have this condition. Also unique to this group within *Cyprinella* is the reduction of preorbital tubercles to the anterior lacrymal. As discussed earlier for the *lutrensis* clade, the reduction of lacrymal tubercles is derived over what outgroups and most *Cyprinella* have. Because the tubercle reduction in this clade is quite different from that discussed earlier for the *lutrensis* clade (exclusive of *ornata*), these two conditions are not homologous.

***Cyprinella nivea-leedsi-callisema-callitaenia* species group** (Suite 24). The monophyly of these four species is supported by 17 derived osteological features: 1) short and broad ectopterygoid, 2) frontal bones narrow, 3) metapterygoid-interhyal articulation narrow, 4) anterior margin of ceratobranchial 1 expanded anteriorly, 5) basibranchial 1 with an hourglass shape, having a strongly developed median constriction, 6) mesethmoid long, 7) anterior notch of vomer very deep, 8) optic and hypophyseal foramina completely separated by pterosphenoid, 9) palatine elongate, 10) dorsal margin of premaxilla serrate, 11) premaxilla strongly bent, 12) anterolateral edge of palatine expanded into elongate process, 13) rostral process of maxilla bent into L-shaped rod, 14) isthmus of maxilla moderately shallow, 15) premaxillary process of maxilla extremely tall, 16) caudal skeleton narrow, and 17) scapula with small dorsoposterior process.

***Cyprinella leedsi-callisema-callitaenia* species group** (Suite 25). These three species share seven derived characters: 1) ventromesial process of palatine short, 2) anterior ceratohyal with foramen ventral to anterior fork, 3) anterior neck of ceratohyal narrow, 4) mentomeckelian short and cone-shaped, 5) no pharyngeal teeth in secondary tooth row, 6) flank scales above lateral line with a single central tubercle, and 7) flank scales below lateral line with a single central tubercle.

Based on parsimony argumentation, the loss of the secondary tooth row in *callisema* and *leedsi* is considered a derived condition for this clade, with a reversal to the 1, 4-4, 1 count in *callitaenia*. All three of these species share the unique conditions of having a single tubercle located centrally on flank scales both above and below the lateral line. When central tubercles are present in other species of the genus they are scattered and number more than one. Thus, the single central tubercle condition of these species is derived.

***Cyprinella callisema-callitaenia* species pair** (Suite 26). These two species are very similar morphologically and are here consid-

ered sister species based on three osteological characters. These species share: 1) a narrow interopercle, 2) a lacrymal strongly tilted

ventrally, and 3) a connection between the frontal and dermopterotic bones.

SUMMARY

The primary intent of this study was to resolve species relationships of the traditionally recognized subgenus *Cyprinella* of *Notropis*. Based on comparisons with other cyprinids, the genus "*Notropis*" as traditionally used is not a monophyletic group (*sensu* Hennig) and can no longer be considered as such. Thus, in addition to the recognition of *Cyprinella* as a distinct genus, other subgenera of *Notropis* are elevated to generic status and some genera of North American cyprinids are rearranged taxonomically. The resulting taxonomic changes have been done to maintain consistency between the phylogenetic relationships of species and our existing classification.

sis of osteological variation.

Variation in osteology and secondary sexual characteristics of North American cyprinids suggests that many eastern North American species form a monophyletic group. Included in this group are species traditionally placed in the genus *Notropis* (except *Aztecucula sallei*), and the genera *Cyprinella*, *Luxilus*, *Lythrurus*, *Pteronotropis*, *Oregonichthys*, *Clinostomus*, *Richardsonius*, *Yuriria*, *Hybopsis*, *Pimephales*, and a clade inclusive of *Hybognathus*, *Exoglossum*, *Dionda*, *Campostoma*, *Nocomis*, *Platygobio*, *Macrhybopsis*, *Extrarius*, *Phenacobius*, and *Erimystax*. Relationships of all of these species were not fully resolved and polytomies were obtained. Basally, a multichotomy exists between a clade inclusive of the genera *Pteronotropis*, *Cyprinella*, *Luxilus*, *Lythrurus*, a restricted *Notropis*, and each of the remaining clades above. The genus *Pteronotropis* forms the basal sister group of the first clade and the *Lythrurus-Luxilus-Cyprinella* clade is the sister to the restricted *Notropis* clade. The genus *Lythrurus* is hypothesized as the sister group to *Luxilus* plus *Cyprinella*. Within the restricted *Notropis* clade, the subgenus *Notropis* is sister to the more inclusive *Notropis texanus* species group. This clade forms a polytomy with the *Notropis volucellus* species group and the subgenera *Hydrophlox* and *Alburnops*.

Monophyly of the genus *Cyprinella* is supported by 38 characters. Species relationships based on 206 character transformations produced a fully resolved phylogeny of the genus. Within the genus, two major clades are recognized: the primarily southwestern United States and Mexico *lutrensis* clade and the eastcentral United States *whipplei* clade. Species of the *lutrensis* clade include *ornata*, *lutrensis*, *garmani*, *formosa*, *bocagrande*, *lepida*, *rutila*, and *xanthicara*. Species of the *whipplei* clade include *spiloptera*, *camura*, *whipplei*, *analostana*, *chloristia*, *venusta*, *galactura*, *pyrrhomelas*, *xaenura*, *caerulea*, *trichroistia*, *gibbsi*, *callistia*, *nivea*, *leedsii*, *callisema*, and *callitaenia*. A detailed account for each species is presented, as well as an analy-

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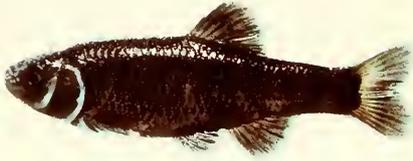
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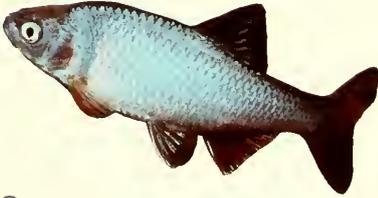
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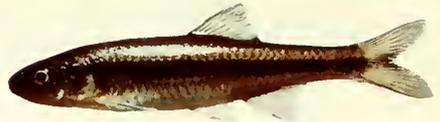


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Plate I. A) *Cyprinella ornata*, male, 54 mm SL, Río Papagochic, Guerrero, México; B) *Cyprinella ornata*, female, 46 mm SL, Río Papagochic, Guerrero, México; C) *Cyprinella lutrensis*, male, length and locality unknown, photo by W. N. Roston; D) *Cyprinella garmani*, male, 50 mm SL, Río Nazas, Durango, México; E) *Cyprinella garmani*, female, 59 mm SL, Río Nazas, Durango, México; F) *Cyprinella formosa*, male, 47 mm SL, Río Casas Grandes, Chihuahua, México; G) *Cyprinella bocagrande*, male, 43 mm SL, Ojo Solo, Chihuahua, México; H) *Cyprinella lepida*, male, 52 mm SL, Nueces River, Real Co., Texas, photo by L. M. Page.



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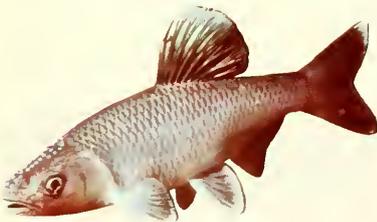
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Plate II. A) *Cyprinella rutila*, male, 39 mm SL, Río San Juan, Nuevo León, México; B) *Cyprinella xanthicara*, male, 46 mm SL, Cuatro Ciénegas, Coahuila, México; C) *Cyprinella proserpina*, male, 46 mm SL, Devils River, Val Verde Co., Texas, photo by L. M. Page; D) *Cyprinella panarcys*, male, length not listed, Río San Pedro, Chihuahua, México (UMMZ 198786), photo by R. R. Miller; E) *Cyprinella spiloptera*, male, 65 mm SL, Little Beaver Creek, Kankakee Co., Illinois, photo by L. M. Page; F) *Cyprinella spiloptera*, male, length unknown, Shoal Creek, Newton Co., Missouri, photo by W. N. Roston; G) *Cyprinella camura*, male, length unknown, Terrapin Creek, Graves Co., Kentucky, photo by B. M. Burr; H) *Cyprinella camura*, male, 89 mm SL, Terrapin Cr., Graves Co., Kentucky, photo by B. M. Burr.



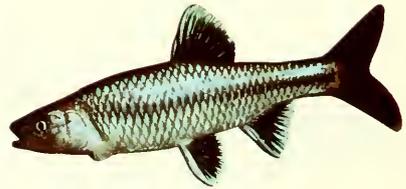
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Plate III. A) *Cyprinella whipplei*, male, 89 mm SL, St. Francis River, Wayne Co., Missouri, photo by L. M. Page; B) *Cyprinella analostana*, male, 64 mm SL, Morgan Creek, Orange Co., North Carolina, photo by L. M. Page; C) *Cyprinella chloristia*, male, 78 mm SL, Pacolet River, Spartanburg Co., South Carolina, photo by L. M. Page; D) *Cyprinella chloristia*, male, length unknown, North Carolina, photo by W. N. Roston; E) *Cyprinella venusta*, male, 80 mm SL, Guadalupe River, Kerr Co., Texas, photo by L. M. Page; F) *Cyprinella galactura*, male, 101 mm SL, Beaver Creek, Taney Co., Missouri, photo by L. M. Page; G) *Cyprinella galactura*, female, 79 mm SL, Buffalo River, Lewis Co., Tennessee; H) *Cyprinella pyrrhomelas*, male, 72 mm SL, South Saluda River, Pickens Co., South Carolina.



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Plate IV. A) *Cyprinella caerulea*, male, length and locality unknown, photo by W. N. Roston; B) *Cyprinella trichroistia*, male, 80 mm SL, Rock Creek, Murray Co., Georgia, photo by B. M. Burr; C) *Cyprinella trichroistia*, male, 70 mm SL, Schultz Creek, Bibb Co., Alabama; D) *Cyprinella gibbsi*, male, 65 mm SL, Enitachope Creek, Clay Co., Alabama; E) *Cyprinella callistia*, male, length unknown, Conasauga River, Polk Co., Tennessee, photo by W. N. Roston; F) *Cyprinella callistia*, male, 85 mm SL, Turkey Cr., Tuscaloosa Co., Alabama; G) *Cyprinella nivea*, male, 87 mm SL, Pacolet River, Spartanburg Co., South Carolina, photo by L. M. Page; H) *Cyprinella callisema*, male, 63 mm SL, Oconee River, Clark Co., Georgia.

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