

Six distinctive Cyprinid fish species
referred to *Dionda* inhabiting segments of
the Tampico Embayment drainage of Mexico

Carl L. Hubbs and Robert Rush Miller

ABSTRACT.—Six sharply differentiated species of Cyprinidae that seem to be referable to the genus *Dionda* inhabit the drainage basin of the Río Pánuco of eastern México. One also occupies five minor stream systems intervening between Río Pánuco and the abrupt physiographic and faunal break north of Veracruz. These species contribute to the diverse and highly endemic character of the moderately rich fish fauna of the Río Pánuco stream complex. Three of the six species have been named recently, and two, *D. catostomops* and *D. dichroma*, are described as new. The six species constitute three allopatric, physiographically separated pairs.

RESUMEN.—Seis especies bien diferenciadas de Cyprinidae, que se pueden referir al género *Dionda*, habitan la cuenca del Río Pánuco en el este de México. Una de las especies ocupa además cinco cuencas pequeñas situadas entre el Río Pánuco y la fractura fisiográfica y faunística que se presenta en el norte de Veracruz. Estas especies contribuyen a la diversidad y elevado endemismo característicos de la ictiofauna, relativamente rica, que habita el complejo sistema del Río Pánuco. Tres de las seis especies han sido descritas recientemente, y aquí se describen dos especies nuevas, *D. catostomops* y *D. dichroma*. Las seis especies mencionadas constituyen tres pares alopátricos fisiográficamente separados.

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INTRODUCTION AND GENERAL DISCUSSION

All of the six clearly distinct species of minnows herein referred to *Dionda* occupy parts of the drainage basin of the Río Pánuco, the major affluent of the Tampico Embayment (Muir, 1936) of the Gulf of Mexico, and all, *D. ipni* (Alvarez and Navarro) alone excepted, are confined to that stream system (Fig. 1). *Dionda ipni* occurs also, as the only cyprinid, in the five stream systems of consequence (those of ríos Tuxpan, Cazonés, Tecolutla, Nautla, and Misantla) that discharge into the Gulf between Laguna de Tamiahua, just south of Tampico, and the rugged coastline north of Veracruz, where the eastern margin of the high Mexican Plateau very closely approaches, and slopes steeply to, the vicinity of Punta del Morro, with no significant streams over the lava-flow terrain. This rugged coast marks the extreme known southern limit, on the tropical Atlantic coastal-plain drainage, for the entire family Cyprinidae, in fact for any cyprinoid except "*Hybopsis*" *moralesi* (De Buen, 1956), of the upper Papaloapan system, which species probably originated by stream-capture from the Río Lerma system, and the catostomid *Ictiobus meridionalis* (Günther); or of any additional fluviatile fishes conceivably of Nearctic origin except *Ictalurus meridionalis* (Günther), *Lepisosteus tropicus* (Gill), and *Aplodinotus grunniens* Rafinesque. The latter two, moreover, are rather questionably Nearctic vagrants, and may well have attained their far southern habitat at some remote, cool time, perhaps before the volcanic flow just referred to; or, perhaps, when a broader coastal plain resulted from lowered sea level.

According to our now rather extensive and detailed data, the six cyprinid species of east-central México that we refer to *Dionda* comprise three pairs of quite distinct species, between which pairs there appears to be complete allopatry, whereas within each pair there is a large degree of sympatry.

In sequence, from the lowland, coastwise portion of the Río Pánuco system, the first of the three pairs of species comprises, as already noted (Hubbs and Miller, 1974), *Dionda ipni* (Alvarez and Navarro) and *D. erimyzonops* Hubbs and Miller. Both of these species occur in the northern, Río Tamesí section of the Río Pánuco / Río Tamesí complex (which streams are connected near the coast), as well as in the lowlands of the Río Pánuco system proper, whereas *ipni* alone appears to represent the genus in the upper, southern tributaries of the Río Pánuco, including notably the seemingly disjunct and now isolated type locality of the species, and, as noted above, in the five disjunct stream systems southeast of the Pánuco basin. As indicated by Hubbs and Miller (1974: 7-8), the two species have been taken together in the same collection in these specified ratios (*ipni* : *erimyzonops*): 14 : 33 in Río Guayalejo, tributary to Río Tamesí, at Llera, Tamaulipas (UMMZ 192501 : 192500); 7 : 3 in Río Forlón, tributary to Río Tamesí, at Forlón, Tamaulipas (FMNH 4477 : 16548-50); 2 : 1 in Río Axtla, tributary to Río Pánuco, at Axtla, San Luis Potosí (UMMZ 124358 : 129680); and 5 : 14 in Río Valles, tributary to Río Pánuco, at Valles, San Luis Potosí (UMMZ 97457 : 97469). Sympatry in this species combination seems to be limited by the special habitat requirements of *erimyzonops* as contrasted with the more generalized habitat of *ipni*, and perhaps also by the special spawning habitats of *ipni* (p. 331).

The second at times sympatric pair, comprising *Dionda rasconis* (Jordan and Snyder) and *D. catostomops* n. sp., is seemingly restricted to what we treat as the lower of the two intermontane areas within the Río Pánuco system proper—the one drained by the Río Gallinas (= Río Frío or Río Ojo Frío), in San Luis Potosí. The two species have been taken together at both localities from which there are collections, in the indicated ratios (*rasconis* : *catostomops*): 67 : 1 in Río Gallinas,

near Rascón, San Luis Potosí (UMMZ 196693 : 196692); 15 : 6 in Río Tamasopo near Tamasopo, San Luis Potosí (UMMZ 193509 : 195950); 13 : 58 at the same locality (UMMZ 196345 : 196346-47), when an apparently breeding population of *catostomops* was encountered. The low indicated incidence of sympatry in the population from near Rascón seems to be attributable to the limited development there of the riffle habitat, for which *catostomops* seems to have a strong predilection.

In the third pair, comprising *Dionda dichroma* n. sp. and *D. mandibularis* Contreras-Balderas and Verduzco-Martínez (1977), sympatry seems to occur only in the Río Verde system within the higher intermontane basin, containing the highly distinctive La Media Luna faunal association, in San Luis Potosí. The two species involved were taken together, in this stream system, in three of the somewhat more prolific collections in the following ratios (*dichroma* : *mandibularis*): 7 : 7 at Puerta del Río, the source of Río Verde, San Luis Potosí (LSUMZ 1216: 405 & 407), 72 : 33 at same locality (UMMZ 196338 : 196339); 16 : 6 at spring-fed marsh 10 km south of Río Verde (UMMZ 196701-02 : 196703). Sympatry of this pair seems to be limited by the rarity of *mandibularis* and by its restricted habitat. In describing that species Contreras-Balderas and Verduzco-Martínez did not indicate its partial sympatry with any other species of the genus.

Despite the degree of sympatry found between the two species in each of the three pairs, no evidence of interspecific hybridization has been encountered. This is in line with the evidence that interspecific hybridization among fishes is particularly characteristic of regions that have been profoundly disrupted by continental glaciation (Hubbs, 1955: 18).

The sharp endemism and the localized distribution displayed by the subjects of this report are mirrored by the endemism and localism displayed by the other fishes that inhabit the Río Pánuco drainage system (Fig. 1). The Río Pánuco fish fauna as a whole comprises a remarkable admixture of Nearctic, Neotropical, Middle American, and Mexican Plateau affinities. These diverse elements comprise, for the complex here referred to *Dionda*, as for the fish fauna in general, four remarkably distinct faunal subregions:

I. The coastal-plain section of the Río Pánuco complex, including the largely lowland basin of the Río Tamesí, harbors, as already noted, two of the six Pánuco species that we refer to *Dionda*, namely *erimyzonops*, which is strictly endemic to the combined system, and *ipni*, which to the southeastward occurs in all five significant stream systems to the major distribution block, and to the southwestward penetrates into considerably higher elevations. Another essentially Pánuco endemic, *Gambusia panuco* Hubbs, has been taken in the two systems next southward, those of Río Tuxpan and Río Czones. Other fishes that rank as Pánuco endemics are the sucker known as *Ictiobus labiosus* Meek, a very distinct species (possibly generically separable) that ascends into the main upper Río Santa María tributary, but not to the far-headwater creeks (of category IV) that contain minnows of the Lerma fauna; the catfish *Ictalurus mexicanus* Meek, which, like *Ictiobus labiosus*, occurs also in the lower intermontane area (II); and the minnows *Notropis lutrensis forlonensis* Meek and *Notropis tropicus* Hubbs and Miller (1975). So far as known, two poeciliids, *Gambusia aurata* Miller and Minckley and *Poecilia latipunctata* Meek, are endemic in the Río Tamesí system, and two others, *Gambusia atrora* Rosen and Bailey and *Xiphophorus pygmaeus* Hubbs and Gordon, are, so far as known, endemic only to the Río Pánuco drainage basin proper, at relatively low elevations.

II. The fish fauna of the lower of the two intermontane tributaries of the Río Pánuco system, that of the Río Gallinas (= Río Ojo Frío), comprises, on the basis of collections long made in the vicinity of Rascón, and recently also near

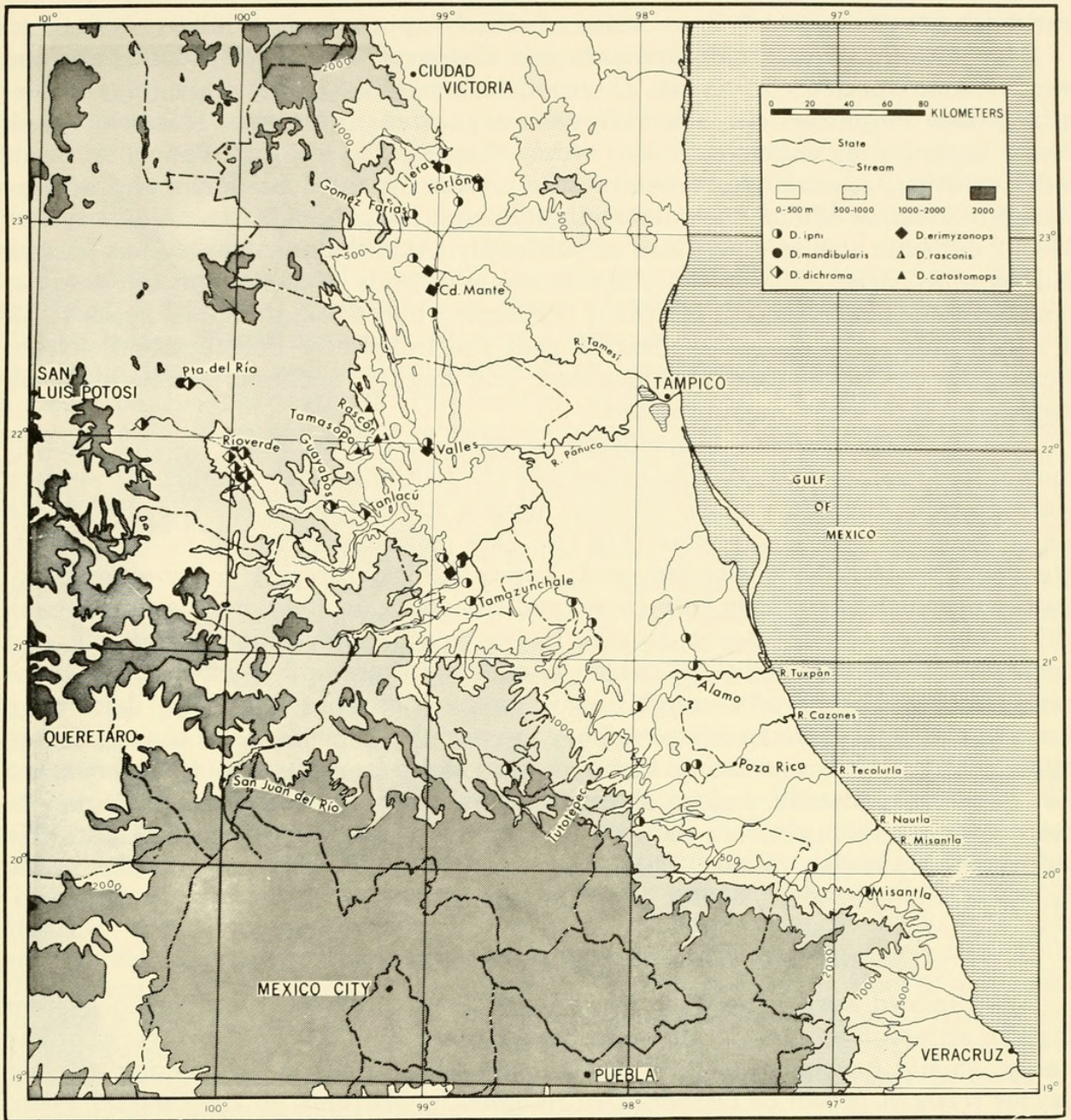


Figure 1. Distribution of the six species referred to *Dionda* in the Tampico Embayment drainage of northeastern México.

Tamasopo, the two sharply distinct species referred to *Dionda*, *D. rasconis* (Jordan and Snyder), long-known, and the trenchantly different *D. catostomops*, herein made known. In addition, this local faunal unit (Fig. 1) has been found to comprise: two widespread species, *Astyanax mexicanus* (Filippi) and *Ictalurus mexicanus*, mentioned above, both shared with the fauna of the upper intermontane area (III); *Poecilia mexicana* Steindachner, and two other poeciliids, *Gambusia panuco* and *Xiphophorus montezumae* Jordan and Snyder, both widespread Pánuco endemics; and three cichlids, the true *Cichlasoma steindachneri* Jordan and Snyder, endemic here, the widespread *C. "steindachneri"* of most authors, and *C. cyanoguttatum* (Baird and Girard). Thus the lower intermontane area has yielded only three endemic species, whereas the upper intermontane area (III) has seven, of which two represent endemic genera, and one constitutes an endemic subfamily.

The very sharp faunal distinctness of the upper intermontane section of the Pánuco complex seems to be related to partial hydrographic isolation: the discharge becomes a rushing torrent, which throughout its narrowly constricted

trench, drops precipitously in a series of closely approximated falls.

III. The upper intermontane area has displayed (Fig. 1), in addition to the two endemic species of *Dionda*, *D. mandibularis* and *D. dichroma* (herein described): the ubiquitous characin *Astyanax mexicanus*; a catfish, *Ictalurus mexicanus*, regarded as endemic to but widely dispersed in the Río Pánuco system; and five other, remarkable endemics—the unique cyprinodont genus and species *Cualac tessellatus* Miller; the outstandingly primitive goodeid, *Ataeniobius toweri* (Meek), endemic also as genus and as subfamily (Ataeniobiinae), as well as species (Hubbs and Turner, 1939); and three endemic cichlids of the genus *Cichlasoma*, namely *C. bartoni* (Bean), *C. labridens* (Pellegrin), and a still unnamed species. All of which illustrates the generalization that the freshwater fish fauna in eastern Mexico tends to be sharply localized and highly endemic, particularly in segregated intermontane subregions.

IV. A very different assemblage of species, not including, so far as yet known, any referable to *Dionda*, comprises the fish fauna of the high, far-western headwaters of the Río Pánuco system, namely Río San Juan del Río, Río Santa Maria, and (or) Río Moctezuma (Fig. 1). This subfauna includes: two cyprinids, *Algansea tincella* (Valenciennes) and *Aztecuela* (or *Notropis*) *sallaei* (Günther), neither of which is endemic only there; and the goodeids *Xenotoca variata* (Bean), which is not endemic, *Goodea gracilis* Hubbs and Turner, which is endemic, and *Xenophorus captivus* (Hubbs), which is endemic there and nearby. All of these were presumably derived through headwater capture from the highly distinctive fauna of the high Mexican Plateau. They are peripheral members of the even more highly distinctive Lerma faunal complex, that spreads over much of the southern part of the vast plateau, and involves some now differentiated members of remote Nearctic origin, along with a majority of endemic types, mostly in the Goodeidae and the Atherinidae (Meek, 1904; Regan, 1906-08; Hubbs and Turner, 1939; De Buen, 1946a-b, 1947; Miller and Fitzsimons, 1971).

RICHNESS OF THE RÍO PÁNUCO SYSTEM CYPRINID FAUNA

It is indeed surprising that the only moderately large Río Pánuco system (Fig. 1), although so near to the extreme southern limit in the New World of the family, should harbor so rich an assemblage (10 species) of Cyprinidae: the six species referred herein to *Dionda*; two retained in *Notropis*, in the Coastal Plain, namely *N. lutrensis forlonensis*, clearly of northern affinity, and the sharply endemic dwarf, *N. tropicus*; and the species *Algansea tincella* and *Aztecuela sallaei*, both of the Río Lerma complex. No matter what generic reference is accepted, all ten cyprinids of this stream system are clearly distinct forms, and the percentage of endemism is unusually high.

GENERIC STATUS OF THE SIX SPECIES HERE REFERRED TO *DIONDA* GIRARD

In the introduction to our description of *Dionda erimyzonops*, one of the six species reviewed herein, we (Hubbs and Miller, 1974:2-4) discussed at some length the problem of recognizing and delimiting *Dionda* as a genus. We are still confronted with the not infrequent apparent breakdown in this complex of the classificatory value of the presence *vs* absence of a maxillary barbel, and of the simple compressed-S form of the intestine *vs* a moderately coiled pattern, both long accorded prime taxonomic significance. Indeed, the confusion seems to be particularly evident in the Mexican cyprinid fauna. We do still have the impression that the species we are treating here do indeed constitute a natural grouping, as the zoogeographical data also seem to indicate. However, our decision to so treat them is still in large measure impressionistic, and provisional. This circum-

stance, nevertheless, does not diminish the evidence of the sharp specific distinction of the six species herein recognized and compared.

We do have some evidence inconsistent with the reference of any or all of the six species to *Hybognathus*. In the past *Dionda* was long treated, for example by Meek (1904: 48), as a generic synonym or as a subgenus of *Hybognathus*, which may or may not be its closest relative. *Dionda*, as we recognize it, differs from that genus in a combination of characters, which, taken together, seems impressive. These characters include: (1) the nature of the pharyngeal process on the basioccipital bone, treated below; (2) the comparatively thick lower jaw, lacking the hard symphyseal knob and the sharp edge characteristic of *Hybognathus*; (3) the larger, less transverse and less U-shaped mouth; (4) the comparatively short and typically well-hooked, rather than long and at most only incipiently hooked, pharyngeal teeth; (5) the location of the dorsal-fin origin over to well behind, rather than somewhat in advance of, the insertion of the pelvic fins; and (6) the considerably dark-pigmented, rather than generally silvery, body coloration that characterizes all species of *Hybognathus*. Two particular features of coloration seem to set *Dionda* apart from *Hybognathus*: each species referred to *Dionda* has a prominent dark lateral stripe running from the tip of the snout to the caudal base and ending in a black basicaudal spot, both lacking in *Hybognathus*; and nuptial males of *Dionda* have jet-black, yellow, or bluish fins, whereas these fins in *Hybognathus* consistently lack bright colors.

In the six species currently recognized and assigned to *Hybognathus*, William L. Pflieger (pers. comm., 1975) has found that the posterior process of the basioccipital bone is dorsoventrally flattened, thin, and broad, except in *H. placitus* Girard, which has this process relatively narrow and rather rodlike, although still dorsoventrally compressed (Bailey and Allum, 1962, pl. I, Figs. C-D; Cross, 1967, Fig. 14). The process is typically angled downward in *Hybognathus*, sometimes rather strongly so. In the eight species assigned by us to *Dionda* (*D. episcopa* Girard, *D. diaboli* Hubbs and Brown, and the six herein treated—all occurring in México), the posterior basioccipital process extends straight back from the pharyngeal pad, and is either laterally compressed and narrow (but spatulate in *D. erimyzonops*) or resembles the process in *H. placitus*, but is thicker and tends to have a ventral keel (*diaboli*, *episcopa*, *rasconis*, and *mandibularis*). The degree of resemblance shown by this structure in the species we refer to *Dionda* and in *H. placitus* alone of the species referred to *Hybognathus* is further believed by Pflieger to represent convergence, for he feels that the configuration of the process that characterizes all other species of *Hybognathus* represents the ancestral condition in that genus.

The problem of the generic placement of the six species herein referred to *Dionda* is greatly complicated by the circumstance that the brightly colored species long treated as *Dionda nubila* (Forbes) has recently been referred by Camm C. Swift (in thesis), to *Notropis*, despite its herbivorous habit and elongate intestine, by the description of a species from North Carolina with a coiled intestine as *Notropis mekistocholas* Snelson, by the discovery that *Notropis anogenus* Forbes also has a coiled intestine, and by the discovery of incipient coiling in other American cyprinids (Snelson, 1971). This complication has also been referred to by Contreras-Balderas and Verduzco-Martínez (1977).

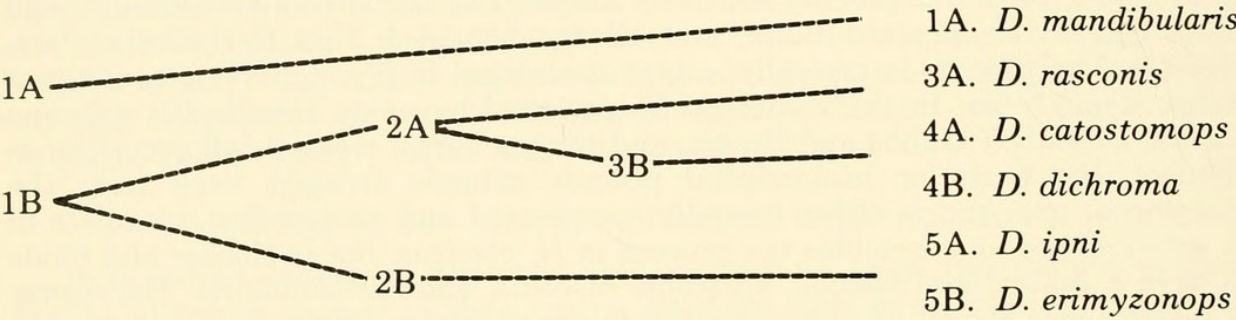
It is abundantly obvious that much of the generic placement in American cyprinids is in a chaotic state, and that the prime significance attributed to intestinal coiling *vs* the single compressed-S configuration, and to the presence *vs* absence of a maxillary barbel, in the taxonomy of the group, has been very considerably discredited. All six species here treated have rather extensively and rather variably coiled intestines, and the development of the barbel fluctuates: *ipni* and *erimyzonops* seem to consistently lack this structure; *mandibularis* ordinarily also lacks a barbel, but a small one was found on one side of one specimen; *rasconis* and *dichroma* normally have at least a very small barbel on each

maxilla; and *catostomops* seems to consistently have a rather larger one on each side. No trace of a barbel has been found in either of the two other species left in the genus, *D. episcopa* (a complex?) and *D. diaboli*, of northern México and adjacent parts of the United States. All eight species have a black peritoneum with a silvery base, but this is the usual characteristic of herbivorous minnows.

It may well be of some bearing in this case to mention that Barbour and Miller (1977), in their revision of the Mexican genus *Algansea*, almost surely a natural unit, have shown that it fluctuates widely in the degree of intestinal coiling and in the presence or absence of the maxillary barbel. In mentioning this circumstance, we (Hubbs and Miller, 1974: 4), added that "It may be more than a coincidence that the breakdown in the putative generic criteria seems to occur conspicuously toward the southern limit of the family, in México, where some ancient types may be retained."

Problems treated above have also been discussed by us in the paper just cited, along with further reference to some of the background studies. We proceed now to present an analytical comparison of the six species referred to *Dionda* that inhabit the Río Pánuco complex of eastern México, and then to follow with a detailed account of each.

ANALYTICAL COMPARISON OF THE SIX SPECIES OF CYPRINIDAE
OF EAST-CENTRAL MEXICO REFERRED PROVISIONALLY
TO *DIONDA*¹



Couplet 1:

- 1A. RAKERS on first gill-arch normally confined to region of angulation, rarely extending as far as the middle of the unusually elongated lower limb; very rarely one or very few near front. MANDIBLE longer (about as long as or longer than postorbital, and more than 10% of standard length), and conspicuously more trenchant (lower edge largely free of flesh; posterior tip sharply produced downward as a very obvious angulation of head contour; anterior end varying from moderately included to sharply protruding). LOWER-LIP GROOVES each 3-5 times as long as anterior interspace. HEAD disproportionately developed anteriorly: length before rear of orbit more than two-thirds length of orbit longer than postorbital. PHARYNGEAL ARCH (Fig. 2A) short and heavy, lower limb broad, with strong lateral ridges (sometimes lacking); upper limb with strongly recurved, pointed tip, and often with a dorsally directed, retrorse spur. Grinding surface of two posterior teeth with crenulate margins. SENSORY CANALS OF HEAD narrowly to very widely interrupted around the upper-posterior bend of the infraorbital canal and along the preoperculomandibular canal just behind mandible. MELANIC COLORATION more boldly streaked (midlateral jet-black streak bordered above by a rather broad and very conspicuous light stripe; scale rows above light stripe marked off by both the subhorizontal lines comprising the light scale-pocket centers and the similarly linear dark lines following the conjunctions of the darkened margins of adjacent longitudinal scale rows); no trace of mid-dorsal dark streak before or behind dorsal fin. *Inhabiting the Río Verde upper-intermontane portion of the Río Pánuco system, along with Dionda dichroma* *Dionda mandibularis*
- 1B. RAKERS on first gill-arch extending forward from the region of angulation to about midway along, or to the front of, the less attenuate exposed border of lower limb (rakers obsolete over most of the greatly foreshortened exposed margin of lower limb in *D. erimyzonops*). MANDIBLE

¹Excluding the populations of northern México referred to *Dionda episcopa* and to *D. diaboli*. Further comparisons of some of the six species are entered in the following accounts of the individual species.

shorter (distinctly shorter than postorbital, and shorter than 10% of standard length), and less trenchant (largely to wholly concealed in fleshy lower-jaw area, without any sharp protrusion of anterior or posterior tip). LOWER-LIP GROOVES each about, to twice, as long as anterior interspace. HEAD not so elongated anteriorly: length before rear of orbit less than two-thirds length of orbit longer than postorbital. PHARYNGEAL ARCH (Fig. 2B) more elongate, not thick and heavy; lower limb with, at most, weak lateral ridges; upper limb with, at most, weakly curved tip and without a retrorse spur; crenulations on teeth weakly developed (in *dichroma* and *rasconis*) or absent (Figs. 2-3). SENSORY CANALS OF HEAD normally continuous (except in a moderate proportion of the *rasconis* population, and often, attributable to dwarfing, in *erimyzonops*). MELANIC COLORATION much less sharply streaked (midlateral streak obsolescent to moderately strong, bordered above by a weak to obsolete light stripe; scale rows of upper sides and back not definitely streaked; mid-dorsal dark stripe developed before and behind dorsal fin, except in *erimyzonops*) Couplet 2

Couplet 2 (from 1B):

- 2A. BARBEL almost invariably formed at end of maxilla, at least as a minute rudiment. BODY in general relatively slender and attenuate, with contours rather symmetrically conical anteriorly (least so in some specimens of *dichroma*). RAKERS (Table 8) on first arch normally 8 or more. ANAL RAYS (Table 4) normally 8 except usually 9 in one part of the range of *dichroma*. CAUDAL PEDUNCLE (Table 9) about, to more than twice, as long as anal-fin base (except often somewhat less than twice longer in *dichroma*). HEAD DEPTH (Table 10) 16-19% of standard length. SCALES (Table 5) more numerous (37-45 along lateral line to caudal base and in 15-23 predorsal rows, except for intermediate values, 33-36 and 14-18, in *rasconis*). COLOR PATTERN relatively simple (lacking the dorsal striping on top of head of *erimyzonops* and the general blackening of whole body and jet-black blotching of nuptial males of *ipni*). *Inhabiting lower- and upper-intermontane tributaries of the Río Pánuco system* Couplet 3
- 2B. BARBEL consistently wholly lacking. BODY relatively robust, with anterodorsal contour rather strongly arched, and front of head gibbous, even in young. RAKERS (Table 8) on first arch normally 8 or fewer. ANAL RAYS (Table 4) normally more than 8. CAUDAL PEDUNCLE (Table 9) normally less than twice as long as anal-fin base. HEAD DEPTH (Table 10) 20-23% of standard length. SCALES (Table 5) fewer (31-37 along lateral line and in 11-14 predorsal rows.) COLOR PATTERN more distinctive and bolder (see Couplet 5). *Inhabiting streams of the coastal plain of the Río Pánuco system and southeastward.* Couplet 5

Couplet 3 (from 2A):

- 3A. FINS all sharply pointed at tip; the rays all slender and fragile. SCALES largely obsolescent to obsolete over far-forward angle of breast and over shoulder girdle; usually somewhat fewer, numbering (Table 5) 33-36 along lateral line (to caudal base); and (Table 6) 14-18 predorsal rows. VERTEBRAE (Table 7), except for rare variants, 18-19 + 16-17 = 34-36. RAKERS on first gill-arch typically extend forward from region of angulation to about midway along the moderately attenuated exposed border of lower limb. LOWER-LIP GROOVES each about twice as long as anterior interspace. PHARYNGEAL ARCH with upper limb very elongate, slender, and sinuous, with a gently curved, sharp tip (Fig. 2C-D). GROUND COLOR very light above as well as below the particularly jet-black (though narrow) midlateral streak (thus not yielding a distinctly bicolored effect); particularly backward, a broad stripe just above the black streak seems to be considerably devoid of pigment; above this stripe, the blackish pigment is chiefly evident as extremely narrow dark lines along edges of scale pockets; body below black streak apparently not developing melanophores. DORSAL FIN of nuptial males neither sooty on preservation nor blue-edged in life. SIZE smaller (standard length only slightly exceeding 50 mm, and nuptial males are as short as 32-40 mm). NUPTIAL TUBERCLES apparently confined to pectoral fin, where they form an irregular, narrow band rather than merely bifurcating on top of each enlarged outer ray. *Inhabiting the Río Gallinas lower-intermontane section of the Río Pánuco system* *Dionda rasconis*
- 3B. FINS all rounded at tip; the rays all robust and strong. SCALES continued forward over anterior breast and over shoulder girdle, though reduced there in size and tending to be imbedded; usually (Figs. 5-6) more numerous (37-45 along lateral line; 15-20 predorsal rows). VERTEBRAE (Table 7), except for rare variants, 19-20 + 17-19 = 37-39. RAKERS on first gill-arch extend forward from region of angulation to, or very nearly to, front end of the rather short exposed border of lower limb. LOWER-LIP GROOVES about as long as, to about half longer than, anterior interspace. PHARYNGEAL ARCH with upper limb not elongate, sinuous, and sharp-tipped. GROUND COLOR rather evenly sooty above the midlateral stripes, contrasting with that of the lower sides even where they have become slightly to moderately dark-dappled (thus yielding an

overall bicolored appearance); light stripe margining above the blackish streak weak and narrow to obsolescent; above this stripe the scale-pockets are not conspicuously dark-margined; in adults, the lower sides develop melanophores. DORSAL FIN in nuptial males becoming sooty, and, in life, conspicuously blue-edged. SIZE somewhat larger (reaching about 65 mm in standard length, and nuptial males are generally longer than 40 mm). NUPTIAL TUBERCLES strong and numerous, widespread over the head, body, and fins of the considerably darkened breeding males; those on pectoral rays in one series branching once. *Inhabiting lower- and upper-intermontane sections of the Río Pánuco system* Couplet 4

Couplet 4 (from 3B):

- 4A. MOUTH entirely below eye, overhung by the sharply downturned snout, with a projecting terminal flap overhanging front of mouth; tip of snout, both lips, and chin on an essentially common, and nearly horizontal plane. LIPS much more conspicuously swollen; the lower wholly or almost wholly devoid of pigment and widely separated, with their inner grooves very short (only about as long as anterior interspace). BARBEL ordinarily conspicuous and obviously pendant. PHARYNGEAL ARCH slender and rather narrow; upper limb well curved; posterior tooth arising above shaft of arch. BODY much more terete (greatest depth less than twice the greatest width). DORSAL AND ANAL FINS, in normal moderate expansion, with posterior edge sloping forward from tip; that of dorsal slightly, and that of anal rather deeply, falcate; with indentation not obliterated by a moderate down-stretching of that fin. CAUDAL VERTEBRAE (Table 7) predominantly 19. MID-DORSAL DARK STREAK obsolete along and behind dorsal fin. *Inhabiting the Río Gallinas lower-intermontane section of the Río Pánuco system* *Dionda catostomops*
- 4B. MOUTH not entirely below eye, rising obliquely to above level of lower orbital margin; not definitely overhung at front by a distinct terminal flap of snout; tip of snout, upper lip, and chin forming a rather oblique, and not evenly continuous, line. LIPS much less conspicuously swollen; the lower well pigmented, with inner grooves each about one-half longer than anterior interspace. BARBEL normally very small to rudimentary, seldom either definitely pendant or not observable. PHARYNGEAL ARCH heavier; upper limb more broadly curved, and usually with retrorse tip; posterior teeth not, or scarcely, elevated above shaft of arch. BODY less terete (greatest depth much more than twice the greatest width). DORSAL AND ANAL FINS, in normal slight expansion, with posterior edge sloping backward from tip; posterior edges straight or slightly rounded (or anal at most only incipiently falcate). CAUDAL VERTEBRAE (Table 7) predominantly 18. MID-DORSAL DARK STREAK moderately to strongly developed. *Inhabiting the Río Verde upper-intermontane section of the Río Pánuco system* *Dionda dichroma*

Couplet 5 (from 2B):

- 5A. ANTERIOR CONTOUR before eye sloping at about 54°; upper lip largely or wholly below level of lower margin of orbit. LOWER-LIP GROOVES in adult separated at front by about the length of either. ORBIT distinctly narrower than interorbital. ANAL-FIN BASE longer (in nuptial males longer than caudal peduncle). PECTORAL RAYS (Table 6) 13–17, modally 15. RAKERS on first gill-arch extending from vicinity of angulation forward about to middle of the much foreshortened exposed margin of lower limb. LATERAL STREAK sooty black, weak to obsolete on head before opercle, obscured in nuptial males by general blackening of whole body. PHARYNGEAL ARCH moderately heavy; lower limb expanded distally; upper limb with a ventrally-keeled triangular facet at its end. V-SHAPED BLACK PATTERN on top of head lacking. BLACKENING OF FINS in nuptial males comprising a large jet-black blotch on median part of most or all fins. NUPTIAL TUBERCLES strong and widespread, clumped over top of head, most of snout, and backward on suborbital region; on upper sides forming definite rows, one per scale; strong also on lower fins. SIZE generally small, but less dwarfed (nuptial males encountered 31–74 mm in standard length). *Inhabiting the coastal-plain section of the Río Pánuco system and other streams south-eastward almost to the great lava blockade at Punta Delgado, Veracruz; reaching farther inland and to higher elevations southward* *Dionda ipni*
- 5B. ANTERIOR CONTOUR before eye strongly arched downward, to become vertical above front of mouth; front of upper lip opposite lower part of eye. LOWER-LIP GROOVES separated at front by about half the length of either. ORBIT about as wide as interorbital. ANAL-FIN BASE shorter (in nuptial males shorter than caudal peduncle). PECTORAL RAYS (Table 6) 12–15, modally 13. RAKERS on first gill-arch attaining the least development (confined to the posterior curve, with 0–1 above and 1–3 below the angle). LATERAL STREAK always jet-black, continued forward around snout. PHARYNGEAL ARCH rather slender; lower limb no wider distally than basally; upper limb with an elevated crest on its dorsal surface (no triangular facet below). V-SHAPED BLACK PATTERN on top of head conspicuous. BLACKENING OF FINS in nuptial males restricted to membranes between anterior rays. NUPTIAL TUBERCLES enlarged and relatively few, generally aligned over top of head and across snout, and along the somewhat sharpened ridge on either

side of caudal peduncle; at most a few minute ones on lower part only of suborbital; very small on body scales; minute on pectoral fin and hardly evident on other fins. SIZE much dwarfed (observed range in standard length of mature adults 21–39 mm). *Inhabiting the coastal-plain section of the Río Pánuco system, particularly in the Río Tamesí section . . . Dionda erimyzonops*

SPECIES ACCOUNTS

Dionda mandibularis Contreras-Balderas and Verduzco-Martínez

Figure 4A–B

Dionda mandibularis.—Contreras-Balderas and Verduzco-Martínez, 1977: 259–265, Figs. 1–3 (original description; types from an arroyo 7 km SSE of Río Verde, San Luis Potosí; also from a spring-fed marsh 9.7 km S of Río Verde and from Puerta del Río 20 km S of Cerritos, San Luis Potosí; relationships largely on basis of intestinal coiling).

Synonymy, Nomenclature, and History.—This species was first collected but not adequately distinguished by Richard T. Gregg in 1956, for his unpublished doctoral dissertation at Louisiana State University. He designated his material as a new subspecies of *Dionda rasconis*, but fully confounded it with the very distinct, partially sympatric species that we are now describing as *Dionda dichroma*. In fact, the designated type series of the “subspecies,” taken at Puerta del Río, comprises, we find, about equal numbers of *mandibularis* and *dichroma* (Gregg’s material of this form from La Media Luna has not been located for reexamination by us, but may represent either or both of the species; his material from the lower Río Verde at Guayabos and Tanlacú, on re-examination, is found to comprise *dichroma* only). Gregg’s material, so far as re-examined by us, is mentioned, with Louisiana State University Museum of Zoology (LSUMZ) numbers in the lists of material examined, under *D. mandibularis* and *D. dichroma*. This species was recognized also by Jorge Armando Verduzco-Martínez in 1972, in his unpublished dissertation for the degree of “Biólogo,” as a new subspecies of *D. rasconis*, which we now recognize and describe as *D. dichroma*.

It has been our pleasure to withhold our treatment of this species pending its description by our Mexican colleagues, Contreras-Balderas and Verduzco-Martínez.

Diagnosis.—Rakers on first gill-arch confined to vicinity of its angulation. Mandible about as long as, or longer than, postorbital, and longer than 10% of standard length; more distinctly trenchant, with obvious posterior angulation; and nearly to greatly protruding forward. Head before rear of orbit longer than postorbital. Sensory canals narrowly to widely interrupted about upper posterior part of infraorbital canal and along preoperculomandibular canal just behind mandible. Melanic pigmentation very bold. Barbel virtually absent (present on one side in only one of the 51 specimens examined by us).

Comparisons.—*Dionda mandibularis* differs trenchantly from each of the five other species of *Dionda* of the Río Pánuco stream complex in numerous characters, supplementing the unique features epitomized in the foregoing Diagnosis, and it contrasts strongly also with *D. episcopa* Girard and *D. diaboli* Hubbs and Brown. It differs from the three other species (*rasconis*, *catostomops*, and *dichroma*) of the upland-interior segments of the Río Pánuco system, in almost invariably lacking even a trace of the maxillary barbel (in which respect it secondarily almost always agrees with the two otherwise very different lowland species, *ipni* and *erimyzonops*). It differs further from the three other upland species in having a blacker lateral stripe, in the much stronger margining light stripe, and in the conspicuously light-centered dorsal scales.

Material Examined.—UMMZ 193474 (11 specimens: 32–52 mm SL), marsh 10 km S of Río Verde, San Luis Potosí (this series was also examined by the describers of the species and was designated by them as paratype); UMMZ 196703 (6: 38–49) and USNM 215783 (7: 35–46), same location; LSUMZ 405 and 407

(7: 39–52), Puerta del Río, “9 km S of Villa Juárez (formerly Carbonera);” UMMZ 196339 (33: 42–58), same location, recorded as “22 km SE of Cerritos” (this series was also mentioned by the authors of the species).

DESCRIPTION

The prime distinctive characters of *Dionda mandibularis* are largely those given as item 1A in the Analytical Comparisons (p. 276), and, above, under Diagnosis and Comparisons.

Size and Form.—This is a moderately small minnow: the largest of the 51 specimens at hand measures 58 mm SL. The dorsal contour rises on the snout at an angle of about 45° , then curves gently to the dorsal-fin origin, with, in some specimens, a weak depression at the occiput; then descends moderately along the base of that fin, before weakly sloping downward, in a very slight curve, to the caudal-fin base. The ventral contour descends along the markedly straight bony edge of the mandible, at an angle usually reversing that of the rostral margin. The ventral contour varies from straight to moderately curved on the breast and rises moderately behind the anal-fin origin, until it becomes about horizontal on the posterior part of the caudal peduncle. In dorsal view the margins of the snout tend to converge rather rapidly to the often pointed tip. The narrow upper lip usually becomes marginal near its middle, and around the front is ordinarily well exposed, in vertically straight dorsal view, as it rises to become nearly horizontal with the lower margin of the pupil. The thin and elongate mandible rises sharply forward to become, variably: only slightly included, even with the upper-lip margin, or, not infrequently, slightly to strongly and angularly projecting. The inner grooves of the lower lip, which converge sharply forward in nearly straight lines to very near the tip of the skin, are 3–5 times as long as the vary narrow anterior interspace. The concealed end of the maxilla lies vertically below either the posterior nostril or the internarial septum. The mandible reaches to below some point between the front of the orbit and the front of the pupil.

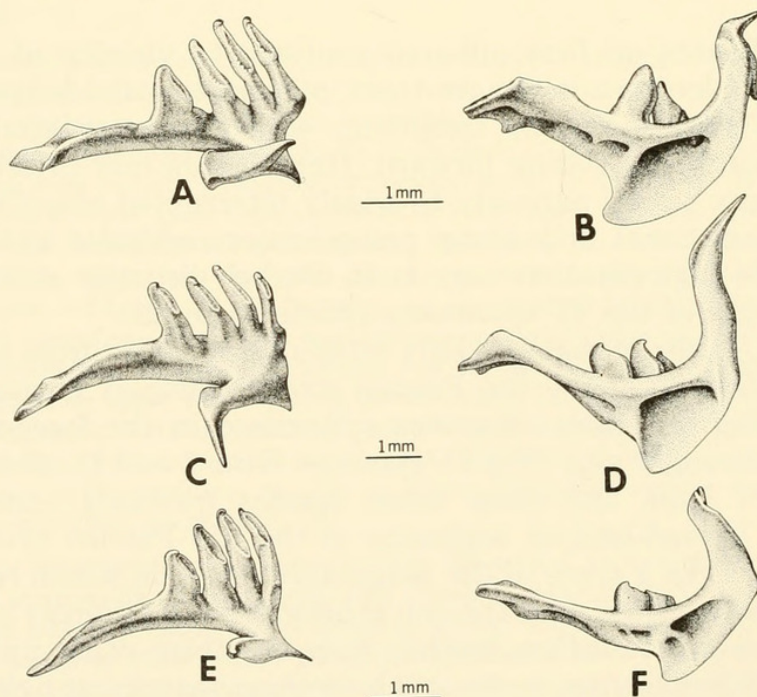


Figure 2. Dorsal and lateral aspects of left pharyngeal arches of three species of *Dionda*. A–B, paratype (52 mm SL) of *D. mandibularis* (UMMZ 193474) from marsh 10 km S of Río Verde, San Luis Potosí. C–D, adult (49.5 mm) of *D. rasconis* (UMMZ 193509) from Río Tamasopo, Tamasopo, San Luis Potosí. E–F, paratype (57 mm) of *D. catostomops* (UMMZ 196347) from Río Tamasopo, Tamasopo, San Luis Potosí.

Proportional Measurements.—The measurements made on *mandibularis*, when compared with those for the five other *Dionda* species of the Río Pánuco complex (Table 10 and separate tables for *dichroma* and *ipni*), demonstrate various interspecific differences. Depth of body, except in the sample from the spring marsh below La Media Luna, is less than in any sample at hand of *dichroma*, and is much less than in *ipni* or *erimyzonops*. Caudal peduncle, except in the same marsh, is definitely slenderer than in *catostomops*, and is distinctly slenderer than in the two lowland species; the peduncle is definitely somewhat shorter than in *catostomops*, consistently with the higher number of caudal vertebrae (Table 7) in that species, but is very much longer than in either *ipni* or *erimyzonops*. Distance from anal origin to midcaudal base is also less than in *catostomops*, but the proportion is essentially the same as in *ipni* and *erimyzonops*, because the much shortened peduncle in those species merely compensates for their very definitely longer anal-fin base. The head is definitely larger than in the three other upland species, but the proportion is about the same as in *ipni* and *erimyzonops*. The lips tend to be less swollen than in the five other species; the width of the upper lip at the symphysis is almost invariably less than in *catostomops*, *ipni*, and *erimyzonops*, and averages less than in *rasconis* and *dichroma*.

Barbel.—Normally the maxillary barbel is totally lacking, but on one side of one specimen (no. 12 in UMMZ 196339), among 51 carefully examined, a minute remnant is evident in the usual position at the lower end of the posterior border of the maxilla.

Gill-rakers.—The rakers on the first arch are found, in 20 specimens, to occupy the diagnostic position indicated in item 1A of the Analytical Comparisons (p. 276). The number (Table 8) varies from 7 to 10, except in one specimen which aberrantly has 12 rakers, of which the 2 foremost are separated from the others by a wide gap.

Pharyngeal Arch and Teeth.—*Dionda mandibularis* has distinctively heavy and short pharyngeal arches (Fig. 2A-B). The broad lower limb is somewhat

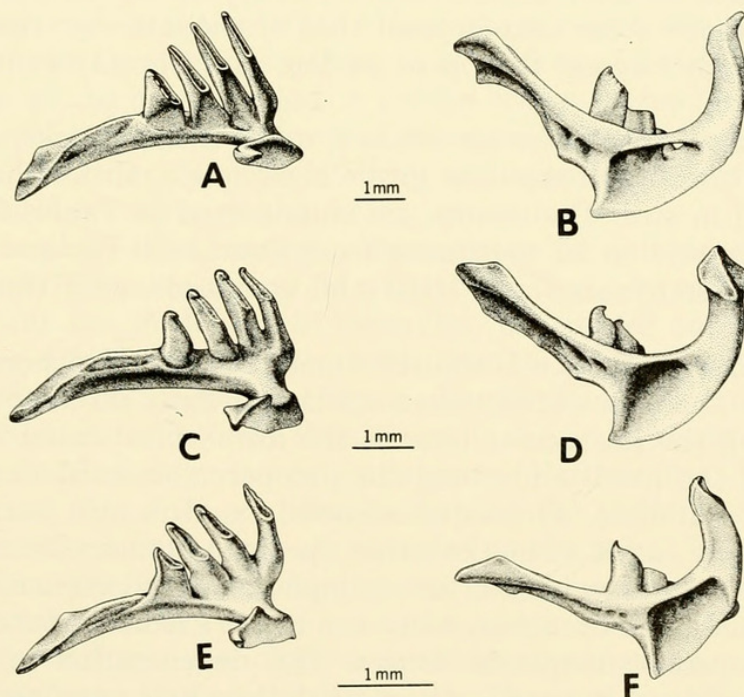


Figure 3. Dorsal and lateral aspects of left pharyngeal arches of three species of *Dionda*. A-B, paratype (55 mm SL) of *D. dichroma* (UMMZ 196338) from Puerta del Río 20 km SE of Cerritos, San Luis Potosí. C-D, adult (48 mm) of *D. ipni* (UMMZ 193492) from tributary of Río San Marcos at Highway 130, Puebla. E-F, adult (27.5 mm) of *D. erimyzonops* (UMMZ 97467-68) from Río Guayalejo near Llera, Tamaulipas.

longer than the upper, and its tip is sharply deflected mesially from the shaft. Its ventral edge is keeled in advance of its tip, and in some specimens strong lateral ridges are developed. The margins of the lower limb are nearly straight. The moderately curved upper limb is thick and heavy, though not as broad as the lower; it narrows abruptly distally, and has a strongly recurved, pointed tip. Where this arch narrows distally, the shape of the bone along its mesial surface varies from an elevated ridge to a retrorse, dorsally directed, spur.

The two posterior teeth, especially the uppermost one, arise on an elevated crest and are notably smaller than the next two; each has a narrowly crenulated grinding surface, similar to but less pronounced than that in the pugnose minnow (Gilbert and Bailey, 1972: fig. 2C). The long and slender third tooth is larger, and has a well-developed grinding surface. The fourth tooth is enlarged, especially basally, and its grinding surface is either weak, or tends to become molariform. The two posterior teeth are well hooked, the lower two weakly or not.

Intestine.—The highly variable degree of intestinal coiling grades irregularly from hardly more convoluted than the simply sigmoid form characteristic of *Notropis* in general (shown as Fig. 2A by Contreras-Balderas and Verduzco-Martínez, 1977), to at least 3 and often 4 major U-shaped loops (as in their Fig. 2C). The loops are the more obvious on the right side. The main coiling, on this side, takes roughly the form of inverted U's, compact medially, but becoming looser and more longitudinal posteriorly. Usually, the coils are largely lateral and extend through most of the body cavity. The axis of the tight to loose central coiling may be vertical or may slope either forward or backward, but we have not observed in any of the species herein treated the regularly concentric and essentially completely circular coiling that is developed in *D. diaboli* and *D. episcopa* (as shown in Figs. 2G and H of the same set).

Fins.—The dorsal is more or less rounded at its tip; when moderately elevated, its posterior border is weakly convex and usually slopes slightly backward. The anal is slightly pointed at its tip; its nearly straight posterior border slopes strongly backward. When the fins are fully depressed, the tip of the longest dorsal ray extends somewhat beyond that of the last ray; the tip of the anal reaches to or slightly beyond the tip of its last ray. The ray counts are listed in Tables 3 and 4.

Scales.—As in all species herein treated, other than *rasconis*, the squamation over the anterior breast and shoulder girdle is complete, although the scales there are much reduced in size. The counts are enumerated in Tables 5 and 6.

Vertebrae.—Counts on 30 specimens from Puerta del Río and on 16 from the La Media Luna marshy area are listed and compared with those of the other species in Table 7.

Sensory Canals of Head.—Uniquely among the species herein treated, the lateral-line canals and pores of the head are consistently interrupted, narrowly to very widely, along the postocular part of the infraorbital canal from behind the eye to the top of the head, and along the preoperculomandibular series immediately behind the mandible. The supratemporal canal is also narrowly to widely interrupted medially, as it is in the other species. Abnormalities in the system were observed in some specimens; for example, a partial commissure across the frontal region, small side branches, and even a short isolated tube with a definite pore along the opercle/subopercle suture. The degeneration of the lateral-line system in this highly restricted, spring-inhabiting fish parallels what has been observed in other minnows in such isolated waters, notably by Hubbs, Miller, and Hubbs (1974) for those in the Great Basin.

Coloration.—*Dionda mandibularis* is highly distinctive in coloration, and the dark areas are much more extensive in the males than in the females. In both sexes the lateral stripe is intensely blackened. It is strong over the snout, the

front of the iris, across the postorbital except at the opercular margin, along the lateral-line row for a few scales, then immediately above the lateral line on the trunk, and along the lateral-line scale row of the urosome. The stripe ends in a small subtriangular basicaudal black spot, fraying backward on the middle caudal rays, with intervening membranes clear in females but well punctulated in males. Above this stripe the conspicuous light streak is somewhat subdued by fine punctulation in ripe males, but is largely clear in females and in non-breeding males. On the body, the light streak is somewhat narrower than the black one. On the head, the light streak covers much of the narial fossa, but is lacking around the blackened front of the muzzle; it is somewhat obscured, especially in males, above the dark stripe on the postorbital region. From occiput to caudal fin the back, in series, is darkened by wide scale-pocket margins, leaving the center of the pockets much lighter, to form definite light streaks, which are much subdued in the nuptial males by the rather intense general darkening. This light dorsal striping becomes rather indistinct close to the caudal fin. There is no definitive middorsal dark stripe, before, around, or behind the dorsal-fin base. In females, the surface below the dark stripe on the body and head, and behind the muzzle, is clear of pigment, with no trace of a midventral stripe on the caudal peduncle, although there is considerable blackening on either side of the anal base. In the breeding males, the entire lower-lateral and ventral surface of the body is densely punctulate with black. The top of the head, including the snout, is blackish in females and black in ripe males. Both lips are largely darkened, as is also the intergular region in males. In females, the cheeks and opercular regions are essentially unpigmented, but in the ripe males there is much black punctulation there, especially over the opercular regions. The vertical fins are darkened along the branching of the rays, especially in nuptial males. There is no black band just above the base of the anal rays. The paired fins, notably in the males, are especially blackened, particularly along the branching rays.

Color in Life.—The rather plain life colors have been described by Contreras-Balderas and Verduzco-Martínez (1977: 261). Conspicuous colors noted by us, in part by underwater observation with a face mask, were the chalky-blue on the outer margins of the lobes of the pelvic, anal, and caudal fins (evidently lacking on the dorsal fin) of the nuptial male. A golden-bronze stripe lies above and parallels the dark lateral stripe; the two are of about equal width and length. The back is olive-green (at least in the female), with a prominent, narrow, yellowish pre-dorsal stripe; the lower sides of the female are pale.

Nuptial Tubercles.—The nuptial tuberculation is well developed on mature males (UMMZ 196703) collected 21 March 1974. The only moderately thickened outermost pectoral ray is devoid of tubercles, except for some weak ones in a single row on the outer half. The succeeding several enlarged rays bear numerous tubercles, several per ray segment; they are hardly developed at the base and are uniserial for a short distance only. Where the fin is somewhat arched upward, the tubercles form a band of about 3–5 irregular rows. Farther distad, they grade first into two series and then into one, finally leaving the outermost part of the ray smooth. There is only a bare trace of tubercles on the pelvic fin, and none on any of the vertical fins. The largest tubercles are those scattered over the top of the head, partly in rows, usually leaving a nearly bare strip over the frontal bone; they tend to form a single row close around the upper margin of the orbit. The large ones extend forward to a line between the fronts of the narial fossae; farther forward there is an essentially nude transverse strip, beyond which a few tubercles cluster around the front of the snout; usually a few occur in a single series along the lower margin of the narial fossa. The head is completely devoid of tubercles below the posterior horizontal section of the infraorbital canal, below the eye, and ventrad from the series just below the narial fossae over the whole

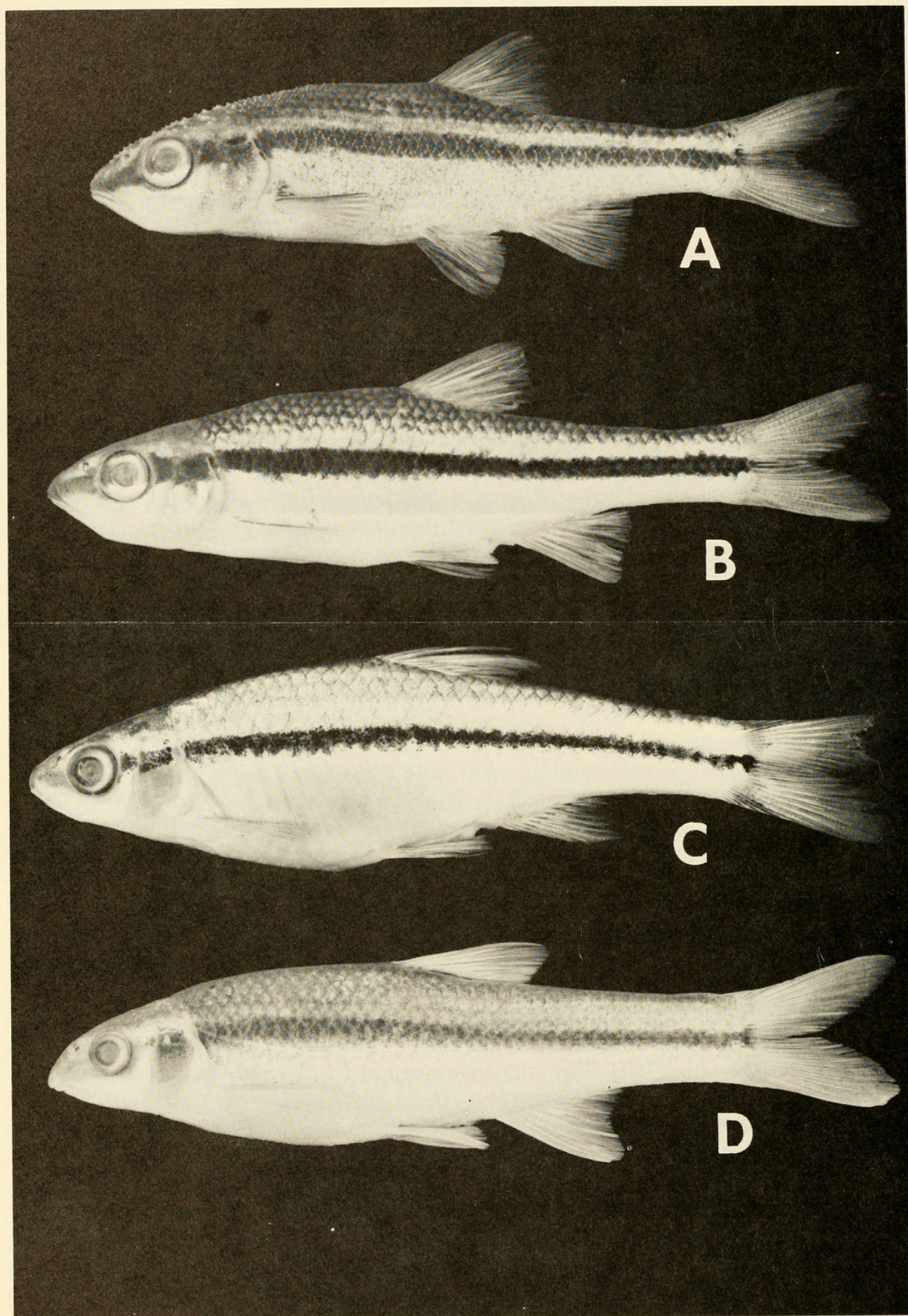


Figure 4. Three species of *Dionda* from Río Pánuco system: **A and B**, nuptial male (51.9 mm SL) and adult female (49.1 mm) of *D. mandibularis* (UMMZ 196703) from marsh 10 km S of Río Verde, San Luis Potosí. **C**, adult (51.3 mm) of *D. rasconis* (UMMZ 193509) from Río Tamasopo, Tamasopo, San Luis Potosí. **D**, adult male holotype (54.7 mm) of *D. catostomops* (UMMZ 196346) from Río Tamasopo, Tamasopo, San Luis Potosí.

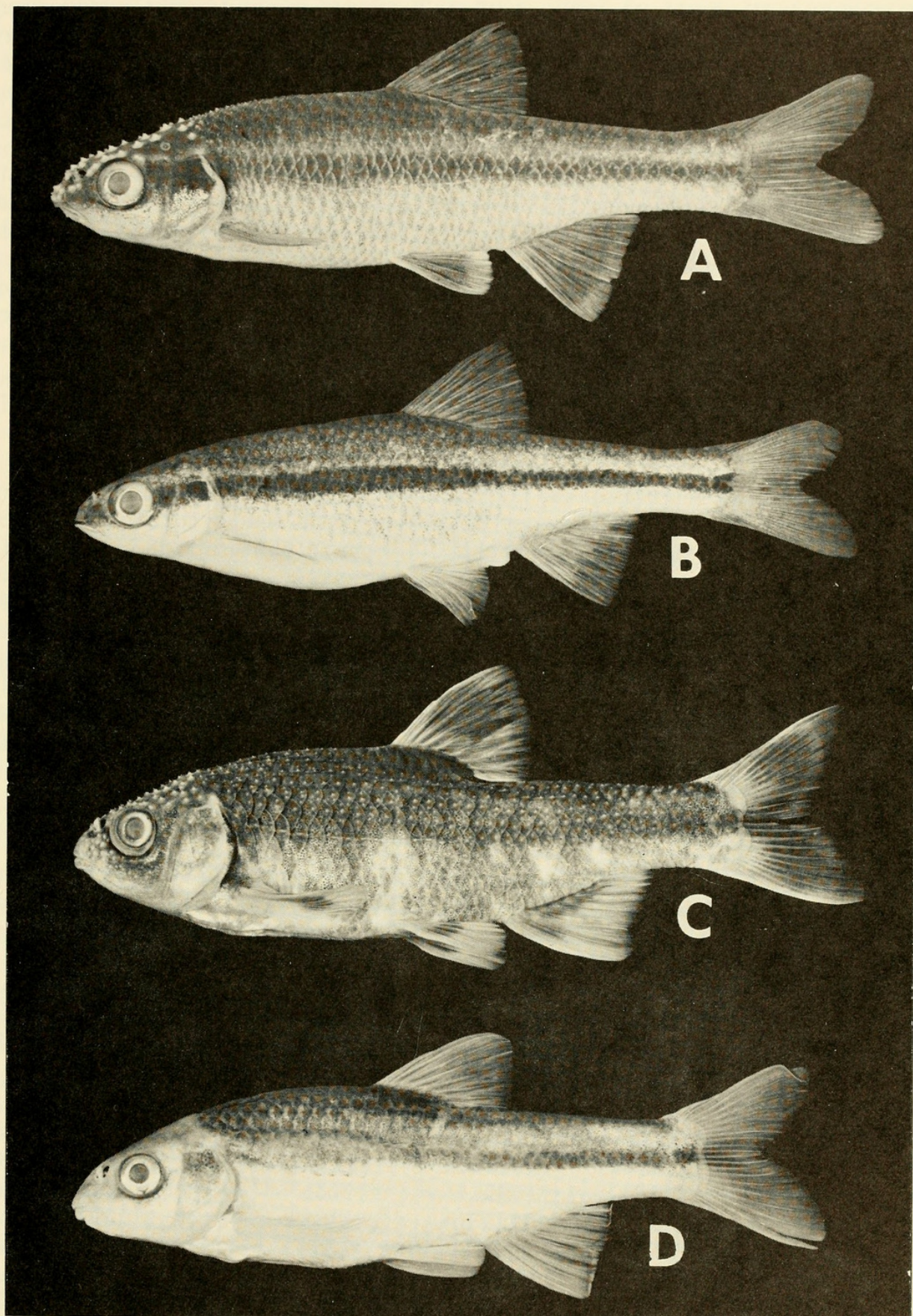


Figure 5. Two species of *Dionda* from Tampico Embayment area: **A and B**, nuptial male holotype (51.7 mm) and female paratype (49.0 mm) of *D. dichroma* (UMMZ 196701-02) from marsh 10 km S of Río Verde, San Luis Potosí (note large eye). **C and D**, high nuptial male (51.5 mm) and prenuptial male (48.0 mm) of *D. ipni* (UMMZ 193492 and 193502), respectively, from tributary of Río San Marcos at Highway 130, Puebla, and distributary of Río Lasan at Highway 180 bridge, Veracruz.

For illustration of *D. erimyzonops* see Hubbs and Miller, 1974: Fig. 1.

ventral region including the chin and lips. Tubercles, mostly rather large, extend over the nape about halfway back to the dorsal-fin origin; these tubercles in part line the scale margins, but are otherwise irregularly arranged. Above the lateral stripe the upper sides and back are almost completely devoid of tubercles. Along the lateral stripe the scales of the lateral-line series, of the next row above, and on the lower part of some scales in the next row above, bear tubercles, which become weak or obsolete close to the head and close to the caudal fin. On the anterior half of the trunk the lower sides are nontuberculate, but farther back the tubercles increase in number over as many as three or four scale rows below the lateral-line series. On the caudal peduncle rather strong tubercles largely line the scales of two rows below the lateral-line series, leaving only the scales of the midventral row unarmed. In general the armature strengthens backward, almost to the lower part of the caudal-fin base. Most of the tubercles are essentially erect, but the large ones on the urosome are moderately antrorse.

Mature females are completely devoid of tubercles.

SEXUAL DIMORPHISM

Except for the features of the nuptial tubercles just treated, and for the sharp sexual differences mentioned under Coloration, little sexual contrast has been observed. Detailed measurements (Table 10) seem to indicate that in the adults the pectoral, pelvic, and depressed-dorsal fins average longer in males than in females, but with very considerable overlap. Furthermore, the pelvic fin extends in the maturing and nuptial males to any point from just past the rear of the anal fossa to considerably behind the origin of the anal fin; whereas in adult females the pelvic extends only to any point from somewhat short of the front, or rarely to the end, of the anal fossa. In each sex the pectoral fin fails by a considerable distance to reach the pelvic insertion. The urogenital papilla of the maturing to mature individuals develops no readily obvious sexual differentiation.

VARIATION

No very marked differences have been observed between samples from the two not far-distant known habitats of this species—Puerta del Río (the great spring source of Río Verde) and the springfed marsh below, in the La Media Luna area.

There does appear to be a greater tendency for the mandible to project forward beyond the upper lip and rostrum in the Puerta del Río material and to be included slightly within the front of the upper lip in the samples from the marsh.

DISTRIBUTION, HABITAT, AND ASSOCIATED SPECIES

Dionda mandibularis, according to the recently expanded reconnaissance of the freshwater fishes of east-central México, seems to be strictly confined to the upper-intermontane portion of the Río Verde division of the Río Pánuco system, in an arroyo and in warm springs in a limited area near the town of Rioverde and in Puerta del Río, the very large source spring of Río Verde about 45 km NW of the town. The total known straightline northwest-southeast range of the species is only about 60 km. The local at least partly sympatric *dichroma* is the only species of *Dionda* that has been taken either in the partly isolated Río Santa Catarina headwater or in the main Río Verde below the turbulent gorge. Nor are there any records of *D. mandibularis* in Río Santa María, Río Gallinas, or Río Valles, nor do we expect it to be found in those streams.

Ecological conditions were noted as follows: water very clear, with considerable vegetation; easily roiled because the bottom was largely of mud or silt; cur-

rent barely perceptible or moderate to none; depth to about 1m; temperature warm (recorded as 25.5° in December, 27° in February, and 24.5° in March). In the spring-fed marsh south of Río Verde, where *mandibularis* and *dichroma* are sympatric, *mandibularis* seems to avoid the spring heads frequented by *dichroma*, preferring, instead, the quieter and deeper water over the flocculent-silt bottom.

Associated fishes, in addition to *Dionda dichroma*, were found to be *Astyanax mexicanus*, *Ataeniobius toweri*, and 2 or 3 species of *Cichlasoma* in both Puerta del Río and the marsh area; *Ictalurus mexicanus* in Puerta del Río only; and *Cualac tessellatus* in the marsh only.

LIFE HISTORY NOTE

Dionda mandibularis appears to be an early-spring spawner. Specimens taken on December 9 were non-nuptial, and those collected on February 5 were in early stage of maturity. On March 21, 4 high-nuptial males and 1 ripe female were collected, and on August 23, females with small ova and postnuptial males were secured.

Dionda rasconis (Jordan and Snyder)

Figure 4C

Notropis rasconis.—Jordan and Snyder, 1900: 121-122, Fig. 3 (original description; compared with [the probably not closely related] *N. nigrotaeniatus* (Günther) of the Río Balsas system; "Río Verde" near Rascón, San Luis Potosí, México). Jordan and Evermann, 1900: 3141-3142 (original account repeated). Böhlke, 1953: 35 (synonymy; types listed).

Hybognathus rasconis.—Meek, 1904: xxxvi, 48, 50, Fig. 10 (in part, excluding the Valles and Forlón records; compared with *H. episcopus*).

Dionda rasconis.—De Buen, 1940: 22 (in part; references and record from basin of Río Pánuco at Rascón, after Meek). Hubbs and Brown, 1956: 71-73 (compared with *Dionda diaboli*; measurements; Rascón). Alvarez, 1959: 80 (presumably in part; characters; Estado de San Luis Potosí); 1970: 67 (in part; characters in key).

Hybognathus episcopus (misidentification).—Regan, 1906-08: 150-151 (reference to *Hybognathus rasconis* and record from "Río Verde" in San Luis Potosí, both in part). Alvarez, 1950: 49 (presumably in part, in key; "norte de México").

Synonymy, Nomenclature, and History.—This well-defined species was referred to *Notropis* by Jordan and Snyder, presumably on the basis of its general appearance, but was transferred to *Hybognathus* by Meek and by Regan, and to *Dionda* by De Buen and by Alvarez, no doubt after it was found to have an elongate intestine. It has been long treated, erroneously, as the nominotypical subspecies of a wrongly assumed intraspecific complex by one of us (Hubbs), in a never completed revision of the fishes of northeastern México, in the 1930's, and, presumably as a result of this incorrect decision, by Richard T. Gregg in his unpublished doctoral thesis of 1956 and by Jorge Armando Verduzco-Martínez in his dissertation for the "Biólogo" degree of 1972. The recent discovery (by Miller) that this species (along with two others apparently related) ordinarily has a maxillary barbel raised further question as to generic placement. Our reference of this and five other species of the Río Pánuco stream system to *Dionda* is herein maintained on a provisional basis, as is explained in the Introduction.

Diagnosis.—Scales obsolescent far forward on breast and on shoulder girdle. Rakers on first gill-arch typically extended forward to about midway along the moderately attenuated exposed border of the lower limb. Scales relatively large, 33-39 along lateral line and 14-18 in the predorsal row. Ground color light above as well as below the jet-black lateral stripe, with narrow dark lines bordering scale pockets above this stripe; sides below virtually unpigmented. Breeding males golden on sides and without bright colors on the fin borders. Nuptial tubercles restricted to a villiform band on pectoral rays.

Comparisons.—*Dionda rasconis* differs sharply from each of the five subsequently described species of the Río Pánuco complex that we also refer to *Dionda*. The normal development of a small maxillary barbel distinguishes it from *mandibularis* and the two very different coastal-plain species (*ipni* and *erimyzonops*). Contrasts with *mandibularis* are elaborated in couplet 1 of the Analytical Comparison (p. 276) and with the four other species in couplets 2 and 3. Its characters contrast trenchantly with those of the one sympatric species of the group, *catostomops*, of the lower-intermontane basin (as stressed in the account of that species, p. 296), as well as with *dichroma* of the upper-intermontane basin (in couplet 3). All distinctive features of *rasconis* outlined in item A of this couplet, with the exception of the vertebral number, the extent of gill-rakers, and the lower-lip groove, distinguish *rasconis* from *mandibularis*, *ipni*, and *erimyzonops*, as well as from the species *catostomops* and *dichroma*, as listed in item B of couplet 2. The very pale coloration of *rasconis* distinguishes it from all other species that we refer to *Dionda*. It is certainly a very distinct, highly localized minnow.

Material Examined.—Holotype CAS-SU 6153 (43 mm SL) and paratypes CAS-SU 6197 (2: 43–44), 25 January 1899, “Rio Verde [*sic* = Río Ojo Frio], near Rascón,” San Luis Potosí. Topotypes: FMNH 4509 (34: 28.0–45.3), 6 May 1903; LSUMZ 406 (10: 19–46), 26 June 1954; UMMZ 196693 (67: 27–49), 20 March 1974. UMMZ 193509, 17 December 1972 (15: 35–50) and UMMZ 196345, 7 February 1974 (13: 36–53), Río Tamasopo near Tamasopo, tributary to Río Gallinas, San Luis Potosí.

DESCRIPTION

The prime descriptive characters of *Dionda rasconis* are given in items 1A, 2A, and 3A of the Analytical Comparisons.

Size and Form.—This is a moderate-sized minnow: the largest among the 145 specimens examined measures 53 mm SL, definitely larger than any example of the greatly dwarfed *Dionda erimyzonops*, but somewhat smaller than the largest of each of the four other species here treated. The lower contour of the body is almost as arched as the upper: a line from the middle of the basicaudal spot to the front margin of the snout passes little below the mid-depth of the trunk. The dorsal contour rises at first rather steeply from near the horizontal through the bottom of the eye, but then flattens out considerably to the occiput, from which it rises rather sharply in a very weak curve to the front of the dorsal fin, with hardly a trace of a break or change in the very even slope at the occiput; the contour slopes downward rather abruptly and sharply along the dorsal base, behind which it gently descends in a nearly straight line. On the head the ventral contour nearly matches the dorsal contour, with a slight protuberance at the end of the mandible. The ventral contour of the trunk curves rather strongly and evenly, until it rises rather rapidly at first along the anal base; then becomes straight or weakly convex to the lower margin of the caudal fin. The upper lip is approximately coterminous with the snout. The rather strongly oblique mouth is generally nearly straight, and the upper jaw extends to a point very slightly in advance of the vertical from the front of the orbit. The mandible, somewhat approaching that of *mandibularis*, extends to slightly before the vertical from the middle of the pupil. The lips are quite full, but less so than in *catostomops*. As seen from below, the mouth is very broadly curved. The inner grooves of the lower lips converge rather gently forward to end well short of the mouth, where they are separated by about two-thirds the length of either (in this respect *rasconis* is rather distinctly intermediate between *catostomops* and all of the other species here treated).

Proportional Measurements.—The measurements made on *Dionda rasconis*, when compared with those for the five other species here treated from the Rio Pánuco complex (Tables 10–12), are particularly distinctive. The body is slenderer than in *ipni* and *erimyzonops*, and in some series of the highly variable *dichroma*, but its depth is comparable to that of the two other species. The caudal-peduncle depth averages slightly greater than in *mandibularis*, distinctly less than in *catostomops*, without overlap, and often less than in *dichroma*, *ipni*, and *erimyzonops*. The peduncle length is shorter than in *catostomops*, with some overlap, but is consistently longer than in *ipni* and *erimyzonops*. The urosome and predorsal measurements are not distinctive. The depressed dorsal is nearly always shorter than in *erimyzonops*. The anal base is usually shorter than in *catostomops*, moderately shorter than in *erimyzonops*, and very much shorter than in *ipni*. The head averages shorter than in *mandibularis*, *ipni*, and *erimyzonops*, but slightly longer than in *catostomops*. Because the dorsal and ventral contours converge anteriorly to a greater degree, the depth of the head averages distinctly less than in *mandibularis* and consistently less than in *ipni* and *erimyzonops*. The head averages distinctly narrower than in *mandibularis*, *catostomops*, and *dichroma*, and is consistently or almost consistently narrower than in *ipni* and *erimyzonops*. The orbit is consistently larger than in *catostomops*, but is usually smaller than in *erimyzonops*. The upper jaw averages distinctly shorter than in *mandibularis* and *ipni*, and slightly shorter than in *erimyzonops*. The interorbital averages definitely narrower than in *ipni* and *erimyzonops*. The mouth is narrower, with no overlap, than in *dichroma* and *ipni*, and is somewhat narrower, with considerable overlap, than in the three other species. The mandible is consistently longer than in *catostomops* and shorter than in *mandibularis*. The symphyseal width of the upper lip is somewhat greater than in *mandibularis*, about the same as in *dichroma*, and commonly less than in *ipni* and *erimyzonops*. The ratio of caudal-peduncle length divided by length of anal base is definitely greater than in *ipni* and *erimyzonops* (Table 9).

Barbel.—With few exceptions, at least a trace of a barbel is developed at the lower tip of the posterior edge of the maxilla, on one side if not on both. On close examination, a barbel was seen on one or both sides of 21 topotypes (UMMZ 193509). A re-examination of the three type specimens indicates that the barbel was probably developed on at least one side and detectable on both (the jaws were somewhat damaged in the attachment of a tin tag). The barbel is commonly visible in ventral view, but to be seen may require careful examination and the extrusion of the jaws. The frequency and degree of development is about the same as in *dichroma*, but the barbel is usually distinctly more rudimentary than in *catostomops*.

Gill-rakers. The rakers (Table 8), about as in *mandibularis*, average slightly fewer than in *catostomops*, definitely fewer than in *dichroma*, definitely more than in *ipni*, and are apparently more numerous than in *erimyzonops*.

Pharyngeal Arch and Teeth.—The lower limb of the pharyngeal arch (Fig. 2C–D) of this species is slender, straight along the dorsomesial border but slightly concave along the opposite edge, and is deflected away from the shaft at its expanded tip; this limb is notably shorter than the upper one, which is also slender, especially distally, very elongate, gently curved, and sinuous, with a sharply pointed tip.

The four teeth are moderately to well hooked at their tips but have only moderately developed grinding surfaces, weakest on the lowermost tooth. Crenulations may appear on any of the teeth.

Intestine.—The extensive coiling of the intestine of the true *Dionda rasconis* has been recognized for about seven decades (Meek, 1904: 50), and the variable

pattern of coiling is under study by Franklin F. Snelson, Jr. Rather casual inspection has disclosed little significant differences in this respect between *rasconis* and the other species here treated.

Fins.—When the rather sharply pointed dorsal fin is well pulled forward, its posterior edge becomes straight or weakly concave, but when the fin is depressed, the edge is considerably concave. The anal fin is rather weakly to sharply pointed at the tip, and the posterior edge of the expanded fin is definitely concave and slopes somewhat backward toward the base. When the dorsal and anal fins are depressed, the tip extends well beyond the end of the short posterior rays. The fins seem to be particularly weak, with slender and fragile rays.

The anal rays (Table 4) usually number 8, as in the three other upland species under treatment (except for the populations of *dichroma* inhabiting the marshy area south of Río Verde), but are almost always one or two fewer than in *ipni* and *erimyzonops*. The ray counts for the other fins (Table 3) are not particularly distinctive.

Scales.—*Dionda rasconis*, alone among the species herein treated, has the scales anteroventrally obsolescent over the median triangular area behind the branchiostegals and thence upward over the shoulder girdle. On the upper sides of the body the scales are especially conspicuous, because they are large and because each scale pocket has a sharply defined and narrow stippled border. The scales appear to be particularly thin and the overlying skin is so thin and delicate that the circuli and radii are especially conspicuous when viewed *in situ*. Not infrequently, the tube on a single scale, or on several in succession, is shortened, or is weakly to abruptly out of alignment, or is even lacking, even when the scale is shown by the complete retention of circuli and radii not to have been regenerated. The scales obviously are especially caducous, for they often show evidence of having been regenerated after loss and are readily removed from preserved specimens by a weak pull (in the other species here treated the scales appear to be so deeply imbedded that they are more difficult to extract). Those along the lateral line, when not regenerated, retain the normal tube and pore structure more consistently.

The scales are usually fewer than in any of the three other upland species in the Río Pánuco system: consistently fewer in the lateral-line count (Table 5), and usually fewer in the various other alignments (Table 6). In comparison with the two lowland species, *ipni* and *erimyzonops*, the counts for the lateral-line series are usually higher than in *ipni* and almost always higher than in *erimyzonops*; the predorsal counts are almost invariably higher, and the counts for other categories average higher to a varying degree.

Vertebrae.—The vertebral formula (Table 7) for *Dionda rasconis* is 18-19 + 16-17, rarely 18 = 34-36, usually 35. There are average differences between this species and the other five here treated in either anterior or posterior section, or in both. *D. rasconis* differs from the sympatric species *catostomops* in the almost invariably lower caudal count and in the apparently invariably lower total count (34-36 vs 37-39).

Sensory Canals of Head.—The sensory canals of the head are particularly (but not uniquely) subject to disruptions and other fluctuations in *rasconis*. Partly to demonstrate individual variation in pattern that may be encountered in this species, and to a somewhat lesser degree in the other five, a detailed study was undertaken:

Variations in the canal and pore pattern of the interorbital and upper-posterior postorbital sections of the head (transformed into a single plane) are illustrated on Figs. 6 and 7, for eight specimens selected from the topotypic series (UMMZ 196693). The most nearly normal and regular pattern, of specimen labelled no. 6, and the most disrupted and irregular pattern, of no. 14, are con-

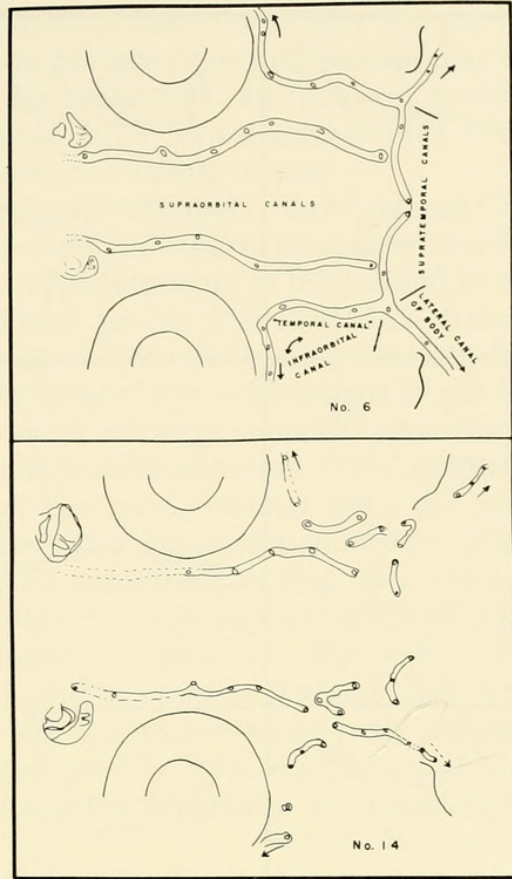


Figure 6. Most nearly normal and most disrupted of eight selected portrayals of the superficial cephalic sensory canal and pore system of the interorbital and upper-postorbital areas (drawn as on a single plane) of *Dionda rasconis* topotypes (UMMZ 196693); selected from the series of 67 specimens.

trasted in Fig. 6; and six variously intermediate patterns are illustrated on Fig. 7. In specimen no. 6 the supraorbital canal is complete on both sides, as it usually but not invariably is (note the left side on the sketch of specimen no. 24). In no. 6 this canal continues backward almost to contact with the supratemporal canal. The two sides of the supratemporal canal in no. 6 almost unite. The posterior, horizontal section of the infraorbital canal (the postocular commissure of Reno, 1969: 740) continues in this specimen, but not in most, around the junction with the postorbital vertical section of the infraorbital canal. Furthermore, in no. 6 the supratemporal and infraorbital canals uninterruptedly branch off from the anteriorly upturned end of the lateralis canal of the body (interruptions in this area are not infrequent in this species).

Variations in the extent of the canal system or the degree of disruption have been tallied for 18 specimens from near Rascón (UMMZ 196693) and in 21 from near Tamasopo (UMMZ 193509 and 196345). Since no obvious regional difference is shown, the data for all 39 examples are combined in the four following paragraphs:

The midline break between the left and right temporal canals was judged to be lacking in one specimen (no. 9 in UMMZ 196345) and hardly developed in one other (UMMZ 196693, Fig. 6, no. 6); very slightly or rather so in 9; moderately so in 16 (one of which has another break on one side); slightly on one side, very widely on the other side in 2 (Fig. 6, no. 23 and especially 21); widely or very widely in 10.

The degree of backward extension of the supraorbital canal in reference to the suture between the frontal and parietal bones of the skull varies spectacularly. The canal ends short of the suture on one side in one specimen, just past on the other side in 2; approximately to or slightly past suture, with some bilateral dif-

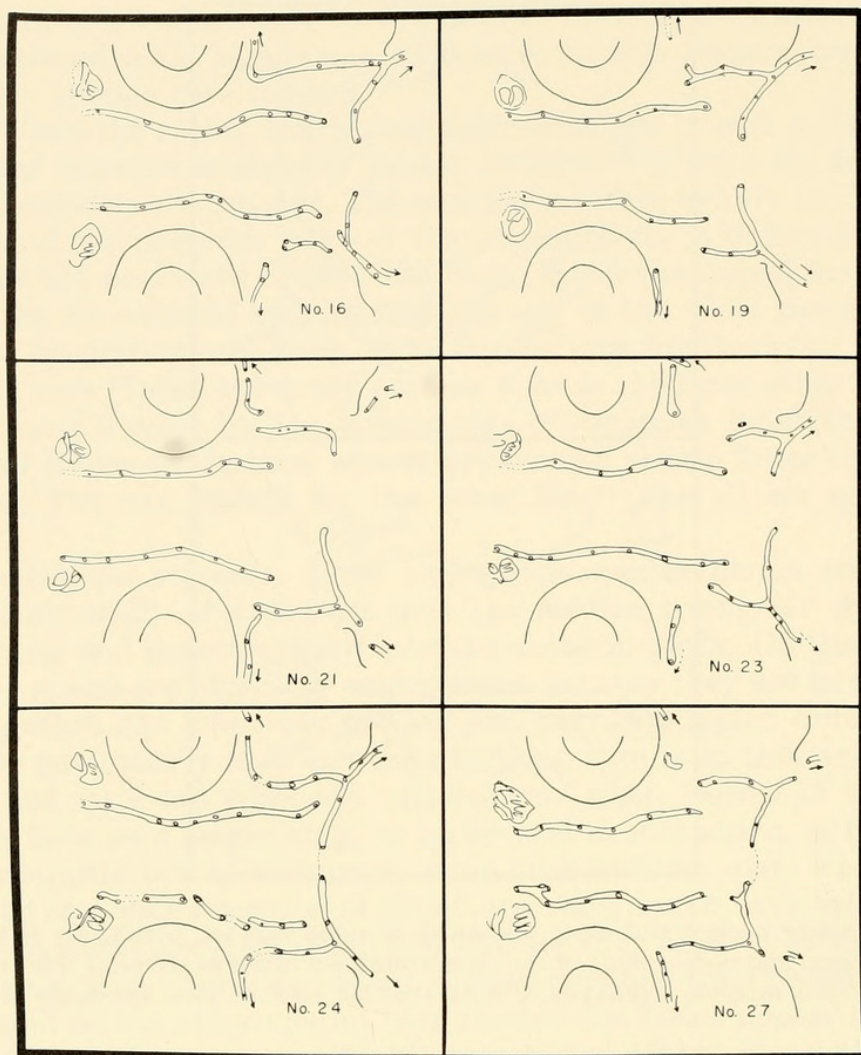


Figure 7. Six additional, less extreme variants in the cephalic sensory canal and pore systems exhibited by *Dionda rasconis* topotypes (UMMZ 196693). The numbers in figures 6 and 7 correspond with those attached to the specimens.

ference, in 16; moderately within parietal in 12; about halfway across parietal in 5, with a sharp downward curve in one; more than halfway across parietal in one; far beyond midway of parietal, very nearly to supratemporal canal in one (Fig. 6, no. 6). In addition, each of two specimens of UMMZ 193509, neither figured, diverges in a special way: in one (no. 5) the right supraorbital extends slightly beyond the suture but the left one overlaps the suture on a retrorse curve; in the other specimen (no. 1) each canal ends near middle of parietal, the left one without terminal curvature, but the right one with an abrupt turn to become, strangely, continuous with the right infraorbital at the middle of its posterior horizontal section ("postorbital commissure"); in addition, the right supraorbital gives off a side branch to near the right edge of the bony interorbital and takes a sharp incurve farther forward.

The infraorbital canal is extremely variable and not infrequently bilaterally asymmetrical. Particularly extreme disruptions and nonalignments are shown on Fig. 6 for no. 14 on both dissimilar sides, and for no. 23 on one side. Counting the two sides separately there were no breaks in 30, a single break in 36, two breaks in 3, and three breaks in one. Other breaks occur near posterior origin of canal in 4, along the posterior horizontal section in 5, near the point of downward curvature in one, and farther downward and then forward in 3. There are other malalignments, and some other complicated arrangements, but the basic pattern is obvious.

The preoperculomandibular canal is usually broken just behind the mandible, in effect typically yielding preopercular and mandibular tubes. Counting the sides separately, the tally is: no break in 7, an incipient break in 2, a moderately wide break just behind mandible in 73, two breaks in one, a break within the mandible in one, and a second, posterior break in one.

Coloration.—The general, uniquely light-colored aspect of the preserved specimens well shown in the type figure, obviously drawn by Chloe Leslie Starks, and in our Fig. 4C, from a photograph) is intensified in each sex by the relatively narrow and sharply defined jet-black stripe that extends from the side of the snout to the basicaudal spot. This distinctive black stripe may be rather intensified on the snout as a horizontal bar, which usually continues around the front of the snout just above, or even intrudes somewhat on, the upper lip. A continuation across the iris may or may not be apparent. This stripe continues strongly across the postorbital region of the head, usually with the melanophores more or less reduced in number on the upper cheek but consistently bold across the upper part of the opercle, leaving the membranous flap clear, in some specimens conspicuously so. The stripe is often more or less interrupted, narrowly, at the junction of the fleshy and bony postorbital area. On the body the stripe uniquely remains narrower than the pupil, and in some specimens narrows more or less just before the almost solidly inky-black, somewhat variously shaped, basicaudal spot, which is smaller than the pupil and is less puncticulated than the stripe. The spot streams out backward along the especially blackened extreme edges of the median caudal rays.

The black lateral stripe is bordered above by a relatively diffuse light streak, which in some specimens is more or less obsolescent forward but is usually at least moderately bold posteriorly, where it tends to be somewhat or even almost entirely devoid of melanophores. This clearish area uniquely tends to expand toward the caudal fin, so as to restrict the darkened area there to the upper edge of the peduncle. The light streak tends to be broader than in the other species here treated except *mandibularis*, in which it is even more conspicuous, because the sides above the streak are much darker. The rather weakly darkened area above the light streak is very characteristically pigmented: the scale margins here are sharply, narrowly, and regularly blackish-bordered and the rest of this surface is very evenly and thickly covered with melanophores, which are so small as to leave the area hardly more than whitish. Across the postorbital area the broad light streak is particularly conspicuous and is largely devoid of any melanophores, especially upward and backward from the orbit. There is also a rather conspicuous, largely unpigmented, area on and about the nostrils, but otherwise, the surface of the head above these much lightened areas is blackened by very thick-set melanophores. From the blackish occipital region a rather conspicuous middorsal dark stripe extends to the dorsal fin, the extreme base of which is very intensely blackened. The middorsal area between the dorsal and caudal fins is usually diffusely darkened, without being definitely dark-striped, but some adults, especially smaller ones, do have a moderately definite stripe there.

Below the black lateral stripe the head and body are very characteristically almost totally devoid of any melanophores, but a few are sometimes inconspicuously developed around the dorsal edge of the upper lip, both laterally and anteriorly, and rarely there are a few across the chin. The base of the anal fin as well as that of the dorsal is very narrowly streaked with jet-black, but there are, except rarely, and chiefly in small adults, no melanophores along the ventral edge of the caudal peduncle. These melanophores behind the anal fin, when visible (though only under a microscope), are very seldom in more than a single file. A very faint blackish border is visible, under due magnification, along the very

edges of some or all of the rays in the dorsal and anal fins, most inconspicuously near the base of the last one to 3 rays. The procurent caudal rays are definitely darkened, and the main rays of the fin are very narrowly darkened on the extreme margins, obsolescently so on the continuation of the upper-lateral pale stripe of the body. The pectoral fin is darkened along the upper edge and along the sides of several following rays; the pelvic fin is not noticeably darkened along its outer ray, but several of the following rays may be very weakly lined by melanophores.

Color in Life.—In the field, at the Río Tamasopo near Tamasopo, it was noted that this species can be distinguished very readily at sight from the sympatric *Dionda catostomops* by its life colors. The large specimen of *rasconis* (Frontis-piece, upper pair) had a golden overcast over the silvery sides, both above and below the lateral line; and the base of the pectoral fin and to a lesser extent that of the anal was orange. In this collection, the fins lacked any trace of bright colors, even in adult males, in contrast with the bright blue seen here on the fins of *catostomops* (as also of *dichroma* in the Río Verde system).

Nuptial Tubercles.—The very minute breeding spinelets of the mature males comprise loosely branching series on the top of the thickened and somewhat upturned submedian parts of the several outer, enlarged pectoral rays following the outermost one, which has only one row of rudimentary pearl organs. These tubercles are arranged too irregularly to form two definite rows after the first branching, but do not comprise a thickly set villiform band as they do in *mandibularis*. The tubercles, very minute, are scattered over the top of the head, but are hardly evident on the snout, and are apparently lacking on the other fins.

SEXUAL DIMORPHISM

Except for the possibly slightly darker general coloration of the males, the sexes of *Dionda rasconis* are hardly distinguishable in general appearance. The chief external sexual dimorphism appears to be confined to the nuptial tuberculation, which is weak in males and seemingly wholly lacking in females. The trend toward larger size in females has been indicated by examination of unselected collections (see below, under Life History Notes).

Detailed measurements of adults, 13 males and 7 females (Table 10), suggest that the males may differ from the females, on the average, in somewhat deeper bodies, slightly longer urosomes (therefore shorter trunks), larger dorsal and pectoral fins, and larger eyes (presumably attributable to the smaller size of the fish)—but none of the differences are large and some may be spurious.

VARIATION

No significant differences in the proportional measurements (Table 10) of this small species appear in the analysis of the collections from near Rascón and from near Tamasopo, the two known localities, not far apart in the same stream system. As noted above under Sexual Dimorphism, the adults of the sexes are hardly distinguishable in general appearance, and the indicated differences in proportions are quite minor.

DISTRIBUTION, HABITAT, AND ASSOCIATED SPECIES

Dionda rasconis, along with the sympatric, recently discovered *catostomops*, represents the complex we are referring to *Dionda* in what we are distinguishing as the "lower intermontane" division of the Río Pánuco stream system, in the state of San Luis Potosí, México (Fig. 1). The two species appear to be particularly characteristic of, and are nearly confined to, the generally swift waters of Río Tamasopo (elevation at Tamasopo, 460m), a main western headwater of Río

Gallinas. That major stream is formed by the Río Tamasopo and the parallel-flowing Río Agua Buena (just to the north), which join about 8 km east of Agua Buena; the Gallinas then continues eastward and south of Rascón to join the Río Ojo Frío southeast of that town. The Río Ojo Frío (also called by some the Río Gallinas, Río Frío, and even "Río Verde"), flows in a north-south direction from well north of Rascón to its junction, in the lowlands, with Río Santa María; it describes a short westward bend about 1 km north of Rascón (where it is locally called Río de la Mula), and it is here at the bridge crossing that the types of *rasconis* were taken. We were told that just above its mouth the Río Ojo Frío forms a series of cascades some 300 m long; these may well provide an effective barrier to upstream migration of some fishes. *Dionda rasconis* and *catostomops* are probably confined to the montane area that lies far above the streams wherein *ipni* and *erimyzonops* co-occur. However, the main course of Río Gallinas remains to be explored. The nearest known collections of *Dionda*, downstream, are of *dichroma* at Tanlacú, near the mouth of Río Verde, and of both *ipni* and *erimyzonops* at Valles (elevation only 87 m) on Río Valles (Fig. 1). However, the whole lower Río Santa María below the mouth of Río Verde, which flows through steep-walled canyons, remains to be ichthyologically explored.

Both *rasconis* and *catostomops* are now known to occur near Tamasopo, where collections have only recently been made (in 1972 and 1974), and in the waters near Rascón (elevation 310 m), which have been explored since 1899 (because Rascón has long been a railroad station). In addition, *catostomops* was taken in 1976 in Río Ojo Frío 11.2 km north of Rascón.

The two sharply differentiated species we are calling *rasconis* and *catostomops* have been taken together three times, in 1972 and 1974, at two localities, in the upper Río Tamasopo and in Río Frío just north of Rascón. The field experience and records, together with the sharply contrasting body form of the two species (Figs. 4C-D), strongly indicate some partial segregation in habitat. Although the actual supporting data are limited and much less definitive than we desire, we are of the opinion that *rasconis* tends to select rather deep and open, more or less slow-moving water with somewhat soft, sandy-silt bottom, whereas *catostomops* is more adjusted to hard-bottomed, stony riffles and pool heads, where the current is stronger. The basis for this conclusion is presented below (p. 306), in the account of *catostomops*.

Other fishes that have been taken at each of the two known localities for *rasconis* (and *catostomops*) are *Ictalurus mexicanus*, *Astyanax mexicanus*, *Gambusia panuco*, *Poecilia mexicana*, *Xiphophorus montezumae*, and three species of *Cichlasoma*. Meek (1904: xxxvii, 146, and 226) listed two other fishes from Rascón, namely *Xiphophorus variatus* (Meek) and *Gobiomorus dormitor* Lacépède. None other was reported from Río Gallinas (misnamed "Río Verde") by Jordan and Snyder (1900: 116), or by any other authors.

LIFE HISTORY NOTES

The evidence that adult males of *Dionda rasconis* tend to be smaller than the females (Table 1) suggests that they grow more slowly or die sooner (or both). Early maturity of the males is definitely shown by the circumstance that all 9 males in the collection made near Rascón by Meek on 6 May 1903, measuring only 34 to 39 mm SL, are in nuptial condition, and that the 20 females in the same collection, 35 to 46 mm, contain ripe ova. All but the very smallest males in the series, 28 to 44 mm long, collected on 20 March 1974 at the same place had also reached or had approached breeding condition.

These dates indicate that this species spawns quite early in the year, which, considering the far-south habitat, is not surprising.

TABLE 1. Standard lengths of all mature males and females of topotypes of *Dionda rasconis* in each of two collections.

	Standard lengths by three-millimeter groups								No.	\bar{X} from ungrouped data
	28-30	31-33	34-36	37-39	40-42	43-45	46-48	49-51		
UMMZ 196693 March 20, 1974										
Mature males	7	8	7	2	5	3	-	-	32	34.97
Mature females	-	14	3	1	12	3	-	2	35	37.11
FMNH 4509 May 6, 1903										
Mature males	-	-	4	5	-	-	-	-	9	36.78
Mature females	-	-	2	9	6	2	1	-	20	39.75

Dionda catostomops, n. sp.
Figure 4D

Synonymy, Nomenclature, and History.—In so far as we can determine, this species has completely escaped the attention of previous collectors.

Diagnosis.—Mouth almost strictly ventral, beneath the strongly downturned snout, and overhung in front by the terminal rostral flap, which, along with both lips and chin, is on an essentially common and nearly horizontal broad plane. Lips conspicuously swollen, the lower ones wholly or almost devoid of pigment and very widely separated; grooves on outer side of lower lips weakly convergent forward and very short, each only about as long as their anterior interspace. Barbels, ordinarily, relatively conspicuous and often obviously pendant. Body form terete, with greatest depth less than twice greatest width. Dorsal and anal fins, when moderately expanded, with most of posterior edge sloping forward from tip, that of dorsal slightly, and that of anal rather deeply, falcate, with indentation not obliterated by a moderate down-stretching of that fin. Vertebrae normally totaling 38 or 39, with little or no overlap on any other Pánuco species of the genus except *dichroma*. Intestine with relatively few loops located far forward in body cavity and largely ventrally.

Comparisons.—This species contrasts with *mandibularis* in all respects treated in the Analytical Comparison under couplet 1, from *rasconis* under couplet 3, from *dichroma* under couplet 4, and from both *ipni* and *erimyzonops* under couplet 5. The contrast with the one sympatric species, *rasconis*, is particularly striking, involving at least 11 character complexes listed in item 3B; in the 4 items on mouth, lips, barbel, and caudal vertebrae number in item 4A; also in various differences in proportional measurements (Table 10): consistently deeper caudal peduncle; usually longer urosome (anus to caudal base); usually shorter depressed length of dorsal fin; usually shorter and slenderer but almost consistently broader head; often longer snout; a consistently and markedly smaller eye; usually narrower mouth; consistently shorter mandible; and usually wider symphysis of the upper lip. Furthermore, *catostomops* appears to reach a somewhat greater standard length than *rasconis* (67 vs 53 mm).

Material Examined.—Holotype UMMZ 196346 (a mature male 54.7 mm SL) and Paratypes: UMMZ 196347 (57: 44-67) and 195950 (6: 20-38) and USNM 213790 (12: 42-69), Río Tamasopo 1.4 km N of Tamasopo, San Luis Potosí; UMMZ 196692 (1: 49), Río Gallinas 1.3 km N of Rascón, San Luis Potosí, and UMMZ 198793 (4: 47-56), Río Ojo Frío, 11.2 km N of Rascón.

TABLE 2. Standard lengths of all mature males and females of *Dionda catostomops* in the one large collection available for measurement.

	Standard lengths by six-millimeter groups					\bar{X} from ungrouped data
	44-49	50-55	56-61	62-67	No.	
UMMZ 196346-47 February 7, 1974						
Mature males	4	14	8	–	26	54.07
Mature females	2	5	12	10	29	59.41

DESCRIPTION

The prime descriptive characters of *Dionda catostomops* are given in items 1B, 2A, 3B, and 4A in Analytical Comparisons and under Diagnosis and Comparisons.

Size and Form.—The largest of the 81 known specimens of this moderately large minnow measures 69 mm SL, and the size exceeds 50 mm in a large proportion of the series. In this species, in contrast particularly with *ipni*, the females appear to reach a larger size than the males (Table 2; see also p. 305).

The lower contour of the whole fish is much less curved than the upper, so that a line from the middle of the basicaudal spot to the extreme bottom of the front margin of the snout passes well below the depressed part of the lateral line, and well below the middle of the trunk at a point which, in projection, is about twice or not much less than twice as far from the dorsal origin as from the pelvic insertion. The bottom of the head is nearly straight and horizontal. The top of the head in side view rises in a weak curve from the very sharply decurved snout tip to the occiput, behind which the contour is moderately convex to the front of the dorsal. There is usually only a slight depression between the preoccipital and postoccipital segments of the dorsal outline. The dorsal contour at the front of the dorsal fin is relatively weakly elevated and the dorsal base slopes downward much less conspicuously than in the other species here treated. The contour behind the dorsal fin is relatively flat and nearly horizontal, due in part to the unusually deep caudal peduncle and to the posteriorly attenuated urosome. The ventral contour behind the anal fin is almost straight and horizontal, and before the anal fin is rather strongly curved to the extremely low and flat lower contour of the head.

The considerably swollen, but smooth, lips are definitely overhung by the sharply downturned snout, which forms a terminal flap extending distinctly in advance of the upper lip. The lower margin of this flap, both lips, and the whole chin are on an unusually broad, essentially common, nearly horizontal plane. In correlation with their essentially flat, horizontal, and ventral position, the lower lips and the whole lower jaw area are completely or almost wholly devoid of melanophores. The grooves within the lower lips converge rather weakly forward and remain widely separated anteriorly by a distance equal to or nearly equal to the length of either groove.

Proportional Measurements.—The values for *Dionda catostomops*, when compared with those for the five other *Dionda* species (Tables 10-12) of the Río Pánuco complex, demonstrate numerous differences. The body is about as slender as in *mandibularis* or *rasconis*, but, with some inconsistency and much overlap, slenderer than in *dichroma* and almost always slenderer than in *ipni* or *erimyzonops*, with the dividing line at about 28% of the standard length. The caudal peduncle is consistently deeper than in *mandibularis* and *rasconis*, often

but not consistently deeper than in *dichroma*, and comparable with *ipni* and *erimyzonops*. The peduncle is notably elongate, usually longer than in *mandibularis* or *rasconis*, nearly always longer than in *dichroma*, and always longer than in the two lowland species. The length of the urosome is usually to always longer than in any of the five other species. The length of the depressed dorsal fin is not conspicuously distinctive, except in being consistently less than in *erimyzonops*. The anal base is about the same as in *dichroma*, somewhat shorter than in *mandibularis* and *rasconis*, usually shorter than in *erimyzonops*, and very much shorter than in *ipni*. The head is usually shorter than in *rasconis* or *dichroma*, but consistently shorter than in the three other species, *mandibularis*, *ipni*, and *erimyzonops*. The orbit is consistently smaller than in *rasconis*, *mandibularis*, and *erimyzonops*; the value varies greatly in *dichroma* (see also p. 315, Fig. 9) and in *ipni*. The upper jaw is often shorter than in *erimyzonops* and, with very slight overlap, is shorter than in *ipni* and in *mandibularis*. Despite the broadening of the head ventrally the least interorbital width is often narrower than in the five other species. The mandible is often shorter than in the variable *dichroma* and in *ipni*, and consistently shorter than in *rasconis*, *erimyzonops*, and *mandibularis*. The upper-lip width, at symphysis, is much wider than in *mandibularis*, but often less so than in *ipni* and *erimyzonops*.

Barbel.—The maxillary barbel is much better developed in this species than in any of the other five here treated. It is always evident on both sides, even without opening the mouth, and it is often somewhat pendant.

Gill-rakers.—As is indicated in item 1B of the Analytical Comparisons, the rakers extend forward about to or well beyond the middle of the lower limb of the first arch (as in all of the species herein treated except *mandibularis* and *erimyzonops*). The numbers are specified in Table 8.

Pharyngeal Arch and Teeth.—The lower limb of the pharyngeal arch of this species is similar to that of *rasconis*; it is slender and nearly straight, but it has a shallow concavity along the mesial border; its length about equals that of the upper limb. The latter is well curved, broad basally but narrowing to a bluntly pointed tip that may be slightly recurved. In overall shape, the arch is more like that of *ipni* than that of *rasconis* (Fig. 2E-F).

All four teeth have moderately hooked tips, the uppermost least so; each has a grinding surface—least developed on the lowermost tooth and best displayed on the two middle ones. The uppermost tooth is moderately elevated above the arch.

Intestine.—The intestinal coiling is of much the same general type as in the other Río Pánuco stream system species now referred to *Dionda*. The course of the intestine, which varies markedly in length and in the amount, direction, and location of coiling, may be indicated by the pattern observed in one of the larger specimens, in which much of the closely impacted surrounding adipose tissue had largely been cleared away. The somewhat thickened anterior segment extends backward well toward the end of the body cavity, then abruptly reverses course to near the center of the cavity. Here it describes a tight vertical coil in the body cavity, which in this species is especially restricted ventrally by reason of the flattened ventral contour and the well arched dorsal contour. This coil, largely on the right side, is closed above and open below, and lies on the tangential plane. From near the bottom of this coil the intestine runs forward nearly to the front of the cavity, where, after some twisting, it turns back to describe another vertical loop tight against the first major coil. The intestine then returns to an anterior position in the cavity, with some circuitry in different planes; it then turns backward again to continue, with some twisting, to the rectum. In detail, various other patterns are followed.

Fins.—The dorsal fin, as in the sympatric species *rasconis*, is rather sharply pointed, instead of being rounded at the tip; the posterior border of the moder-

ately extended fin is weakly concave and subvertical. The anal fin has a weakly rounded tip and its posterior border is weakly to strongly concave, rendering the fin distinctively falcate. When the dorsal fin is fully depressed its tip extends to well behind the tip of the last ray, and the tip of the anal usually reaches to somewhat behind the tip of its last ray.

The fin-ray counts for 31 specimens (UMMZ 196346, holotype, modal for all fins, and 196347) are specified in Tables 3 and 4. The specimen from Río Gallinas has counts modal for each fin, except 13–12 for the pectoral.

TABLE 3. Ranges and means of fin-ray counts (except for anal fin) for the east-central Mexican species of *Dionda*.¹

Species (No.)	Dorsal	Caudal	Pectoral	Pelvic ²
<i>mandibularis</i> (20)	7–9 (8.15)	18–19 (18.95)	12–15 (13.25)	8–9 (8.05)
<i>rasconis</i> (30)	7–8 (7.93)	19 (19.00)	11–15 (13.05)	5–8 (7.77)
<i>catostomops</i> (31)	8 (8.00)	19 (19.00)	12–15 (13.76)	6–9 (8.02)
<i>dichroma</i> (85) ³	7–9 (8.01)	18–19 (18.97)	12–15 (13.24)	0–9 (7.81)
<i>ipni</i> (48)	8–9 (8.02)	18–19 (18.96)	13–17 (15.08)	7–9 (7.98)
<i>erimyzonops</i> (37–40)	8–9 (8.03)	18–19 (18.97)	12–15 (12.86)	6–9 (8.03)

¹Counts for anal rays are detailed in Table 4. The paired fins were counted on both sides.
²Odd counts for pelvic rays (other than 8) are: for *mandibularis*, 9 in 2; for *rasconis*, 5 in 1, 7 in 11; for *catostomops*, 6 in 2, 7 in 1, 9 in 6; for *dichroma*, 0 in 1, 3 in 1, 4 in 3, 7 in 9, 9 in 1; for *ipni*, 7 in 5, 9 in 3; for *erimyzonops*, 6 in 1, 7 in 4, 9 in 8.
³For the dorsal-ray count 25 additional specimens (from Guayabos) are included.

Scales.—The squamation over the anterior breast and shoulder girdle is complete. Counts of the scales along the lateral line are detailed in Table 5 and the enumerations for other series are summarized in Table 6.

Sensory Canals of Head.—As in the other species herein treated, *mandibularis* excepted, the infraorbital and preoperculomandibular series of the lateral-line system are normally complete in the adult. The supratemporal is usually somewhat interrupted medially. The supraorbital canal, with pores complete, extends to or slightly beyond the suture between the frontal and parietal bones, so that the terminal pore lies close to the supratemporal canal, not far from the horizontal posterior part of the infraorbital canal. Very rarely a short supernumerary canal appears on the opercles.

Vertebrae.—The counts (Table 7) were based on radiographs of 38 specimens from near Tamasopo and on the single one (with count of 19 + 20 = 39, from near Rascón). The precaudal counts average slightly higher than in *dichroma*, distinctly higher than in *rasconis*, very much higher than in *ipni*, and higher with no overlap than in *mandibularis* or *erimyzonops*; the caudal counts average higher than in any of the five other species, with no overlap on *erimyzonops*, but with a strong overlap on *dichroma*. The total counts are consistently higher than in the other species, save for a very slight overlap on *ipni* and a strong overlap on *dichroma*.

Coloration.—The mature males are hardly perceptibly more pigmented than the mature females: this circumstance may be related to the fact that the nuptial tubercles are extremely weak in the mature males and are incipiently developed in the ripe females.

TABLE 4. Counts of anal rays in the east-central Mexican species of *Dionda*.

Species	7	8	9	10	11	12	No.	\bar{X}
<i>mandibularis</i>	1	42	-	-	-	-	43	7.98
<i>rasconis</i>	3	86	3	-	-	-	92	8.00
<i>catostomops</i>	1	30	-	-	-	-	31	7.97
<i>dichroma</i>	14	371	95	8	-	1	489	8.21
Río Sta. Catarina	3	54	5	1	-	-	63	8.06
Puerta del Río	-	32	5	-	-	-	37	8.13
Vic., Media Luna to Río Verde	6	197	33	2	-	1	239	8.14
7-10 km S of Río Verde	2	16	47	5	-	-	70	8.79
16 km SE of Río Verde	1	21	2	-	-	-	24	8.04
Río Verde, Guayabos	-	23	2	-	-	-	25	8.08
Río Verde, Tanlacú	2	28	1	-	-	-	31	7.97
<i>ipni</i>	-	6	235	365	46	5	657	9.71
Tamesí drainage	-	3	113	21	-	-	137	9.13
Pánuco drainage	-	2	88	217	19	2	328	9.79
Metztlilán drainage	-	-	-	27	21	3	51	10.53
Tuxpan drainage	-	1	15	54	1	-	71	9.77
Cazones drainage	-	-	7	37	3	-	47	9.91
Tecolutla drainage	-	-	4	4	2	-	10	9.80
Nautla drainage	-	-	1	2	-	-	3	9.67
Misantla drainage	-	-	7	3	-	-	10	9.30
<i>erimyzonops</i>	-	5	92	14	-	-	111	9.08
Tamesí drainage	-	4	75	11	-	-	90	9.08
Pánuco drainage	-	1	17	3	-	-	21	9.10

The lateral stripe is distinctly less blackened than in the other upland species here treated. It is rather indistinct on the head. On the snout the stripe is developed on the side only, and because the mouth is so completely inferior the stripe is angled rather sharply downward from the front of the eye. Behind the eye the stripe is represented by a small and very weak, in some specimens obsolescent, mark that extends backward and somewhat dorsad to the upper end of the preopercle. The postocular portion of the stripe connects with the trace on the snout along a definite punctulate band bordering the lower orbital margin. On the opercle the stripe is expanded into a blackish blotch covering most of the bone except along the unpigmented bony margin and on the membranous flap. On the body the rather diffuse and weak stripe covers the scale row just above the lateral-line series where the sensory canal is depressed on the mid-trunk, but then continues, on the urosome, along the lateral-line row. The stripe tends to pinch out just before the generally roundish and blackish, approximately pupil-sized, basicaudal blotch.

On the body there is only the slightest trace of a light streak on the trunk above the dark stripe, and virtually no trace of this light streak on the urosome. On the head, in contrast, a moderately conspicuous but somewhat disrupted, weakly pigmented streak extends above the blackened opercle forward and somewhat downward to the upper-posterior rim of the orbit. Farther forward, the

TABLE 5. Counts of lateral-line scales in the east-central Mexican species of *Dionda*.

Species	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	No.	\bar{X}
<i>mandibularis</i>	-	-	-	-	-	-	2	2	4	6	2	2	1	-	-	19	39.74
<i>rasconis</i>	-	-	1	16	9	3	-	-	-	-	-	-	-	-	-	29	34.48
<i>catostomops</i>	-	-	-	-	-	-	9	16	4	2	-	-	-	-	-	31	37.97
<i>dichroma</i>	-	-	-	-	-	-	4	7	27	30	43	34	18	7	4	174	40.92
Santa Catarina	-	-	-	-	-	-	1	1	7	2	11	6	2	-	-	30	40.57
Puerta del Río	-	-	-	-	-	-	2	2	4	3	5	4	-	-	-	20	39.95
Media Luna & Rioverde	-	-	-	-	-	-	1	2	4	7	10	9	8	1	2	44	41.25
7-10 km S of Río Verde	-	-	-	-	-	-	-	-	-	-	4	8	6	5	2	25	42.72
16 km S of Río Verde	-	-	-	-	-	-	-	1	3	7	4	3	2	-	-	20	40.55
Río Verde, Guayabos	-	-	-	-	-	-	-	1	3	6	7	3	-	-	-	20	40.40
Río Verde, Tanlacú	-	-	-	-	-	-	-	-	6	5	2	1	-	1	-	15	40.13
<i>ipni</i>	-	14	53	55	10	2	1	-	-	-	-	-	-	-	-	135	33.53
<i>erimyzonops</i>	1	16	18	3	-	-	-	-	-	-	-	-	-	-	-	38	32.61

narial flaps are nearly white, and there is a scarcely pigmented area of considerable size just behind and above the posterior nostril. Above the lateral dark stripe the body is rather evenly dusky, with diffuse dark margins on the scale pockets, and, anteriorly, weakly lightened scale-pocket centers, which are very much less conspicuous than in *mandibularis*. Below the dark stripe and above the broad unpigmented ventral surface, the scale pockets are narrowly and rather weakly margined behind by a definite stippled border. On the urosome this pattern becomes less definite and is confined to from one to two scale rows below the lateral-line series. Between the occiput and the dorsal fin there is a broad, somewhat diffuse, dusky middorsal band, in some specimens quite weak, which extends backward rather weakly along either side of the dorsal base, and then continues, in some fish rather faintly, to the upper base of the caudal fin. There is virtually no trace of a dark midventral streak behind the anal fin, but usually traces of short dark lines extend upward and forward from the anal base.

The top of the head is blackish, becoming only weakly dusky on the top of the snout, and still lighter toward the backward-deflected snout tip. The cheeks, except as noted above, the branchiostegal surface, and the entire chin are definitely unpigmented, as is also the lower lip except, rarely, for a few melanophores laterally; the upper lip commonly bears melanophores near the outer margin, but these are so deeply embedded as to be inconspicuous.

The lower fins are also largely deficient in melanophores. The dorsal, however, is finely punctulate marginally along the rays, and is blackened very close to the base. The anal is almost devoid of melanophores, except for very small ones along the margins of the rays toward their bases, and except also, in general, for at least a trace of melanophores along the extreme base of the fin. The caudal is rather weakly darkened along the very edges of the rays. The pectoral is almost totally devoid of pigment on the outer surface, as is the inner surface except on the outer ray and on the narrow margin of the next few, enlarged rays. The pelvic is totally devoid of black pigment cells except for a close-set line of very minute specks along the extreme inner edge of one to a few of the outer rays, on the upper side.

TABLE 6. Ranges and means of scale counts (except those in lateral line) for the east-central Mexican species of *Dionda*.¹

Species (No.)	Predorsal Scales	Predorsal Rows	D Fin to Lateral Line	A Fin to Lateral Line	P ₂ Fin to Lateral Line	Body above Lateral Line	Body below Lateral Line	Around Body	C Ped. above Lateral Line	C Ped. below Lateral Line	Around C Peduncle
<i>mandibularis</i> (15-20)	18-20 (19.00)	17-20 (18.60)	7-8 (7.15)	5-7 (6.05)	4-7 (5.00)	14-16 (14.83)	15-19 (16.33)	31-36 (33.17)	7-9 (7.75)	6-8 (7.15)	15-19 (16.90)
<i>rasconis</i> (21-23)	16-20 (17.86)	14-18 (15.86)	5-8 (6.09)	4-6 (4.74)	4-5 (4.30)	11-15 (12.96)	13-16 (14.30)	27-32 (29.26)	5-8 (6.67)	5-7 (5.81)	12-17 (14.48)
<i>catostomops</i> (30)	16-21 (18.20)	15-19 (16.20)	6-7 (6.30)	4-6 (5.23)	4-6 (4.40)	13-15 (13.63)	13-16 (13.97)	28-33 (29.60)	7-8 (7.03)	6-7 (6.70)	15-17 (15.73)
<i>dichroma</i>	17-24 172 (20.5)	15-23 73 (18.33)	6-8 75 (6.77)	5-7 75 (5.88)	4-7 75 (5.28)	11-17 75 (14.46)	13-21 75 (16.36)	26-39 174 (31.56)	7-9 75 (7.37)	5-9 75 (6.89)	14-20 75 (16.27)
<i>Sta. Catarina</i> (30)	19-24 (21.63)	17-23 (19.47)	6-8 (6.97)	5-7 (6.27)	5-7 (5.73)	13-17 (15.01)	15-21 (17.67)	31-39 (34.80)	7-9 (7.57)	6-9 (7.17)	15-20 (16.73)
<i>Puerta del Río</i> (18-20)	17-22 (18.94)	15-20 (17.22)	6-7 (6.30)	5-6 (5.30)	4-5 (4.80)	11-15 (13.05)	13-17 (15.05)	26-34 (29.70)	7-8 (7.05)	5-7 (6.55)	14-17 (15.60)
<i>Vic. Ríoverde</i> (25) ²	18-24 (19.84)	16-20 (17.76)	6-8 (6.92)	5-7 (5.88)	4-6 (5.12)	13-17 (14.92)	14-18 (15.84)	26-36 (31.84)	7-9 (7.40)	5-8 (6.84)	14-18 (16.24)
<i>Lower R. Verde</i> (35) ³	18-23 (19.80)	- -	- -	- -	- -	- -	- -	27-33 (29.34)	- -	- -	- -
<i>ipni</i> (41-42)	12-15 (13.66)	11-14 (12.57)	5-7 (6.12)	4-6 (4.88)	3-5 (3.93)	11-13 (12.43)	11-14 (12.19)	24-29 (26.62)	5-7 (6.71)	5-6 (5.10)	12-15 (13.81)
<i>erimyzonops</i> (37-38)	12-15 (13.62)	11-13 (12.27)	5-6 (5.18)	3-4 (3.95)	3-4 (3.74)	9-13 (10.87)	10-12 (10.87)	21-26 (23.74)	5-6 (5.03)	4-5 (4.95)	11-13 (11.97)

¹Counts for lateral-line scales are detailed in Table 5.
²The predorsal scales and those around the body were enumerated on 89 specimens.
³These specimens are from Tanlacú and Guayabos, and are in flabby condition.

TABLE 7. Counts of vertebrae in the east-central Mexican species of *Dionda*.

Species	Precaudal							Caudal							Total									
	16	17	18	19	20	No.	\bar{X}	15	16	17	18	19	20	No.	\bar{X}	33	34	35	36	37	38	39	No.	\bar{X}
<i>mandibularis</i>	-	23	23	-	-	46	17.50	-	-	21	24	1	-	46	17.57	-	6	31	9	-	-	-	46	35.07
<i>rasconis</i>	-	-	41	26	-	67	18.39	-	22	41	3	-	-	66	16.71	-	6	49	14	-	-	-	69	35.12
<i>catostomops</i>	-	-	-	17	22	39	19.56	-	-	-	9	21	9	39	19.00	-	-	-	-	1	15	23	39	38.56
<i>dichroma</i>	-	-	5	103	68	176	19.36	-	-	20	115	50	1	186	18.17	-	-	-	6	82	69	5	162	37.45
<i>ipni</i>	4	135	125	25	-	289	17.59	-	40	193	54	2	-	289	17.06	13	141	132	41	7	3	-	337	34.69
Tamesí drainage	2	64	12	1	-	79	17.15	-	7	61	11	-	-	79	17.05	6	59	16	1	1	-	-	83	34.18
Pánuco drainage	2	59	72	23	-	156	17.74	-	26	97	31	2	-	156	17.06	6	58	61	25	6	3	-	159	34.85
Tuxpan drainage	-	9	25	-	-	34	17.74	-	3	23	8	-	-	34	17.15	1	22	21	5	-	-	-	49	34.61
Cazones drainage	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	22	2	-	-	-	26	35.00
Tecolutla drainage	-	3	7	-	-	10	17.70	-	3	7	-	-	-	10	16.70	-	-	6	4	-	-	-	10	35.40
Misantla drainage	-	-	9	1	-	10	18.10	-	1	5	4	-	-	10	17.30	-	-	6	4	-	-	-	10	35.40
<i>erimyzonops</i>	-	27	13	-	-	40	17.33	1	21	18	-	-	-	40	16.43	13	24	3	-	-	-	-	40	33.75
Tamesí drainage	-	18	12	-	-	30	17.40	1	15	14	-	-	-	30	16.43	8	19	3	-	-	-	-	30	33.83
Pánuco drainage	-	9	1	-	-	10	17.10	-	6	4	-	-	-	10	16.40	5	5	-	-	-	-	-	10	33.50

TABLE 8. Counts of all rakers on outer side of first gill-arch for the east-central Mexican species of *Dionda*.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	No.	\bar{X}
<i>mandibularis</i>	-	-	-	-	-	-	1	8	4	6	-	1	-	20	8.95
<i>rasconis</i>	-	-	-	-	-	-	3	11	9	5	1	1	-	30	8.77
<i>catostomops</i>	-	-	-	-	-	-	-	1	9	15	5	-	-	30	9.80
<i>dichroma</i>	-	-	-	-	-	-	-	4	6	14	11	9	1	45	10.40
<i>ipni</i>	-	-	-	1	8	26	23	11	2	-	-	-	-	71	6.58
<i>erimyzonops</i> (?)						(?) ¹	-	-	-	-	-	-	-	?	?

¹The counts of the very rudimentary rakers, for an unspecified number of specimens, is given in the original description as 0.3 + 1.3, yielding the total possible limiting variation of 1.6.

The early-juvenile color pattern of *Dionda catostomops*, very likely specifically distinctive, is displayed by a 20-mm specimen in the series (UMMZ 195950) collected on December 17. The lateral dark stripe is more intensely blackened than in the adult and is nearly continuous across the head; on the trunk it is about three rows of large melanophores wide and on the urosome it becomes densely stippled. The axial septum of the body muscles is marked toward the head by a single file of melanophores running just above the black stripe, but this pattern grades backward into a continuous black streak dropping to the middle of the stripe. Above the stripe the stippled scale-pocket borders are developing. Dorsolaterally, conspicuously large melanophores form hardly more than a single file on each side, flanking the finely stippled middorsal band, which is a definite narrow streak before, but a wider dusky band behind, the dorsal fin. The very base of that fin is narrowly blackened. The short oblique streaks arising from the base in the adult are intensely blackened. From the jet-black basicaudal spot short streamers extend backward between the bases of the rays. Along the trunk each lateral-line scale is marked by specklets, generally vertically paired but in part single. A few small and inconspicuous melanophores are scattered along the ventral edge of the caudal peduncle. Except as indicated, the body is unpigmented below the midlateral black stripe.

Color in Life.—The distinctive colors of this species were observed during the one significant collection of adults, fortunately when the fish were in breeding condition. The fins of the mature males were seen to be colored like those of *dichroma*, as seen when collected in 1970—particularly in respect to the blue borders. The color contrasted sharply with that of the breeding specimens of *rasconis* taken in the same collection (see p. 294, and Frontispiece). The field notes taken of *Dionda catostomops* on 7 February 1974 are here paraphrased as follows. The breeding males were chalky blue on the fins: on the distal part of the caudal lobes, the outer third of the anal and caudal, the outer margin of the pelvic, and the tips of the pectorals; they were dark above, and contrasted with the specimens of *Dionda rasconis* taken in the same collection. On 29 January 1976, 10 females had all fins tipped with milky white, and the bases of the fins (except dorsal) were orange.

Nuptial Tubercles.—The contact organs are relatively small and weak, and are in some respects inconsistent in extent of occurrence over the head, body, and fins of the nuptial males. They are, however, represented to an almost unique degree in the ripe females. In the males rather small and essentially erect tubercles are developed over the whole dorsal surface of the head, from just before the nostrils to the occiput. The patch extends forward between the nostrils, and then, following a largely naked strip across the snout, is replaced on the anterior ridge of the snout by a patch of definitely smaller tubercles, just short of where the snout

turns backward toward the mouth. In some males a few small tubercles extend backward, below the nostril, in a single series along the upper margin of the pre-orbital region. Commonly a few occur in a series or two on the opercle near its dorsal margin, and rarely one or a few develop on the cheek near its upper end. Those on the top of the head are irregularly and rather densely scattered, with linear orientation clearly evident only in a row closely paralleling the dorsal margins of the orbit. Other very small tubercles, usually in single file, ring the margins of a few to many scales near the front of the nape. In some specimens those contact organs extend backward to, or reappear on, some of the scales in front of the dorsal-fin base. In some males a trace of such tubercles occurs also on the dorsal surface of the body behind the dorsal fin, and rarely the scales are margined with tiny tubercles backward to the upper base of the caudal fin. On the inner side of the pectoral fin, very small nuptial tubercles form a single file on the outer part of the not greatly swollen outermost ray, and another single file, branching once, just within the tip of the next several rays. Only bare traces of tubercles appear on the pelvic fins of some males, in much the same pattern as on the pectoral. Occasionally extremely small tubercles are evident, in a single file, along the branched anal rays, but no trace was seen of any on either the dorsal or caudal fin, or anywhere on the lower surfaces of the body, in this obviously bottom-inhabiting minnow.

Most of the mature females exhibit, uniquely, some degree of development of the tubercles on the upper part of the head and on the pectoral fin, in the same pattern as on the adult males.

SEXUAL DIMORPHISM

The extremely slight differences in coloration and the relatively small sexual differentiation in the nuptial tubercles appear to be paralleled by the very slight average differences appearing in the morphometric data on 10 adults of each sex in the series measured (Table 10). Some very slight, very widely overlapping differences do fall in line with the general rule that the trunk size in fishes tends to be the larger in females, and the urosome to be the longer in males (the measurements involved are caudal-peduncle length, anal origin to caudal base, predorsal length, and pelvic insertion to lateral line).

The paired fins in the mature adults are appreciably longer in males than in females, as is usual. The interspace between the tip of the depressed pectoral fin and the insertion of the pelvic fin in the males is shorter, but in the females is longer, than the orbit. The pelvic in males reaches to beyond the tip of the urogenital papilla, or even to beyond the anal origin; whereas in females it extends to some point short of the papilla, and apparently never to beyond the end thereof.

As is usual for most minnows other than the nest-building and nest-guarding species (such as *D. ipni*), the females of *D. catostomops* seem to grow larger than the males (as is noted on p. 297, and Table 2); obviously, the larger size of the females would benefit reproduction. Conversely, nest preparation and care seem to be tied in with larger size in the males, as Hubbs and Cooper (1936: 18) pointed out.

VARIATION

In addition to the very slight degree of sexual dimorphism just noted and the remarkable similarity of the sexes in coloration and in nuptial tuberculation, this species seems to exhibit a very high degree of consistency that may well be related to its highly restricted range and habitat.

DISTRIBUTION, HABITAT, AND ASSOCIATED SPECIES

The distribution of *Dionda catostomops* and associated species are treated in the present account of the closely sympatric *D. rasconis*, but the probably different habitat of the two is discussed here.

These two sharply differentiated species were taken together in Río Tamasopo near Tamasopo twice, as recounted on p. 295 (see also below).

Field notes for the collections near Tamasopo appear to define the habitat of *D. catostomops*. Those for 1972 (when the two species were not distinguished and only 6 young to small adults of *catostomops* were taken with 15 specimens of *rasconis*) record that "The *Dionda* habitat is in silt-bottomed pools well below riffle heads but in good current 2–3 feet deep; it does not, apparently, prefer rocks and good riffles," but the notes define the current as "quite swift to slight" (these quotations seem to apply primarily to *rasconis*). The notes for 1974 when the one good collection of mature adults of *catostomops* was obtained, denote that short riffles were interposed between long pools and that the current was "slight to moderately swift." The collections were obtained by seining over the full length of the riffles and into the heads of the pools. In 1976, when observations were made with a face mask and the seining was selective, *catostomops* was found to occur on riffles at least 0.7m deep, either at the ends of long pools or as the riffles swept into pool heads. The records for both 1974 and 1976 indicate that: the water was clear and not readily roiled; the bottom was of rocks, marl, sand, and silt; the depth was to about 1.5–3m; and the vegetation was represented by green algae growing on rocks. The terete, flat-bottomed form of *catostomops* very strongly supports the idea that it segregates in swift water. It is assumed that the breeding specimens of this species were probably secured on the riffles.

In the lower, quieter and less clear, water of Río Ojo Frío near Rascón only a single individual of *catostomops* was taken on 20 March 1974, along with 67 topotypes of *rasconis*, at this the third record (second known location) of joint occurrence. The water of the broad river was recorded as greenish blue, with visibility of nearly 1m; with no vegetation; the bottom of sand, silt, gravel, and stones; and the current swift to slight. However, no special attempt was made to work the riffles, which are sparse at this station; this could explain why only one specimen of *catostomops* was secured.

The 1976 collection of *catostomops* from Río Ojo Frío, 11.2 km north of Rascón (where only this cyprinid, *Astyanax*, and a *Cichlasoma* were taken), came from very clear water over rocky bottom near pool heads, in the strong current in water as deep as 1.4m. The temperature here was cold, 18°C, whereas the Río Tamasopo registered 24.8°C on the following day.

LIFE HISTORY NOTE

The breeding condition of specimens constituting the one good series of *catostomops* taken on 7 February 1974 in water of 27°C, suggests late-winter spawning. The 20-mm (SL) specimen taken on 17 December 1972 (water 22°C) suggests that the reproduction may start early in the winter. It may well be that the spawning season is accelerated to precede late-spring warming of the water, but the paucity of collections and ecological data render this only a tentative hypothesis.

Derivation of Name.—The name *catostomops* reflects the resemblance of this fish in body form to the type genus, *Catostomus*, of the sucker family. The suffix *-ops* is the latinization of $\omega\psi$, face or eye, denoting resemblance. This choice of name parallels that of *erimyzonops*, from the similarity of that species in general form and color pattern to the catostomid genus *Erimyzon*.

TABLE 9. Ratio of lengths, caudal peduncle / anal base, in east-central Mexican species of *Dionda*.

Species	Ratios										No.	Range	\bar{X}
	0.70- 0.89	0.90- 1.09	1.10- 1.29	1.30- 1.49	1.50- 1.69	1.70- 1.89	1.90- 2.09	2.10- 2.29	2.30- 2.49	2.50- 2.69			
<i>mandibularis</i>	-	-	-	-	-	4	13	9	1	2	29	1.82-2.68	2.11
<i>rasconis</i>	-	-	-	-	-	-	9	16	6	2	33	1.96-2.55	2.20
<i>catostomops</i>	-	-	-	-	-	-	3	11	5	1	20	1.99-2.51	2.25
<i>dichroma</i>	-	-	-	1	4	25	18	13	1	1	63	1.49-2.62	1.94
<i>ipni</i>	3	13	17	7	1	-	-	-	-	-	41	0.70-1.57	1.15
34.5-39.7 mm	-	3	4	5	1	-	-	-	-	-	13	1.03-1.57	1.28
40.6-49.6 mm	-	7	12	2	-	-	-	-	-	-	21	0.92-1.34	1.14
50.3-73.7 mm	3	3	1	-	-	-	-	-	-	-	7	0.70-1.10	0.94
<i>erimyzonops</i>	-	-	-	10	8	8	1	-	-	-	27	1.38-1.95	1.60

***Dionda dichroma*, n. sp.**
Figures 5A-B, 10

Hybognathus rasconis.—Meek, 1904: xxxvi, 50 (in part; Río Verde at Río Verde).

Dionda rasconis.—De Buen, 1940: 22 (in part; record from Río Verde, after Meek). Hubbs and Brown, 1956: 73 (in part; Meek's material from Río Verde). Miller, 1956: 14-15 (tributary to Río Verde, La Media Luna). Darnell, 1962: 323 (in part; literature references only).

Hybognathus episcopus (misidentification).—Regan, 1906-08: 150-151 (in part; Río Verde record only). Alvarez, 1950: 49 (presumably in part, in key; "norte de México").

Dionda sp.—Contreras-Balderas and Verduzco-Martínez, 1977: 262 (associated with *Dionda mandibularis*).

Synonymy, Nomenclature, and History.—Material of this species, although known and recorded for more than a third of a century, has been misidentified with the trenchantly distinct species *D. rasconis*, or even with *D. episcopa* (see above).

Status.—This species, as herein delimited, occurs over a wider geographical range than any of the other three upland species among the six herein treated (Fig. 1), and apparently over a greater range of habitat type than any of the other five. Although it appears to be the most variable in several characters among all six, we do not at present regard it as justifiably divisible into species or subspecies. Further analysis, however, may eventuate in such a decision.

This is the species that for many years passed as a synonym, or as a then unnamed subspecies, of *Dionda* or *Hybognathus rasconis* (p. 287). The sharp distinctness of these two species is outlined in couplet 3 of the Analytical Comparisons (p. 277).

Diagnosis.—Rakers on first gill-arch extend forward from angle to or very nearly to front end of lower limb. Barbel typically present at end of maxilla, though small and often rudimentary. Scales continued forward over anterior part of breast and over shoulder girdle. Scales relatively small, 37-45 along lateral line. Caudal peduncle only about half longer than anal-fin base. Ground color rather evenly sooty above lateral stripe, conspicuously lighter below, producing a contrasting, bicolored appearance (Fig. 5A-B). Dorsal fin of nuptial male sooty and blue-edged in life; other fins also blue-edged. Mouth not overhung in front by snout. Greatest depth of body much more than twice greatest width. Dorsal and anal fins with posterior edges straight or slightly rounded. Middorsal streak moderately to strongly developed.

Comparisons.—*Dionda dichroma* contrasts with *mandibularis* in all respects treated in the Analytical Comparisons under couplet 1, from *rasconis* under couplet 3, from *catostomops* under couplet 4, and from *ipni* and *erimyzonops*

TABLE 10. Proportional measurements (permillage of SL) of adults of three species of *Dionda*: indicating range, (mean), and number.

	<i>Dionda mandibularis</i>			<i>Dionda rasconis</i>		<i>Dionda catostomops</i>
	Puerta del Río	Marsh 10 km S of Rioverde	Río Gallinas	Río Tamasopo	Río Tamasopo	
	UMMZ 196339	UMMZ 193474, 196703	UMMZ 196693	UMMZ 196345	UMMZ 196346-7	
Standard length, mm						
Males	40.7-46.7 (44.0)	33.0-48.5 (40.4)	28.8-43.9 (35.7)	This set not sexed	Type, ♂, 54.7 mm	
Females	45.7-57.2 (52.0)	32.6-52.7 (44.9)	40.5-50.2 (44.5)	35.4-52.4 (43.6)	52.5-61.0 (57.0)	10
					56.8-66.1 (61.4)	10
Body depth						
Males	255-299 (274)	224-276 (256)	225-278 (247)	265-295 (279)	Type 265	
Females	260-321 (288)	226-260 (245)	250-280 (263)		251-279 (263)	
					256-281 (265)	
C-peduncle depth					Type 126	
Males	105-115 (110)	91-111 (103)	92-114 (106)	102-118 (112)	118-133 (128)	
Females	102-115 (109)	90-104 (98)	102-113 (107)		121-136 (127)	
C-peduncle length					Type 260	
Males	219-239 (229)	220-255 (232)	227-251 (241)	218-249 (238)	259-269 (266)	
Females	213-231 (223)	226-255 (240)	229-256 (242)		241-271 (259)	
A origin to C base					Type 378	
Males	334-338 (336)	327-355 (345)	339-363 (350)	331-370 (350)	371-391 (382)	
Females	316-343 (331)	323-357 (339)	332-365 (347)		349-386 (372)	
Predorsal length					Type 525	
Males	527-555 (540)	524-558 (540)	496-538 (518)	493-532 (517)	507-525 (516)	
Females	540-570 (549)	522-549 (540)	500-543 (515)		511-541 (528)	
Depressed D fin					Type 237	
Males	225-251 (241) ₃	216-251 (234)	231-276 (254)	240-271 (256) ₁₁	220-237 (229)	
Females	208-227 (216) ₄	208-235 (221)	223-262 (245)		212-237 (224)	
A-fin base					Type 120	
Males	109-120 (114)	100-119 (111)	101-115 (108)	107-119 (112)	109-130 (120)	
Females	103-115 (109)	95-109 (102)	95-116 (106)		105-122 (115)	
P ₁ -fin length					Type 213	
Males	186-213 (204)	185-223 (201)	175-216 (197)	185-218 (197)	204-218 (210)	
Females	179-210 (188)	175-192 (185)	178-203 (159)		188-212 (196)	

under couplet 2. In some respects *dichroma* resembles or approaches *ipni*, for instance in the usual approach toward *ipni* in the blackish markings on the fins and occasionally in the disruption of the dark lateral stripe, in the frequently rounded margins of the fins, in the shortening of the caudal base and elongation of the anal-fin base (Table 9), and in the increased number of anal rays (Table 4). It differs sharply from *ipni*, however, in having the anal base in mature males much shorter instead of longer than the caudal peduncle, in having the black stripe continued forward to the eye rather than being confined to the opercle, in the longer and less separated inner grooves of the lower lip, in having nuptial tubercles seldom and at most weakly continued backward onto the suborbital region, and in the usual development of the barbel. *D. dichroma* contrasts very sharply with *erimyzonops* in having the snout very much less downcurved, the lower-lip grooves shorter and farther apart anteriorly, the gill-rakers much better developed, the fins much smaller, the head lacking the dark dorsal striping, the scales more numerous (Tables 5-6), and in the much less reduced size.

Material Examined.—All from San Luis Potosí, and all UMMZ specimens except as noted: Holotype, 196701 (51.7 mm SL) and paratypes 196702 (15: 38-54), spring-fed marsh 10 km S of Río Verde. Paratypes: 172195 (251: 16-65) and UF 14575 (10: 46-60), Río Santa Catarina, 65 km W of Río Verde; 196338 (72: 31-63) and LSUMZ 1216 (7: 47-61), spring at Puerta del Río, 20 km SE of Ceritos; 187685 (11: 41-59), La Media Luna, 11 km SSW of Río Verde; 188800 (13: 30-58), canal in Río Verde connecting with La Media Luna; 189278 (47: 18-40), Río Verde, 2 km NE of Río Verde; 189573 (113: 39-64) and UNL 1327 (38: 36-62), Río Verde at bridge just E of Río Verde; 192511 (4: 28-53), ditch 8 km S of Río Verde and 4.1 km W of highway; 193448 (24: 13-60), tributary to Río Verde, 16 km SE of Río Verde; 193473 (19: 33-56), type locality; UNL 1031 (10: 31-55) and 1321 (4: 28-36), arroyo 7 km SSE of Río Verde. Non-types: FMNH 3877 (16: 25-51), Río Verde at bridge just E of Río Verde; LSUMZ 23 (3: 17-29), La Media Luna, SSW of Río Verde; LSUMZ 274 (25: 31-53), Río Verde at Guayabos; LSUMZ 408 (31: 37-54), Río Verde at Tanlacú.

DESCRIPTION

The prime descriptive characters of this species are given in items 1B, 2A, 3B, and 4B of the Analytical Comparisons, and under the two preceding sections.

Size and Form.—This is a moderately large minnow: the largest among the 693 specimens studied by us measures 65 mm SL in each sex, and many exceed 50 mm. The ventral contour is about as strongly curved as the dorsal, or nearly so (thus contrasting with the swift-water species *catostomops*). The bottom of the head, however, is rather smoothly curved, but is considerably less oblique than the dorsal margin, which is quite steep and strongly curved on the snout, rounded moderately above the eye, and then about straight to the occiput, just behind which it may be swollen moderately before curving gently to the dorsal-fin origin. The contour through the dorsal-fin base is moderately to weakly deflected downward, and the postdorsal contour is nearly straight to the slight flare at the caudal base. The ventral contour of the trunk is nearly straight to rather strongly curved, and the postanal margin roughly matches the postdorsal.

The edge of the mandible is rather strongly oblique, and is largely to wholly covered by the flesh of the lower jaw area (lacking the rather sharp anterior and posterior tips seen in *mandibularis*). The lips are only moderately developed and the upper is little or not at all concealed by a terminal fleshy flap.

Proportional Measurements (Table 11).—This is usually a moderately deep-bodied minnow over most of its range, with the greatest depth about, or more than, 30% of the standard length (ordinarily less than 30% in the 3 preceding

upland species, *mandibularis*, *catostomops*, and *rasconis*, and in the adults of the two lowland species, *ipni* and *erimyzonops*; but, as in the aberrant though topotypic population of the marshy area south of Río Verde, this species may resemble those three other upland species in slenderness. There is considerable regional and individual variation also in the depth of the caudal peduncle. The head in major dimensions, as in *catostomops* and *rasconis*, is ordinarily considerably smaller, proportionately, than in *mandibularis*, *ipni*, and *erimyzonops*. The mandible length is not particularly distinctive, except for being definitely less than in *mandibularis*. The caudal peduncle, measuring between one-fourth and one-fifth of the standard length, is usually shorter than in the other upland species, particularly *catostomops*, but is somewhat longer than in *erimyzonops* and much longer than in *ipni*. The predorsal length, about 53% of the standard length, averages longer than in *catostomops* and *mandibularis*. The dorsal fin, about as in *catostomops*, is usually shorter than in the other species. The anal-fin base is about as long as in the other upland species, but is shorter than in the two lowland species. The highly variable ratio between anal-fin basal length and caudal-peduncle length approaches, with much overlap, the values for *erimyzonops* and barely overlaps the low ratios for *ipni* (Table 9). The head length constitutes about 25% of the standard length, distinctly less than in *mandibularis*, *ipni*, and *erimyzonops*, but otherwise is not particularly distinctive. The orbit in this species varies spectacularly in size with locality (Fig. 9), as specified under Variation (pp. 315-316).

Barbel.—The barbel, generally minute to small and seldom pendant, is almost always developed on either one or both sides, near the lower-posterior tip of the maxilla.

Gill-rakers.—The rakers on the first arch, unlike those of *mandibularis*, *ipni*, and *erimyzonops*, are developed along nearly the full length of the lower limb and apparently are rather more variable than in the other species, numbering 7 to 13, with the mode at 10 (Table 8).

Pharyngeal Arch and Teeth.—The lower limb of the pharyngeal arch of *dichroma* is of moderate width and irregular shape, broad distally and deeply curved along the mesial border. There is a conspicuous ventral keel well in advance of the mesially-deflected tip. This limb, subequal to the upper limb, is slightly to moderately curved, and it is either recurved at its tip (Fig. 3A-B) or is elongated and has a weakly pointed tip.

The three uppermost teeth have well-developed grinding surfaces and are moderately to weakly hooked, or some may lack hooks; the grinding surface is small to obsolete on the lowermost tooth, which usually has a well-hooked tip. Some or all of the teeth may be weakly crenulated, especially along the posterior margin. The dentition was examined in specimens from four widely separated localities, including Tanlacú which lies farthest downstream in Río Verde.

Intestine.—The general appearance of the rather extensively and consistently coiled intestine is shown in a photograph (Fig. 8) of a 52-mm specimen from Río Verde E of Rioverde. Six major coils are visible despite the fact that the available interspaces, as is usual, are largely filled by lobes of the liver, and, in this specimen, marginally by the mature ovary.

Fins.—The fins are of about the same, moderate size as in *mandibularis* and *catostomops*, but average somewhat smaller than in the three other species herein treated. They tend to have longer bases and greater spread than do those of the other upland species, but to equal the two lowland species in this regard. In the ratios of lengths, caudal peduncle / anal base, this species is intermediate between the other upland species and the two lowland ones (Table 9). The dorsal rays (Table 3), as in the five other species, predominantly number 8. The anal-ray counts diverge from those of the three other upland species, which predominantly also number 8, by having a larger proportion of counts of 9—especially in some



Figure 8. Ventrally exposed, largely convoluted, intestinal coils, *in situ*, of adult female of *Dionda dichroma* 51.0 mm SL (UMMZ 189573). The coil closely margining the exposed lobe of liver remains largely concealed in adipose tissue.

areas of the upper Río Verde near Río Verde (Table 4), thus again showing an approach toward the two lowland species. Pectoral rays are predominantly 13, as in *rasconis*, rather than 12 or 13 (*erimyzonops*), 13 or 14 (*mandibularis*), 14 (*catostomops*), or 15 (*ipni*). Pelvic rays are usually 8, as in all six species.

Scales.—The squamation, contrasting with that of *rasconis*, is complete on the body. The numbers in the various rows counted (Tables 5–6) are of normal variability within localities but vary regionally, even between closely approximated locations. The counts are almost invariably higher than in *rasconis*, *ipni*, and *erimyzonops*, but variously overlap those of *mandibularis* and *catostomops*.

Vertebrae.—The usual counts for *dichroma* are 18 or 19 precaudals, 17 to 19 caudals, and 37 or 38 total. These numbers are overlappingly fewer than in *catostomops*, but are definitely higher than in the other east-central Mexican species referred to *Dionda* (Table 7).

Sensory Canals of the Head.—As in *rasconis* (Figs. 6–7) there is much individual and bilateral variation in the pattern of these canals and their pores, with various interruptions, branchings, interconnections, etc. The preoperculomandibular, infraorbital, and supraorbital canals are usually complete, but occasionally are broken or otherwise aberrant. The supratemporal in some collections is very commonly, or even usually, complete across the midline, but in other lots is ordinarily interrupted, at the midline, narrowly, widely, or variably. In some collections, as of the topotypes (UMMZ 196701–2), the supratemporal usually extends in a generally nearly straight line to just before or just behind the underlying frontoparietal suture. This is particularly so in the far-downstream series from Guayabos and Tanlacú. In the isolated headwater location of Río Santa Catarina the supraorbital canal usually extends well beyond the suture and becomes wavy, with one or even two slight to sharp incurvings. It may end by joining the supratemporal, or end blindly, or send a branch to fuse with the adjacent canals, at any point extending from the median terminus of the supratempo-

ral or to any point along the "temporal" canal. These two contrasting patterns are reasonably consistent in the samples just mentioned. A nearly complete separation could be obtained by comparatively analyzing the canals at the uppermost (Santa Catarina) and lowermost (Guayabos and Tanlacú) series, but the variations found in the complex of habitats about Río Verde and La Media Luna (including also the Puerta del Río headwaters) seem to defy any reasonable segregation.

Coloration.—The general coloration of the adult females and of the young of both sexes is quite well shown by the female (Fig. 5B), which in most respects follows rather well the general features of the species under study. A jet-black stripe runs horizontally straight backward from the rear edge of the eye to more or less connect with the black basicaudal spot, which is essentially its terminus. It is narrowly interrupted at the opercular edge, where the stripe overlies the upper end of the gill-opening. The stripe tends to be broadened, sometimes to nearly the width of the eye, along the middle of the trunk, where it either contacts the lateral line, there weakly downcurved, or is narrowly separated therefrom. Very close to the head the lower edge of the stripe passes somewhat below the lateral line. The stripe, though there weakened and somewhat diffused, is generally resumed across and around the snout. A conspicuous middorsal dusky stripe extends from the occiput to and along the sides of the dorsal-fin base and thence backward to the upper caudal base, but there is at most only a very slight speckling along the lower edge of the caudal peduncle.

The dark lateral stripe tends to be bordered above by a much narrower lighter streak, particularly behind the upper part of the eye, and generally also toward the caudal fin, where it is wider. The whole region between this light streak and the middorsal stripe is darkened, either solidly or by speckling. There is generally almost no pigmentation below the lateral stripe in young and females, except, in some females, for weak stippling around the rear of the scale pockets. In young and females there is also very little pigmentation on the fins, except along the upper edge of the pectoral and along a weak margining of the dorsal.

As the males approach maturity the body above the lateral stripe, and eventually the whole side, becomes darkened, particularly near the scale margins (Fig. 5A). Eventually, as the males reach maturity, the upper parts above the lateral black stripe become further darkened, particularly near the scale-pocket margins. In a few mature males from the extreme headwaters of Río Verde at Santa Catarina the lateral stripe tends to become disrupted into more or less distinct, irregular, and short dark bars, slightly suggestive of much abbreviated parr marks (Fig. 10), but this transformation never attains the very broad crossbanding attained by the advanced nuptial males of *ipni* (Fig. 5C); see also below under Variation.

All fins in nuptial males tend to become sooty, except very near their light margins, and, in some individuals, in a lower-anterior light area (as in Fig. 10); the caudal fin is least so affected.

At no stage is there any suggestion, in this or in any other of the species under special study, of the diagnostic dark striping of *erimyzonops* on the top of the head.

Color in Life.—The sexually dimorphic colors of breeding males and females of *dichroma* were observed, annotated, and photographed in water in the field, just east of Río Verde, on 13 February 1970 (Frontispiece, lower pair, male above and female below). The field notation, based on the male, reads: "tips or margins of all fins are iridescent blue, lacking in female." The dark dorsum and the fins also are the more deeply pigmented on the color slide, bringing out in special contrast the pale centers of the scale pockets. A field note on UMMZ 196702, taken from a marsh on 21 March 1974, reads: "breeding males with milky-blue to cobalt-blue fins," and the note for Río Santa Catarina (UMMZ 172195), taken on 19 March

1955, indicates that males have white on the outer margins of the pectoral, pelvic, and anal fins. The bluish fin margins of the male fade to whitish at other localities, so the Santa Catarina fish may well have had these fins blue-bordered in life (this point needs checking). Breeding males of *catostomops* were found to exhibit similar blue coloring on the fins (p. 304). Field notes on breeding males observed through a face mask on 31 January 1976, in the marsh south of Río Verde, read: Outer margins ($\frac{1}{4}$ to $\frac{1}{3}$) of all fins, including tips of caudal lobes, brilliant cobalt blue; a deep golden orange stripe below, and a golden-bronze stripe above, the dark lateral stripe, these two stripes of similar width and length; tip (including top) of snout also blue. Females with a golden bronze stripe above the dark lateral stripe that is of the same width and length; fins all pale.

Nuptial Tubercles.—Distinctive nuptial tubercles were noted for several series, including UMMZ 188800 and 192511, or are well shown on Figure 5A (out of UMMZ 196702). By far the most conspicuous are the very large tubercles on the head, the largest of which in basal diameter exceed half the width of the pupil; they extend in roughly five lengthwise rows from the occipital line to between and before the nostrils. The arrangement of the pearl organs in these rows is rather irregular, except for those on the outermost row, on each side, that comprise an essentially regular, weakly curved line just within and paralleling the interorbital margin. These huge tubercles atop the head have a rather bulbous basal portion, which, particularly in the middle third of the area covered, is convex posteriorly and concave in front and ends in a constricted tip bent more or less forward. These enlarged head-top tubercles are preceded, beyond a more or less completely naked cross strip, by about three irregularly transverse rows of definitely smaller yet not minute tubercles rounding the snout just above the front of the premaxilla; the more lateral of these organs point outward, the median ones forward. This rostral armament is followed by a few slightly larger tubercles scattered between the anterior nostril and the rostral groove directly below. Several slenderer ones, in part with tips bent forward, are set on the mandible, and are commonly followed by a few below the cheek, between the mandible and the interopercle. Occasionally a few others are set on the lower part of the cheek or on the opercle.

A few tubercles, small but larger than the minute ones margining the scale borders, occur on some specimens (including the nuptial male shown as Fig. 5A) near the middorsal line between the occiput and the dorsal-fin origin. Numerous close-set minute tubercles irregularly line the free margins of nearly all the scales across the back and sides of the entire body, but do not continue across the ventral surface in advance of the anal fin. A few appear elsewhere on the scale surfaces. In some specimens a number rise even from some of the lateral-line pores. Somewhat enlarged and basally crowded tubercles arise on the slightly swollen scales across the lower surface of the caudal peduncle, and, to some extent, just above the anal-fin base; but these do not form there a definite band of strong, very closely juxtaposed tubercles.

Small tubercles extend virtually the full length of all but the innermost rays of the pectoral and pelvic fins, along all the anal rays, and along at least the lower and median caudal rays; also, in some males, along the dorsal-fin rays. These tubercles are uniserial along the outermost or foremost ray on each of the fins, but branch once, beginning close to the base, along the following rays.

Breeding females, including the one portrayed as Figure 5B, exhibit a mere trace of the large head-top tubercles, but apparently none others are represented.

Sexual Dimorphism.—With maturity, the sexes of *dichroma* become moderately different in that the males become more melanistic on body and fins (p. 313, Fig. 5A) and in life their fins become strikingly blue peripherally (see the Fron-

tispiece). Similar differentiation is seen in the sympatric species, *mandibularis*. As just noted, the nuptial tubercles in the mature males are much enlarged atop the head and are developed over almost the entire surface of the body and fins, but are scarcely evident in breeding females.

In line with the general tendency, the posterior parts, as measured by the lengths of the urosome and the anal-fin base, average somewhat longer in males, whereas the trunk region, as measured by the predorsal length, averages longer in females. The fins and the head and head parts average slightly greater in males, but the eye size seems to be similar.

Variation.—*Dionda dichroma* (or possibly species complex) is by far the most variable among the six species herein treated. The most striking difference in proportions is that of the size of the eye. In the four populations measured in detail the average permillage values for length of orbit vary as follows: 59 and 73.5, with virtually no overlap for the two separated headwaters, Río Santa Catarina and Puerta del Río, respectively (Table 11); with high values of 79.5 for the marshy area S of Río Verde and of 70 for Tanlacú near the mouth of Río Verde, farthest downstream. The mean ratios of orbit to snout in the same series are as follows: 1.38, 1.04, 0.95, 1.03. Approximate extremes in ratio of orbit to post-orbital lengths are about 1.5 for the marshy area and 2.5 for Río Santa Catarina. The ratios of orbit length to postorbital length (Fig. 9) show no approach when the values for the very large-eyed population from the isolated marsh 10 km S of Río Verde (UMMZ 196702) is compared with those for the very small-eyed series from Río Santa Catarina (UMMZ 175195). The wide difference between these two series is bridged over by the values for the series from Puerta del Río (UMMZ

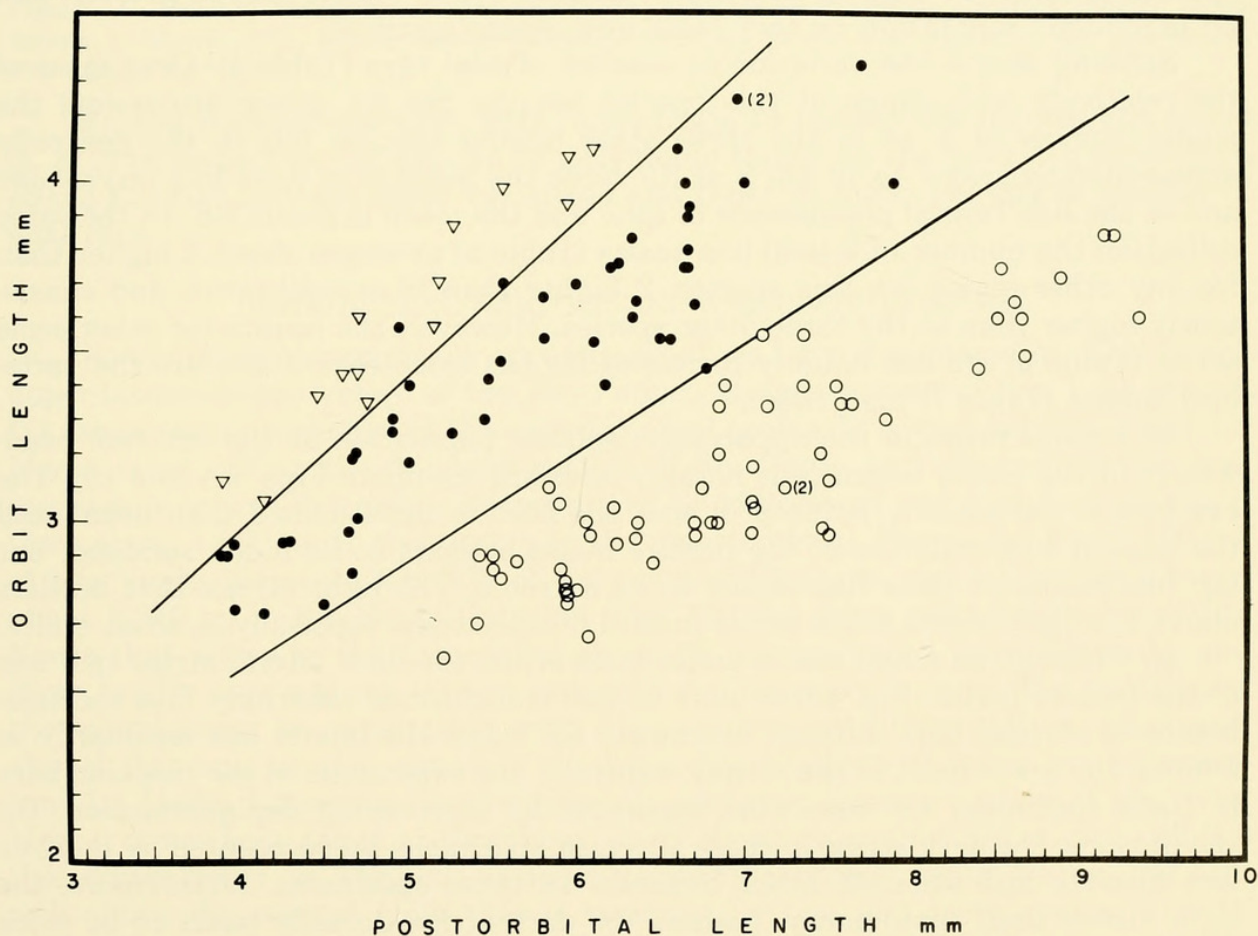


Figure 9. Sharp distinction in size of eye (in relation to postorbital length) between specimens of *Dionda dichroma* from isolated marsh 10 km S of Río Verde (UMMZ 196702, upper left), and those from the two headwater populations: Puerta del Río (196338, middle) and Río Santa Catarina (172195, lower right).

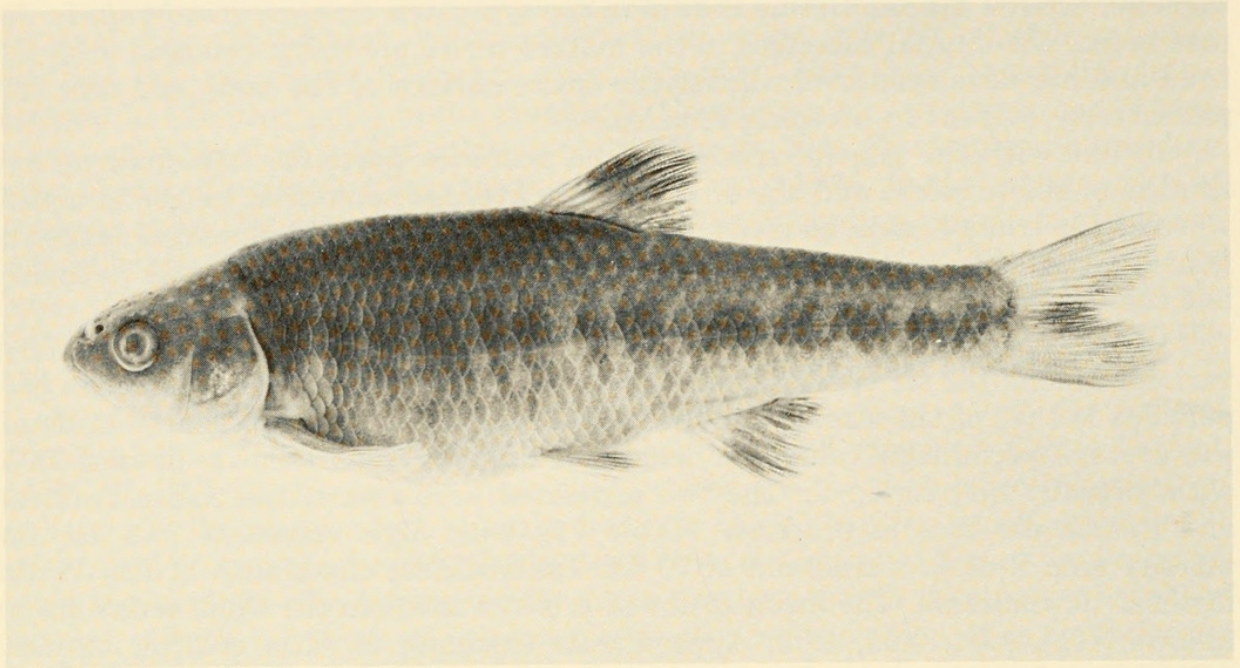


Figure 10. Nuptial male paratype (63.9 mm SL), variant of *Dionda dichroma* (UMMZ 172195, no. 44), from Río Santa Catarina (Fig. 11), isolated headwater tributary of Río Verde, about 65 km W of Río Verde, San Luis Potosí. Note unusual color pattern, small eye, and rather domed head.

196338), with only a slight overlap in either direction. Inspection of other series of specimens tends to suggest that the overlap in the two directions is greater, and no taxonomic separation on this basis now seems justified.

Striking also is the variation in number of anal rays (Table 4). Over most of the relatively wide range of this species (among the six under discussion) the modal number is 8, as in the three other upland species, but in the generally spring-marshy area 7 to 10 km S of Río Verde the mode is at 9, as in *erimyzonops* and in the Río Tamesí populations of *ipni*, and the mean is about 8.8. In the same collection the number of lateral-line scales (Table 5) averages about 2 higher than for any other region for this species, 3 higher than in *mandibularis*, and consistently higher than in the three other species. However, the counts for other scale series (Table 6) are not notably increased for the same region, nor are the vertebral counts (Table 7) high there.

In several respects the apparently isolated population at the extreme headwaters of Río Santa Catarina is notably aberrant (compare Figs. 5A and 10). The eye here is particularly reduced in size, the head is more domed than usual, and the nuptial tuberculation of the mature males appears to be much subdued, but the blackening of their fins seems to be extreme. The light streak that borders above the dark lateral stripe tends toward obsolescence, especially in adult males.

In addition, as noted above under Coloration, the dark lateral stripe in a few of the mature males (Fig. 10) is more or less transformed anteriorly into the semblance of vertical bars diffused downward far below the lateral line (ordinarily in *Dionda* the lower limit of the stripe); ventrally the extensions of the blackish bars in these specimens are somewhat separated by intervening depigmentation. On the urosome the dark stripe in these aberrant specimens is represented by more or less discrete and squarish black blotches. In these specimens, furthermore, the light streak that, customarily, borders the dark stripe dorsally tends to be weak or even largely obliterated. The darkened area of the fins in these aberrant nuptial males tends to be particularly blackened. Their form and coloration gives some impression of an approach toward *ipni*, but we do not believe that these especially far-separated populations are thereby indicated as particularly consanguineous.

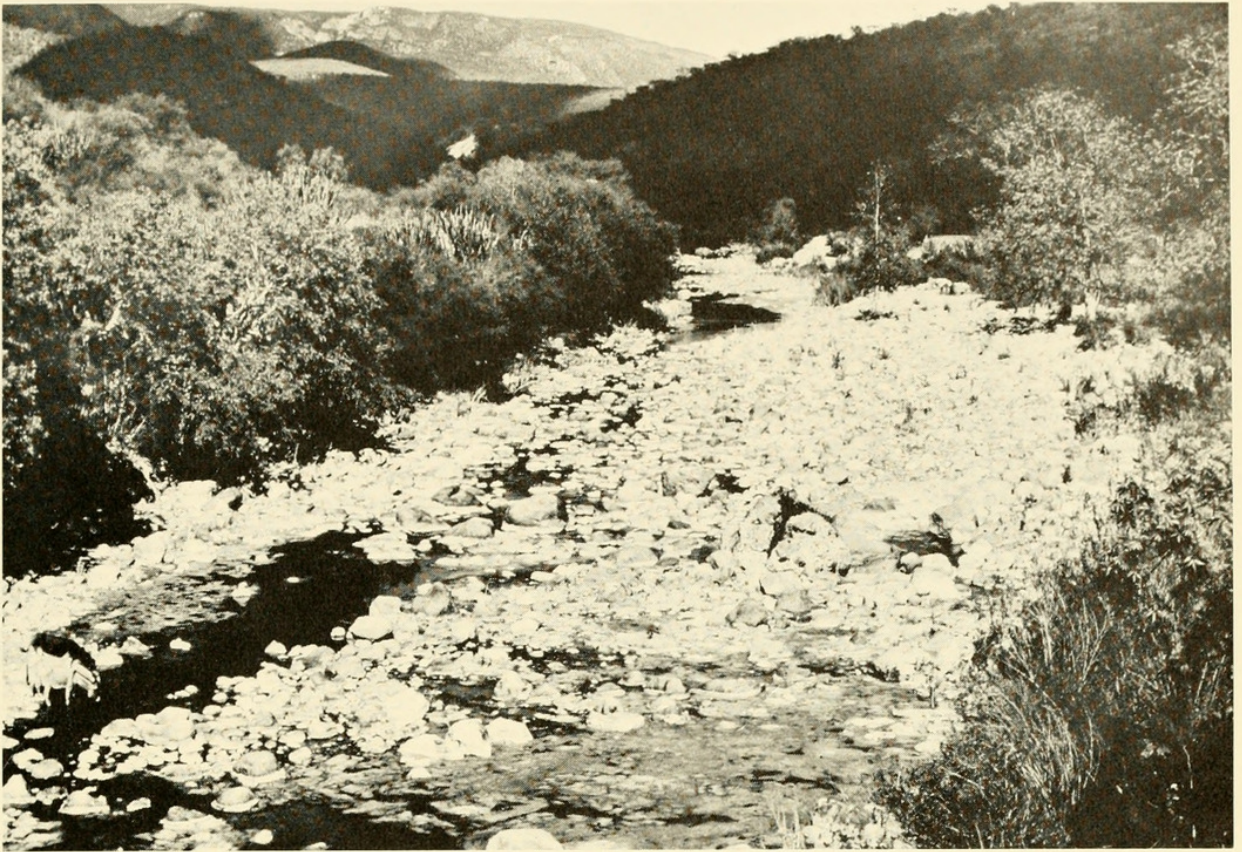


Figure 11. Isolated headwater habitat of *Dionda dichroma* in Río Santa Catarina, looking downstream, in March, 1974, from bridge on Highway 70, about 65 km W of Río Verde, San Luis Potosí. Photograph by Miller.

Marked fluctuations with little relationship to locality are pointed out above (p. 312) in respect to the pattern of lateral-line canals on the head. No correlation seems to exist between these variations and those in either eye size or number of anal rays.

DISTRIBUTION, HABITAT, AND ASSOCIATED SPECIES

Dionda dichroma primarily occupies what we have designated (p. 272) as the upper-intermontane valley of the Río Pánuco stream system in San Luis Potosí. Its range seems to center in the extensive and profusely spring-fed area about La Media Luna, within the drainage system of Río Verde, and throughout this area in streams as well as springs it appears to be widespread and abundant, at elevations about 1,000 m. It also occurs in the reported head, Puerta del Río (1,100 m), of Río Verde, about 45 km NW of the town of Río Verde, and, at an elevation of about 1,250 m, in Río Santa Catarina (Fig. 11), the other main headwater of Río Verde that arises in the mountains about 65 km westward from Río Verde, and flows briefly over a stony stream bed until it disappears in sand. The isolation of the populations is compatible with their moderate differentiation (discussed above). The species also occurs in the lower Río Verde, well below the intermontane La Media Luna area, in the generally eastward-flowing portion of the river. Here it has been taken at Guayabos, at an elevation around 500 m, and still farther downstream, at Tanlacú, at an elevation of probably about 300 m, but still well above the coastal plain that is occupied by *ipni* and *erimyzonops* (Fig. 1). Both Guayabos and Tanlacú lie well below the narrow, torrential gorge of Río Verde that is cut into a lava canyon (reportedly 60 m deep), beginning at Pinahuán (ca. 750 m) about 20 km S of Highway 70 on the road between Rayón and Lagunillas. It seems entirely reasonable to conclude that the far-downstream

TABLE 11. Proportional measurements (permillage of SL) of adults of *Dionda dichroma*: indicating range, (mean), and number.

	Rio Santa Catarina UMMZ 172195	Puerta del Río UMMZ 196338	Marsh 10 km S of Río Verde UMMZ 196701-2	Río Verde, Tanlacú LSUMZ 408
Standard length, mm				
Males	53.8-64.9 (60.0) 10	44.0-56.3 (50.4) 10	Type, ♂, 51.7 mm	This set not sexed
Females	49.2-65.0 (56.7) 10	47.2-65.3 (56.2) 10	40.9-53.6 (48.5) 7	46.3-53.7 (51.0) 10
Body depth				
Males	277-327 (300)	293-327 (309)	Type 264	289-342 (310)
Females	272-339 (301)	254-328 (296)	239-271 (258) 247-268 (259)	
C-peduncle depth				
Males	121-135 (126)	111-126 (120)	Type 115	111-129 (121)
Females	111-123 (118)	104-126 (113)	108-122 (114) 99-104 (101)	
C-peduncle length				
Males	216-246 (229)	214-253 (237)	Type 224	209-236 (221)
Females	195-246 (219)	206-248 (232)	209-236 (219) 198-250 (224)	
A origin to C base				
Males	334-362 (347)	326-364 (353)	Type 353	322-358 (340)
Females	306-356 (333)	322-371 (347)	332-369 (345) 329-350 (340)	
Predorsal length				
Males	507-558 (529)	512-538 (530)	Type 516	516-551 (536)
Females	511-549 (537)	514-543 (529)	516-528 (521) 505-540 (524)	
Depressed D fin				
Males	196-230 (218)	208-231 (222)	Type 230	205-238 (224)
Females	202-230 (213)	201-234 (217) ₈	221-254 (233) 216-231 (222) ₅	
A-fin base				
Males	106-126 (120)	107-136 (116)	Type 131	110-125 (116)
Females	106-121 (114)	103-129 (115)	117-134 (127) 95-133 (117)	
P ₁ -fin length				
Males	179-210 (196)	186-208 (196)	Type 199	186-226 (203)
Females	171-195 (185)	171-202 (185)	197-222 (205) 183-192 (186)	
Lateral line to D origin				
Males	158-186 (174)	157-181 (170)	Type 159	159-182 (169)
Females	158-183 (169)	136-175 (161)	140-166 (153) 140-150 (147)	

Lateral line to P ₂ insertion	Males	123-144 (134)	135-156 (144)	Type 110	125-156 (137)
	Females	128-170 (143)	106-159 (136)	101-122 (111) 114-133 (120)	
Head length	Males	252-292 (266)	245-268 (257)	Type 259	242-269 (255)
	Females	249-264 (255)	235-261 (251)	248-260 (255) 224-250 (241)	
Head depth	Males	183-217 (202)	178-197 (189)	Type 184	181-200 (190)
	Females	185-203 (195)	170-193 (182)	178-194 (186) 164-182 (175)	
Head width	Males	145-166 (157) _g	134-148 (141)	Type 151	125-145 (134)
	Females	136-164 (149)	127-154 (138)	126-151 (137) 122-135 (127)	
Snout length	Males	85- 96 (89)	74- 85 (79)	Type 78	65- 78 (72)
	Females	79- 89 (84)	67- 85 (75)	75- 86 (79) 69- 78 (73)	
Orbit length	Males	54- 65 (58)	69- 86 (75)	Type 79	66- 73 (70)
	Females	58- 62 (60)	68- 77 (72)	75- 82 (79) 78- 82 (80)	
Upper-jaw length	Males	68- 74 (72)	58- 78 (68)	Type 68	63- 78 (68)
	Females	66- 76 (70)	62- 70 (65)	63- 70 (67) 61- 72 (66)	
Suborbital width	Males	41- 49 (44)	35- 49 (39)	Type 36	27- 36 (32)
	Females	33- 45 (41)	28- 41 (34)	34- 42 (37) 30- 37 (34)	
Least interorbital width	Males	97-110 (104)	94-103 (99)	Type 93	80- 95 (87)
	Females	94-104 (100)	86-102 (95)	93-109 (99) 87- 94 (91)	
Mouth overall	Males	68- 80 (76)	61- 72 (66)	Type 64	58- 67 (62)
	Females	68- 80 (73)	55- 69 (62)	60- 69 (66) 54- 67 (60)	
Mandible length	Males	80- 91 (85)	79- 92 (84)	Type 84	73- 90 (83)
	Females	77- 88 (84)	70- 85 (79)	69- 91 (85) 76- 98 (84)	
Upper-lip symphysis	Males	15- 21 (17)	13- 21 (16)	Type 15	11- 20 (15)
	Females	16- 20 (18)	13- 20 (16)	13- 16 (15) 12- 15 (13)	

occurrence of the species is attributable to downward flushing, rather than any upstream wandering.

In the variety of springs, outflow irrigation ditches, arroyos, and the main (upper) Río Verde, where this species has been collected, the water was described as clear but often easily roiled; the vegetation as algae (often the only plant), water lily, a long-leaved submergent, *Scirpus*, water hyacinth, and *Chara*; the bottom as sand, gravel, rocks, and sparse boulders, marl, and silt (deep mud rarely); depth of capture as rarely over 1 m, often somewhat less; and the current as varying from very slight to moderate, rarely swift. The creeks inhabited had attained widths of 10–12 m; in the lower Río Verde up to 50 m. Temperatures in the springs and spring-fed areas were warm, varying approximately from 26° to 29°.

Associated fishes are those listed under the account of *Dionda mandibularis* (p. 287), with the addition of two exotic species that have very recently (since 1970) gained access to the outflow ditches leading from La Media Luna to the Río Verde: *Gambusia panuco* and *Tilapia aurea* (Steindachner).

LIFE HISTORY NOTE

That *Dionda dichroma* has a protracted breeding season, perhaps from late winter to fall, is suggested by the occurrence of young fish and of nuptial males coexisting with females having ripe or ripening eggs. Because some habitats are in warm springs or outflows that are of higher than ambient temperatures, the spawning period may last longer in these habitats than in the streams. The collection of a 13-mm specimen (UMMZ 193448) on November 25, and of another (UMMZ 172195) 16 mm long, on March 19, suggests reproduction from late autumn until late winter.

Derivation of Name: *di-*, combining form of Greek origin signifying twice or double ($\delta\iota\varsigma$, two), and $\chi\rho\omicron\mu\alpha$ (*chroma*), skin or color, regarded as in adjectival, declinable form.

Dionda ipni (Alvarez and Navarro) Figures 5C–D, 12

Hybognathus rasconis (misidentification).—Meek, 1904: xxix, xxxvi, 50 (in part; “Forlon [in part] and Valles” records only).

Dionda rasconis.—De Buen, 1940: 22 (in part; references and records, from basin of Río Pánuco at Forlón and Valles, after Meek). Hubbs and Brown, 1956: 73 (in part; “*Notropis ipni*” erroneously regarded as “a southern race”). Darnell, 1962: 323–324 (in part; reference to Meek’s Río Pánuco records; records from Río Tamesí drainage system, with remarks on habitat and food; males nuptial on 21 December).

Hybognathus episcopus (misidentification).—Regan, 1906–08: 150–151 (reference to *Hybognathus rasconis*, in part, but not record from Río Verde in San Luis Potosí). Alvarez, 1950: 49 (in part, in key; “norte de México”).

Notropis ipni.—Alvarez and Navarro, 1953: 5–8, Fig. 1 (original description; “río Grande de Metztitlán . . . en la cuenca del Pánuco”—“un afluente del río Ama que es tributario del Moctezuma”; inclusion in *Notropis* “indudable”; compared with *N. braytoni* Jordan and Evermann and *N. boucardi* (Günther). De Buen, 1956: 539 (Mexican species of *Notropis* compared). Cortés, 1968: 191 (compared with *N. imeldae* Cortés). Alvarez, 1970: 62 (characters in key; “río y laguna de Metztitlán, Hgo.”).

Dionda ipni.—Hubbs and Miller, 1974: 4, 7, 8, 12–13, 15 (paratypes studied; *Hybognathus rasconis* Meek from Forlón in part as synonym; compared with *D. rasconis* in respect to habitat, characters, and distribution; occurrence with *ipni* in ríos Tamesí and Pánuco, but occurrence alone in ríos Tuxpan, Czones, Tecolutla, and Nautla). Contreras-Balderas and Verduzco-Martínez, 1977: (“senso Hubbs y Miller, 1974”).

Synonymy, Nomenclature, and History.—The designation of this sharply distinct species as *Hybognathus* or *Dionda rasconis*, following the early erroneous conclusion by Hubbs and Gordon (MS) that it should be treated as a subspecies of *Dionda rasconis*, we have now rectified (Hubbs and Miller, 1974). With still newer

and more complete information now available, it has become clearly evident that the true *Dionda rasconis*, having a separate intermontane range farther west in the Río Pánuco drainage system, is trenchantly distinct from *Dionda ipni*, which ranges almost exclusively over the coastal plain of the Tamesí-Pánuco drainage system, and thence southward not exclusively on the plain. The discovery that *Dionda rasconis* has a maxillary barbel led us to regard it as specifically distinct, and this conclusion has now been abundantly verified by the finding of many other clear-cut differences (see Analytical Comparison). A careful study of six paratopotypes and additional topotypes (Fig. 12) led us to conclude that *Notropis ipni* Alvarez and Navarro may be regarded as specifically inseparable from the supposed coastal-plain subspecies of "*Dionda rasconis*." Thus the name *Dionda ipni* becomes available for one of the two coastwise forms.

The nomenclatural history of this distinct species of *Dionda* has been extensively complicated. It was long confounded by us and other students of Mexican freshwater fishes (largely in manuscript) with *Dionda rasconis*, or was treated as a distinct, never formally named, subspecies of that species, primarily on the basis of the usually higher number of anal rays (Table 4). Meek (1904: xxxvi, 50) confounded it (and also *D. erimyzonops*) in part with *D. rasconis*, and Regan (1906-08: 150-151) even failed to distinguish any of those species from the trenchantly different "*Hybognathus*" *episcopus* of more northern waters. Only very recently did we discover that the true *rasconis* differs sharply from all other forms of *Dionda* in usually having a small maxillary barbel, and we now find that in this and many other features *rasconis*, along with four other east Mexican species that we assign to *Dionda*, is specifically distinct from *D. ipni*, as well as from all others referred to *Dionda*. We have found, as was noted by Hubbs and Miller (1974: 4, 7) through an examination of six of the paratypes, that "*Notropis*" *ipni* was based on this distinctive southern form of *Dionda*, which, in the lack of any prior published name, may be called *Dionda ipni*. Examination of the viscera of one of the six paratypes kindly furnished by Dr. Alvarez showed the coiled intestine clearly. The original description of *Dionda ipni* gives the ray number as "D 9-10; A 12-14"; but the six paratypes at hand yield lower counts—dorsal, 8 (5), 9 (1); anal, 10 (3), 11 (3), using the standard count for cyprinoids of principal rays only, with the last one treated as double. Obviously the describers of "*Notropis*" *ipni* included rudimentary anterior rays and (or) counted the last ray unconventionally as 2. A series of 45 topotypes (UMMZ 196682) has 7-9 dorsal rays, mean 8.11, and 10-12 anal rays, mean 10.53 (Tables 3 and 4). The type specimens came from a section of the Río Pánuco system where the water seemingly has little or no present surface-flow connection with the Pánuco, but we suspect surface connection either in flood or in very recent geological time, and find no basis for the specific separation of the population represented by the types of *Notropis ipni*.

Diagnosis.—Barbel lacking. Anterodorsal contour strongly arched. Anal rays (usually 9 in Tamesí drainage and 10 and 11 in Metztitán drainage). Anal base normally more than two-thirds as long as caudal peduncle. Head depth more than one-fifth standard length. Dorsal contour behind dorsal fin nearly straight and horizontal. Inner grooves of lower lips only about as long as the anterior interspace. Scales large (usually 33 or 34 in lateral line). Nuptial males with very strong tubercles, one per scale, forming horizontal lines along scale rows above lateral line, and with a large, bold black blotch on each fin (Fig. 5C).

Material examined.—The material of *Dionda ipni* as studied is listed under major stream systems and states from north to south; then under each system, by serial catalog number in each museum. Except as otherwise indicated, all material is deposited in the Museum of Zoology, The University of Michigan (UMMZ).

Río Tamesí system, Tamaulipas.—97455, tributary of Río Guayalejo 26 km N of Xicotencatl (4 specimens: 34–37 mm SL); 97456, Arroyo de las Animas, 32 km S of Limón (16: 15–35); 164733, Arroyo del Encino at Encino (26: 8–16); 167451, Río Sabinas, 8 km NE of Gómez Farías (28: 20–34); 192501, Río Guayalejo at Llera (14: 24–38); 192894, Río Boquilla ca. 19 km W of Limón (46: 17–30). FMNH 4477, Río Forlón at Forlón (11: 30–34).

Río Pánuco system, San Luis Potosí.—97457, Río Valles at Valles (5: 14–27); 124329 and 162140, Arroyo Palitla at Palitla, 8 km N of Tamazunchale (52: 14–43 and 8: 27–36); 12433, Río Matlapa, 21 km N of Tamazunchale (1: 41); 124345, Arroyo Plan de Jalpilla, 29 km N of Tamazunchale (14: 22–34); 124358, Río Axtla at Axtla (2: 20–24); 164708, Río Moctezuma at Tamazunchale (116: 20–44). Veracruz.—97458, Río de los Hules, 18 km SW of Tantoyuca (14: 15–25); 97459, junction of Río de los Hules and Río Calaboza, 14 km SW of Tantoyuca (44: 14–30). Veracruz-Hidalgo boundary.—97460–61, tributary to Río Calaboza at Chapapoti, 32 km S of Tantoyuca (124: 13–43). Hidalgo.—172496, Río de Metztlán at Barranca de Venados (6 paratypes of *N. ipni*, 21–32); 196682, Río Venados (= Metztlán), 0.5 km below Puente Venado (46 topotypes, 17–64); 196685, Río Amasa, 10 km W of Huejutla (163: 14–47).

Río Tuxpan system, Veracruz.—167520, stream in drainage basin of Río Pantepec, 6 km N of Alamo (1: 15); 193502, tributary to or distributary from Río Lasán, 3 km NW of Potrero de Llano (177: 20–55). Hidalgo.—ENCB 3631, Río Baltrán at San Bartolo Tutotepec (3: 44, 70, 74).

Río Czones system, Puebla.—97464, tributary to Río Czones near Agua Fria, 19 km S of Miahuapán (2: 14–24); 97465–66, Río San Marcos (or tributary near Huilota (15: 26–35); 193492, tributary to Río San Marcos, 42 km WSW of Poza Rica (95: 34–52). Río Tecolutla system, Puebla.—124302, Río Necaxa at La Mesa (= Necaxa) (1: 30); 124307–08, Vaso de Necaxa at La Mesa (10: 17–27).

Río Nautla system, Veracruz.—167490, stream 6 km W of Martínez de la Torre (3: 35–38).

Río Misantla, Veracruz.—ENCB 1312, at Misantla (10: 21–32).

DESCRIPTION

Size and Form.—This medium-sized minnow is definitely larger than *Dionda erimyzonops* (the largest specimen examined is 74 vs 39 mm SL, and the smallest fully nuptial male measures 31 vs 21 mm). The dorsal contour is strongly convex predorsally, especially in males, in which the contour rises about an orbit length above a line from dorsal-fin origin to top of orbit. The dorsal contour is much more curved than the ventral: the greatest distance below a line from midcaudal base to tip of snout is only slightly more than two-thirds the greatest distance to the dorsal contour. Before the occiput the dorsal contour slopes rather steeply and before the nostrils descends rather abruptly (but on a more even curve and at a less steep angle than in *erimyzonops*, not approaching verticality just above the mouth). The contour of the snout before the nostrils forms an angle of only about 50° with the line from midcaudal base to snout tip. The dorsal contour becomes nearly horizontal just before the origin of the dorsal fin, but along the base of that fin drops at an angle of about 20°; behind the dorsal fin the contour extends in an essentially straight, subhorizontal line to the upper caudal base. The ventral contour is gently and rather evenly curved to the front of the anal fin, behind which it rises rather sharply to the front of the caudal peduncle, the lower border of which ascends very gently and in a nearly straight line. The lateral profile before the nostrils forms an angle of about 75° with the body axis. Commonly the tip of the snout somewhat sharply overhangs the rather thick and smoothly swollen, nonplicate, upper lip, or the two may be coterminous. The top of the upper lip is lower than in *erimyzonops*, horizontally even with or slightly lower

than the bottom of the orbit. The roughly semicircular mouth is completely overhung by the upper lip. Very characteristically, the inner grooves of the very short lower lips converge very slightly forward, do not reach nearly to the front of the mouth, and are separated anteriorly, as in *catostomops*, by a very wide space, which in the adult is approximately as wide as either groove is long. In *dichroma*, on the other hand, each groove is about 1.5 times as long as the anterior interspace, whereas in *erimyzonops* and *rasconis* each is about twice as long as the anterior interspace, and in *mandibularis* they are about 3 to 5 times as long. The concealed end of the maxilla lies below the interval between the posterior nostril and the orbit. The mandible reaches somewhat behind a vertical from the front of the pupil. The posterior border of the orbit is approximately half of the ocular length nearer to edge of the opercular membrane than to tip of snout.

Proportional Measurements (Table 12).—The eye is definitely smaller proportionally than in *erimyzonops*: the orbit length is very much less than the least interorbital width and is much shorter than the postorbital length.

Barbel.—No trace of a maxillary barbel was found on any of the many specimens examined from various localities. One hundred specimens in a single collection (UMMZ 193502, from the Rio Lasan basin) were carefully examined on each side, but not a single barbel or rudiment was discerned.

Gill-rakers.—The rakers are much reduced, about as in related species. Counts through the coastal-plain range are 1-2 + 3-7 on the first arch and 2-3 + 11-14 on the second arch (Table 8).

Pharyngeal Arch and Teeth.—The lower limb of the pharyngeal arch of *ipni* is moderately heavy, nearly straight, and widest near its distal end; it is longer than the upper limb, which is short, thick, and well curved, and is somewhat expanded and keeled (ventrally) before its blunt tip (Fig. 3C-D).

The four teeth are well hooked and each of the three uppermost bears a moderate to well-developed, spatulate grinding surface, which may be obsolete on the lowermost tooth; the uppermost tooth is strongly elevated above the shaft. In the one variant seen with 5 teeth on the left arch, the increase from 4 is at the uppermost end, where two small teeth are closely appressed.

Intestine.—As seen in specimens from different localities, the intestine from the right side forms three main loops, of which the anterior two are tighter than the third but hardly semicircular. The peritoneum is black over the usual silvery base.

Fins.—The dorsal fin originates slightly behind or slightly before the pelvic insertion; its tip is broadly rounded and its rear edge at normal expansion of the fin is straight or weakly convex and approximately vertical; when the fin is depressed, its longest ray reaches well beyond the tip of the last ray. The anal has a rounded tip, a concave rear margin, and, when the fin is depressed, its longest ray falls short of the tip of the last ray in nuptial males, but reaches from not quite, to a little beyond, the tip of the last ray in females. The pectoral fin in the female falls short of reaching the pelvic insertion by about an orbit length; in mature males it is notably wide and horizontal, but, when depressed it barely reaches the pelvic insertion, or fails to do so by as much as a pupil length. The pelvic fin in mature females just about reaches the anal origin, or passes well beyond that point, as it usually does in adult males.

The anal rays (Table 4) are more numerous than in any other species referred to *Dionda*, but the usual number ranges regionally from a low of 9 to a high of 10 or 11 (as is mentioned below under Variation). The dorsal and pelvic counts (Table 3) are each usually 8, and the caudal count seldom deviates from the family standard of $10 + 9 = 19$. The pectoral count, in probable correlation with the large size and wide spread of the fin, averages moderately higher than in any of the other species here treated, more than 2 rays higher than in *erimyzonops*.

TABLE 12. Proportional measurements (permillage of SL) of adults of *Dionda ipni*: indicating range, (mean), and number.

	Río Venados Topotypes UMMZ 196682	Río Lasán Tuxpan System UMMZ 193502	Río Beltrán Tuxpan System ENCB 3631	Trib., R. San Marcos Cazones System UMMZ 193492
Standard length, mm				
Nuptial males	55.4-63.3 (60.4) 3	38.3-53.4 (44.6) 10	68.1-73.7 (70.9) 2	45.9-52.0 (48.8) 6
Prenuptial males	40.6-47.4 (43.3) 4	-	-	39.9-46.9 (45.0) 6
Mature females	43.5-48.2 (45.9) 3	34.5-39.4 (36.9) 10	44.3 (one)	40.2-48.1 (42.2) 11
Body depth				
Nuptial males	295-317 (303)	279-305 (293)	278-308 (293)	269-315 (294)
Prenuptial males	271-304 (281)	-	-	283-329 (309)
Mature females	297-320 (303)	271-299 (282)	269 (one)	284-306 (293)
C-peduncle depth				
Nuptial males	125-130 (128)	121-140 (132)	134-137 (135)	123-135 (129)
Prenuptial males	115-131 (124)	-	-	121-136 (131)
Mature females	106-118 (111)	116-126 (121)	122 (one)	115-126 (120)
C-peduncle length				
Nuptial males	149-172 (164)	177-214 (190)	170-192 (181)	184-206 (193)
Prenuptial males	182-194 (189)	-	-	192-214 (202)
Mature females	163-182 (175)	171-200 (192)	182 (one)	187-202 (195)
A origin to C base				
Nuptial males	355-371 (363)	351-386 (365)	353-374 (363)	350-379 (361)
Prenuptial males	349-362 (355)	-	-	342-372 (358)
Mature females	322-325 (324)	316-341 (328)	331 (one)	324-348 (333)
Predorsal length				
Nuptial males	527-533 (531)	518-539 (526)	498-520 (509)	512-537 (525)
Prenuptial males	530-545 (535)	-	-	531-556 (537)
Mature females	531-584 (556)	510-566 (533)	524 (one)	526-547 (533)
Depressed D fin				
Nuptial males	230-244 (240)	242-271 (253)	236-246 (241)	234-253 (242)
Prenuptial males	239-260 (250)	-	-	243-259 (250)
Mature females	229-241 (237)	229-247 (241)	246 (one)	220-257 (241)
A-fin base				
Nuptial males	195-213 (202)	172-195 (180)	182-189 (185)	167-187 (176)
Prenuptial males	157-173 (167)	-	-	145-169 (160)
Mature females	148-163 (155)	126-150 (141)	144 (one)	133-162 (144)
P ₁ -fin length				
Nuptial males	210-227 (216)	215-243 (230)	242-244 (243)	207-229 (218)
Prenuptial males	202-222 (215)	-	-	204-224 (213)
Mature females	193-198 (196)	192-207 (201)	205 (one)	192-243 (230)
Lateral line to D origin				
Nuptial males	164-174 (170)	140-165 (152)	174-189 (181)	156-187 (169)
Prenuptial males	156-169 (160)	-	-	163-187 (175)
Mature females	146-161 (155)	162-183 (172)	153 (one)	140-165 (152)

Lateral line to P₂ insertion

Nuptial males	127-141 (134)	120-144 (137)	129-131 (130)	119-140 (128)
Pre-nuptial males	112-133 (123)	-	-	128-146 (137)
Mature females	133-147 (142)	105-130 (118)	123 (one)	120-144 (137)
Head length				
Nuptial males	279-289 (285)	273-294 (282)	286-288 (287)	269-284 (279)
Pre-nuptial males	268-287 (276)	-	-	275-290 (283)
Mature females	261-285 (272)	267-296 (276)	275 (one)	263-282 (276)
Head depth				
Nuptial males	213-219 (216)	208-229 (221)	214-233 (223)	216-223 (219)
Pre-nuptial males	196-211 (205)	-	-	202-226 (216)
Mature females	195-203 (199)	195-216 (203)	186 (one)	199-219 (209)
Head width				
Nuptial males	166-181 (173)	175-176 (176)	144-162 (154)	160-173 (166)
Pre-nuptial males	148-156 (151)	-	-	147-168 (156)
Mature females	148-170 (163)	149 (one)	149 (one)	147-162 (154)
Snout length				
Nuptial males	101-103 (102)	92-105 (98)	102-104 (103)	84- 96 (92)
Pre-nuptial males	94- 97 (95)	-	-	88- 98 (94)
Mature females	92-100 (95)	84-101 (91)	91 (one)	85- 97 (91)
Orbit length				
Nuptial males	57- 61 (59)	71- 87 (78)	52- 59 (55)	75- 82 (77)
Pre-nuptial males	64- 70 (67)	-	-	77- 84 (81)
Mature females	61- 74 (66)	84- 97 (88)	71 (one)	78- 89 (83)
Upper-jaw length				
Nuptial males	74- 81 (78)	74- 88 (78)	73- 82 (77)	77- 82 (79)
Pre-nuptial males	76- 80 (78)	-	-	74- 84 (79)
Mature females	73- 84 (79)	71- 85 (75)	71 (one)	74- 85 (78)
Suborbital width				
Nuptial males	49- 53 (51)	42- 51 (47)	44- 53 (49)	40- 47 (43)
Pre-nuptial males	41- 46 (44)	-	-	38- 46 (42)
Mature females	44- 48 (46)	37- 48 (44)	43 (one)	37- 43 (40)
Least interorbital width				
Nuptial males	104-112 (108)	98-108 (103)	103-105 (104)	102-106 (104)
Pre-nuptial males	108-115 (112)	-	-	99-110 (106)
Mature females	103-113 (107)	92-101 (95)	96 (one)	99-113 (103)
Mouth overall				
Nuptial males	90- 97 (93)	74- 85 (79)	90- 94 (92)	82- 88 (84)
Pre-nuptial males	81- 87 (85)	-	-	75- 84 (79)
Mature females	81- 92 (86)	67- 81 (75)	80 (one)	72- 86 (78)
Mandible length				
Nuptial males	84- 94 (89)	76- 95 (88)	90- 95 (93)	85- 89 (87)
Pre-nuptial males	87- 95 (91)	-	-	85- 95 (90)
Mature females	73- 90 (80)	81- 94 (89)	82 (one)	90-101 (94)
Upper-lip symphysis				
Nuptial males	22- 23 (23)	19- 23 (21)	20- 22 (21)	20- 23 (21)
Pre-nuptial males	15- 23 (18)	-	-	17- 25 (21)
Mature females	17- 21 (20)	16- 24 (20)	17 (one)	16- 23 (20)

Scales.—The scales, much like those of *erimyzonops* (Hubbs and Miller, 1974: 12), are broadly exposed. The far-anterior scales along and just below the lateral line have the exposed field about twice as high as long. The seriation is relatively even, as is well shown by the regular, horizontal alignment of the large tubercles, one per scale, in nuptial males (Fig. 5C). The lateral-line pores, most noticeably anteriorly, open in advance of the scale margin. On a single scale the ridges are not sharply angulated, are moderately and rather evenly spaced, and rather regularly cross the radii.

The lateral-line scales (Table 5) usually number only 33 or 34, average fewer than in *rasconis* and somewhat more than in *erimyzonops*, and except in a single specimen out of 135 counted are invariably fewer than any of our counts for any specimen of *mandibularis*, *catostomops*, or *dichroma*. The scales around the body generally average somewhat more than in *erimyzonops*, but rather fewer than in the other species (Table 6); at the slenderest part of the caudal peduncle 3 scale rows usually intervene between the lateral-line and the middorsal series, as in *rasconis*, rather than only 2 as in *erimyzonops*, although as in that species also, alone in the whole group, only 2 rows are aligned between the lateral-line series and the midventral row. In general, the scale counts in the various series run somewhat greater than in *erimyzonops*, but usually fewer than in the other species.

Vertebrae.—The vertebral counts (Table 7), with a trace of regional fluctuation, average somewhat more than in *erimyzonops*, somewhat fewer than in *mandibularis* and *rasconis*, and definitely fewer than in *catostomops* and *dichroma*, with little overlap.

Sensory Canals of Head.—The sensory canals of the lateral-line system on the head (Figs. 6–7) are less subject to multiple abnormalities in *ipni* than in some of the other species under treatment. All canals were checked on more than 30 specimens (UMMZ 193492, from a tributary to Río San Marcos), with some duplication for the paired canals. The preoperculomandibular canal is complete and regular in all 32 examined. The infraorbital canal is complete and essentially regular in 30 examined, with a strong upward hook or spur on the temporal section in 2, and is inextricably broken up in that section in 1. The supratemporal canal is complete (continuing across the middorsal line) in 14 specimens, almost complete in 5, very narrow in 3, narrow in 8, and moderately narrow in 1; there is a median dorsal pore in the 12 counted, among which the canal is complete in 9 and interrupted medially in 3.

The major fluctuations and abnormalities involve the anterior, preorbital end of the supraorbital canal, in large part in association with either the upper-anterior, essentially horizontal part, also called the “temporal canal,” of the infraorbital canal, or with the supratemporal canal. In 28 specimens (or sides), the essentially straight and blind end of the infraorbital canal extends backward over the frontal bone, with very limited deviation from a straight course, very nearly to, just to, or slightly beyond, the frontoparietal suture. There is almost no approach to the strong curvature(s) of the canal, or to the forward extension of the canal well beyond the suture, that was seen in the Santa Catarina variant of *dichroma* (p. 312). In 10 additional specimens (or sides) there are various interruptions, disruptions, branchings, and irregularities in the same area; and in one, hardly any trace of the normal tube pattern remains.

Coloration.—The sexual differences in coloration are far more extreme in *Dionda ipni* than in any of the other species here treated, perhaps among the most extreme among any American cyprinids. In the young and females the boldest marking is a dark lateral stripe, which is jet-black on the body. This stripe may be either fully connected with, or largely disrupted from, the round or oblong jet-black basicaudal spot. On the head the stripe is continued, angled downward.

It is usually jet-black over most of the area where it crosses the opercle, but is generally disrupted just back of the eye. The stripe is hardly suggested on the iris, the upper part of which is rather uniformly punctate. It is continued, sloping sharply downward, on the side of the snout below the nostrils, but does not round the snout tip; in general it lies over the lateral line, but is usually separated therefrom near the middle of the trunk, where the lateral line is most decurved. On the anterior part of the trunk black speckling is incipient beside the lateral-line pores. Above the stripe the back is almost uniformly darkened, although commonly a narrow dusky streak runs just above and parallel with the stripe, fading on the caudal peduncle. The weak and narrow middorsal dusky streak is especially faint and diffuse before the dorsal fin, behind which it is moderately strong in some individuals. This streak does not continue as a definite border on the body along the sides of the dorsal-fin base as it does in *rasconis*, but the highly characteristic blackish mark on the base of the dorsal fin is diffusely expanded onto the adjacent back. Except for the conspicuous row of deep-lying black specks at the extreme base of the main anal rays, the entire body below the black streak is silvery, and devoid of melanophores. On the head below the stripe the dark speckling is almost entirely restricted to the rim just below the orbit and to the sides and front of the upper lip. The fins are almost entirely clear, except for the dorsal-fin base, for rows or specks along the anterior dorsal rays and along the caudal rays (particularly beyond the basicaudal spot), and for a slight speckling along the outer rim of the pectoral fin.

Gradually, as the males mature, the pigmentation becomes rather fantastically transformed (Fig. 5C-D). The whole back above the lateral line, and most of the head, become almost black, and irregular dusky bars often extend across most of the side. Much of the upper pectoral base is jet-black at the lower end of the sooty border of the shoulder girdle. The black speckling at the base of the anal fin is intensified and expanded. The black streaks on the median caudal rays are also intensified. Near the middle of the base of the dorsal, pectoral, and pelvic fins, and more toward the base on the anal, there develops on the otherwise clear fins a large jet-black blotch or bar, and a similar blotch is often developed also on each lobe of the caudal fin, which elsewhere is not as conspicuously clear as the other fins.

Color in Life.—In mid-December 1972, when nuptial males were observed in streams of the Río Tuxpan and Río Czones systems (UMMZ 193492 and 193502), the fins were seen to vary from yellow-brown to amber to pinkish tan; at one site the top of the head was metallic green. In all these males intense and broad blackish brown bars had developed along the middle of each of the fins, and were outstandingly conspicuous on the pectorals.

Nuptial Tubercles.—The nuptial tuberculation of the males of *ipni* (Fig. 5C) provides, along with the unique nuptial coloration (just described), an impressive body of evidence indicating the distinctness of *ipni* from *rasconis* as well as from *erimyzonops*.

The following account of high nuptial tuberculation is based on the following specimens: 3 topotypes 55–63 mm long from Río Venados (UMMZ 196682); 2 from Río Beltrán, of the Río Tuxpan system (ENCB 3631); 66, 35–55 mm, collected on a breeding riffle in a tributary to Río San Marcos of the Río Czones system (UMMZ 193502, one of which is illustrated in Fig. 5C); 17, 45–52 mm, from a breeding riffle in a tributary to Río Lasán of the Río Tuxpan system (UMMZ 164708); and 1, 37 mm, from a tributary of Río Guayalejo of the Río Tamesí system (UMMZ 97455). Our study has been supplemented by an examination of subnuptial males from these and other localities. It may be concluded that the nuptial characters are not only highly distinctive but also consistent throughout the relatively long range of *ipni*.

The largest of the many tubercles, none however half as wide at the base as the pupil, extend from the occipital line to between the anterior nostrils and from the side of the snout backward normally at least to below the front part of the eye; a few very commonly extending somewhat farther back, occasionally, scattering, as far as the front margin of the preopercle. Those on the top of the head are usually separated by a space exceeding one of the basal diameters, whereas the larger ones on the side of the snout are commonly closer together than one basal width. The lateralmost of the dorsal tubercles on the head uniserially closely follow the upper margin of the orbit and continue downward anteriorly to opposite the middle of the posterior nostril, whence a short gap separates this series from a similar file close to the anterolateral part of the orbit. A partly to wholly naked area broken by at most a very few tubercles crosses the snout in a broad band from directly between to just in advance of the anterior nostrils, and is connected with a generally smooth area about as large as the pupil on the front midline of the snout. Ordinarily only a few tubercles invade these connected smooth areas. There are no tubercles whatever on or between the mandibles, or on the following intergular area.

The most conspicuous tubercles on the body are, diagnostically, usually located one per scale, subcentrally, but often two on the scales of the lateral-line row on the urosome and, not rarely, on the adjoining scale row above. As the scale rows are quite regular, so also are the series of these enlarged body tubercles. The tubercles on the body scales become smaller upward, and are minute across the back between the dorsal and caudal fins. The regular seriation of large tubercles, single per scale, continues on rows on the trunk above the lateral line, often with a small supplementary spinelet, but the regular pattern disappears in the elongate triangle on the nape between the occiput and the front of the dorsal fin. On the trunk the tubercles abruptly and almost completely terminate downward at the lateral line, except, often, for a few above the pelvic fin. Posteriorly, a single row of strong tubercles, supplemented by some smaller ones, extends along the series of scales just below the lateral-line row, becoming irregular toward the caudal fin. Just above the somewhat elongate anal-fin base, in a rather conspicuous and diagnostic band, the tubercles increase in number and size over a very rough and swollen surface. To a slight degree the tuberculation tends to be similarly modified on the lower part of the caudal peduncle, but the ventral edge of the peduncle is nearly smooth.

On the fins the nuptial tubercles, as though in compensation for their high development on the head and body, tend toward obsolescence. On the pectoral a few small to extremely minute slender ones are discernable in some specimens in a single row mostly toward the base of the very fleshy outermost ray. At high development, the edge of a thickened interradiial and hardened structure between the first and second rays bears a file of minute slender spinelets, and some also appear on the second interradiial structure. On most subsequent strengthened rays rather small hooklets form one row branching once; occasionally, on the second interradiial space, with some secondary bifurcation. On the pelvic fin the tubercles, also branching once distally, are obsolete or obsolescent on the outer ray and very weak on the subsequent rays. On the anal fin the arrangement is similar except that the single branching is more median. On the caudal fin the extremely weak tuberculation is virtually confined to the edge of the upper rudimentary rays. On the dorsal fin the thickened front edge may be sparsely studded basally with minute spinelets, and extremely weak ones, branching once submedially, form a basal band on a few following rays.

On breeding females a bare trace of slender tubercles may be discerned on the top of the head and on the snout.

Urogenital papilla.—Adult females have a very distinctive and enlarged urogenital papilla that overlaps the first short anal ray. It fills the large recess in front of the anal fin so fully as to project prominently into the ventral contour of the belly, by forcing outward the margining scales. The papilla bears a pair of lateral flaps near its tip, and the anus opens on the front margin beyond the middle of the papilla, which has a rather sharp edge on each outer-posterior flap.

The papilla of males is very much smaller, relatively round and almost sunk in the preanal depression, just behind the scales and rather far from the anal-fin origin.

SEXUAL DIMORPHISM

Nuptial males become different from young and females in some other respects. The body becomes more compressed and the peduncle usually deepens. The anal fin enlarges, so that the urosome (measured as the distance from the anal-fin origin to the caudal-fin base) tends to measure consistently more instead of less than 35% of the standard length (Table 12). In contrast, as though in compensation, the anterior parts, as measured by the predorsal length, usually shorten proportionately. The distance from the lateral line to the pelvic-fin insertion on the average becomes less. The males, although they mature at a small size (see above), attain a larger size than the females. Because the ratio of lengths, caudal peduncle / anal base, tends toward lower values with increasing size (Table 9), and because males often attain a larger size, the anal base tends to be proportionately longer in males (Fig. 12). The larger size of the males is indicated by the length of the larger specimens of each sex that were picked out for the tabulation of proportional measurements (Table 12).



Figure 12. Low nuptial male (62.6 mm SL) and female (48.0 mm) topotypes of *Dionda ipni* (UMMZ 196682), from Rio Venados, Hidalgo.

A particularly striking difference between mature males and females lies in the increasing robustness of the fin rays in the maturing males, as well as in the intense black blotching of all the fins in the males only (Fig. 5C-D). In high males the pectorals are especially expanded transversely and the outer rays thicken notably.

VARIATION

In addition to being outstandingly and consistently distinct in unusually many characters, *Dionda ipni* displays some local differentiation over its unusually broad geographic and ecologic range. The local variation in number of anal rays (Table 4) in *ipni* exceeds that of *dichroma* and very much exceeds that of any of the other species. The number is preponderantly 9 in the Tamesí drainage system, but 10 in the basally conjoined Pánuco system. Coastwise southward the mean number in the successive stream systems seems to gradually decrease (from 10.53 to 9.30). In the presently seemingly disjunct type locality, which is mapped (Fig. 1) as lying nearer the 2,000 m than the 1,000 m contour (probably near 1,700 m), the number of rays is uniquely high: 10-12, predominantly 10 or 11, and the mean is 10.53 (Table 4).

On comparing the two largest series, respectively from Río Lasán of the Río Tuxpan system (UMMZ 193502) and from a tributary of Río San Marcos of the Río Cazonés system (UMMZ 193492), several differences are noted. The lateral-line scale counts for 21 specimens from each of these two stations are, respectively, 32-34 (mean 32.57), and 33-35 (mean 33.95). The basicaudal spot is definitely the more sharply distinct and the rounder in the San Marcos series, in the females as well as in the breeding males. The black blotches on the fins of the nuptial males average larger, and the blotch on the pelvic fin is more consistently strong, in the Río Lasán set. However, the highest male from Río San Marcos has the fin blotches extremely well developed (Fig. 5C). The mark on the pelvic fin in the San Marcos series tends to be a cross band on each fin whereas in the Río Lasán lot it tends to be a roundish median spot.

DISTRIBUTION, HABITAT, AND ASSOCIATED SPECIES

Dionda ipni is known to occupy various streams in east-central México (Fig. 1), from the Tamesí-Pánuco complex southward almost to the stretch of mountainous, volcanic coastline north of Veracruz, where the eastern margin of the high Mexican Plateau very closely approaches and slopes steeply to the coastline of the Gulf of Mexico. That coastal area has, very understandably, served as a major barrier, on the Atlantic slope, to the southward extension of the Nearctic fluvial fauna and to the northward spread of the tropical freshwater fauna. This species occurs farther south than any other known cyprinoid in the tropical Atlantic drainage, the lowland *Ictiobus meridionalis* excepted. That species, like *Aplodinotus grunniens* and, especially, *Lepisosteus tropicus*, may be ancient relicts. A few other cyprinids live farther south on the Mexican Plateau and in mountain headwaters of a few streams, on both the Pacific and Atlantic sides. *D. ipni* seems to be largely confined in the northern part of its range to the western edge of the coastal plain, which it shares with *erimyzonops* and two species of *Notropis*, namely *N. lutrensis forlonensis* and *N. tropicus* Hubbs and Miller, 1975, leaving the upland part of the Río Pánuco system to *Dionda rasconis* and *D. catostomops* in the Río Gallinas basin, and to *D. mandibularis* and *D. dichroma* in the Río Verde basin.

In the more southern part of its long latitudinal range *ipni* seems to occur, as might have been expected, more inland and at elevations higher than the coastal plain. Thus it occupies the relatively high Río Metztitlán (approaching 1,700 m),

far from the coastal plain, in the extreme southwestern extent of the Río Pánuco system, where the connection with that system is said to be by percolation (Alvarez and Navarro, 1953, and Alvarez, 1970: 62). In the shorter, coastwise streams south of the Río Pánuco complex, at least in the drainage basins of five relatively small rivers (Tuxpán, Cazones, Tecolutla, Nautla, and Misantla), *ipni* is the only known cyprinoid, and it seems to be largely limited to the elevations somewhat above the coastal plain proper; in the Río Tuxpan drainage basin it occurs at least as high as 600 m.

On tallying some habitat features from the field records for specimens listed above, we note that they were collected predominantly where the water was clear; the vegetation variable, but generally rather slight or even lacking, and not rarely consisting of algae; the current about as often slight as rapid; and the bottom variable, but usually at least partly firm, of sand, gravel, rocks, or boulders. As is noted below, nuptial males have been seen congregated on rocky riffles.

LIFE HISTORY NOTES

On two consecutive rainy days in mid-December, 1972, very brief observations were made of the pre-spawning behavior of nuptial males of *D. ipni* in the basins of Río Cazones and Río Tuxpán (UMMZ 193492 and 193502). Temperatures varied between 16.7° and 19.4° in the water and 10.6° and 16.7° in the air. At each station nuptial males congregated on and near the clear, rocky riffles that separate the pools, where presumably the females were concealed. The males faced upstream near midwater or rather close to the bottom, swimming against the moderate current. Attention was immediately drawn to the more active and brighter of these individuals by a characteristic behavior. This involved intermittent, lateral (almost jerky) flicking of the pectoral fins in an almost horizontal plane, thus flashing the dark markings so prominent on these fins. The pectorals are especially large and strong (typically with 15 rays) for such a small fish, evidently as an adaptation for this highly visible, signalling behavior. No young were observed or collected, although 272 specimens were preserved.

These very brief notes indicate that the reproductive behavior of this species is very distinctive and worthy of careful study. Since the males develop strong nuptial tubercles and prominent fin markings in mid-winter, the best time of year for observations would probably be during January through April. The smallest specimens in our collections from the Tamesí-Pánuco complex to the north, 8 and 13 mm SL, were collected between 17 April and 7 May, thus indicating that successful spawning had been underway for some time.

Dionda erimyzonops Hubbs and Miller

Hybognathus rasconis (misidentification).—Meek, 1904: xxxvi, 50 (Forlón record, in part).

Dionda sp.—Darnell, 1962: 324–325, 331–332 (distribution and habitat in the Río Tamesí drainage basin; associated with the similarly colored *Gambusia vittata* Hubbs). Miller and Minckley, 1970: 257 (associated species in Río Tamesí basin).

Dionda erimyzonops.—Hubbs and Miller, 1974: 1–17, Figs. 1–2 (nomenclature and history; diagnosis; generic reference; synonymy; habitat, numerical association with *D. ipni*; description; references); 1975: 129 (Río Axtla near Xilitla; associated dwarf species). Contreras-Balderas and Verduzco-Martínez, 1977: 000 (related to *D. mandibularis*; intestine *re* generic reference).

Diagnosis.—The original diagnosis (Hubbs and Miller, 1974: 5) is still applicable.

Material Examined.—No additional specimens have come to light. We find none among the extant specimens that Richard T. Gregg utilized in his never formally published doctoral thesis entitled “A Distributional Survey of the Fishes of San Luis Potosí, México” at Louisiana State University and Agricultural and

Mechanical College, dated August, 1956 (copy at hand, reproduced by University Microfilms, Inc., Ann Arbor, Michigan). He recognized in this thesis three subspecies of *Dionda rasconis*: (1) *D. r. rasconis*, based on topotypes of the species (reexamined); (2) a new subspecies based primarily on material from "Puerta del Río" (nominal type locality), La Media Luna, Guayabos, and Tanlacú (which we have reexamined and herein list as *D. dichroma*); and (3) another nominal new subspecies described from "Río Axtla at the ferry to Xilitla," with additional material "in poor condition" from Arroyo Palitla, Río Matlapa at Matlapa, and Arroyo Plan de Jalpilla. Of this third "subspecies," apparently all that remains is the nominal holotype from Río Axtla (the 25 nominal paratopotypes as well as the additional material appear to have been lost). Gregg gave the ray counts of the holotype as dorsal 9 and anal 10, but the standard counts on the specimen are those usual in *Notropis tropicus*, and the other characters are typical of that species. The other material of Gregg's third nominal subspecies of "*Dionda rasconis*," for which he gave ray counts of dorsal 9 and anal 9-11, usually 10, in all probability included *Dionda erimyzonops*. Gregg also gave the dorsal rays as 9 for the two other "subspecies."

DESCRIPTION

The only additional descriptive material that we have to add applies to:

Pharyngeal Arch and Teeth.—The lower limb of the pharyngeal arch of this small species (Fig. 3E-F) is much like that of *catostomops*: slender, nearly straight, and slightly deflected mesially at its tip; it is longer than the upper limb, which is moderately curved and moderately thick, rather short, blunt at its tip (which may be slightly recurved), and the crest on its mesial surface is elevated.

The four teeth are moderately to well hooked and their grinding surfaces, especially on the two middle teeth, are usually well developed. The two uppermost teeth are well elevated above the shaft.

MERISTIC AND MORPHOMETRIC COMPARISONS OF THE SIX SPECIES

The meristic and morphometric data acquired in the distinction of the six species of the Río Pánuco stream complex is now reviewed, for further bearing on their particular differentiation and for a more general understanding of speciation in the Cyprinidae. We discuss the meristic pattern first.

Among the fin-ray counts the least variable is that for the dorsal fin (Table 3), which is almost uniformly 8, as it is for the minnows of the Great Basin and for a large proportion of small American cyprinids (Hubbs, Miller, and Hubbs, 1974: 85-86). This number holds, with almost no exception, for the myriad species referred to *Notropis*. This consistency is truly remarkable.

The caudal rays (Table 3) hold with few exceptions to the formula of $10 + 9 = 19$, that is normal for the Cyprinidae. In a total of 254 specimens the only rare variants, in four of the six species, have 18 rays. It has generally been assumed that the number of caudal rays in the family is virtually constant, but among the cyprinids of the isolated waters of the north-central Great Basin the count has been found to range from 14 to 21, with relatively large numbers at 18 and 20 (Hubbs, Miller, and Hubbs, 1974: 86-87). The fluctuating variation in the Great Basin may well stem from isolation and very limited predation, which would not be expected in the Río Pánuco system.

In five of the six species the mean number of pectoral rays (Table 3) approximates 13, with a range from 11 or 12 to, in all five species, 15. The number is markedly increased only in *D. ipni*, which yielded a mean of 15.08 and range of

13-17. As noted on p. 323, this increased number seems to be correlated with the obvious dilation of this fin in *ipni*.

The pelvic fin (Table 3), like the dorsal, exhibits a mode of 8 in all six species, as indeed in small American cyprinids in general. Perhaps in line with the not very infrequent diminishment or even total loss of the pelvic fin in fish species in general, the count ranges downward: to 7 in one species (*ipni*), to 6 in two species (*catostomops* and *erimyzonops*), to 5 in one (*rasconis*), to 0 in one (*dichroma*); only *mandibularis* has shown no reduction below 8. The variance from a count of 8 is highly asymmetrical: in 254 counts the number was increased to 9 (and no higher) in 20; whereas the number of counts diminished to below 8 in 39, with 30 at 7, 3 at 6, 1 at 5, 3 at 4, 1 at 3, and 1 at 0.

The fluctuation in number of anal rays (Table 4) is more frequent in this group of six species. In the three most localized species, *mandibularis*, *rasconis*, and *catostomops*, however, deviations from the count of 8 are rare, and this is true also for *dichroma*, except at one nearby locality, where counts of 9 predominate. In the very restricted range of *erimyzonops*, the counts average about 9.1, but in the relatively wide-ranging *ipni* the counts fluctuate markedly in the different drainage systems, as is specified in Table 4 and outlined on p. 323.

The counts for scales in the lateral line (Table 5) are particularly distinctive, grading upward in the six species in the following sequence: *erimyzonops* (most dwarfed) → *ipni* → *rasconis* → *catostomops* → *mandibularis* → *dichroma*. The counts for the first three just-named overlap widely, with means of 32.61, 33.53, and 34.48; but there is only the barest trace of overlap between these three as a group and the other three. The counts for the three smaller-scaled species overlap widely, and there are rather marked differences between localities within the highly variable *dichroma*, and in this species the definitely highest average count occurs just where the anal rays show the most pronounced increase. Other scale-series counts (Table 6) often follow the same pattern, with some deviations, seemingly involving the arching of the back in *ipni*, for example.

The number of vertebrae (Table 7) grades from the lowest in the most dwarfed species (*erimyzonops*), with much overlap through the rather similar values for *ipni*, *mandibularis*, and *rasconis*; with a slight further average increase in *dichroma*, to the highest counts in the elongate *catostomops*. There appears to be a complete distinction only between *erimyzonops* and *catostomops*.

Gill-raker counts on the outer side of the first arch (Table 8) are definitely lowest in the most dwarfed species, *erimyzonops*; grade upward with overlap to those for *ipni*; then, again with overlap, to the rather similar values for *rasconis*, *catostomops*, and *mandibularis*; finally to a further slight increase in *dichroma*. The distinction seems to be about complete only between *erimyzonops* and the other species, excluding *ipni*.

In general, the morphometric values (Tables 10-12) overlap widely but there are some marked differences in proportional measurements (expressed in per-millage of the standard length). Some of the sharpest differences are evident when one set of permillage values are compared with another set. A notable example involves the ratio of the length measurements, caudal peduncle / anal base (Table 9). The extreme low ratios, for *ipni*, stand out sharply, with considerable overlap on the values for *erimyzonops* and slight overlap on those for *dichroma*, but with seemingly no overlap on the ratios for *mandibularis*, *rasconis*, and *catostomops*; the ratios for *dichroma* overlap the values for those three species more than for the values of *ipni*. It may be noted that the ratios for the two relatively wide-ranging species, *dichroma* and *ipni*, seem to be rather more variable than for the other three, more localized ones.

Scrutiny of Tables 10-12 discloses in general relatively little variation within

species in the proportionate size of the various parts of the body and of the head. The lesser orbit length of *dichroma* in the upper Río Santa Catarina (first column in Table 11), and the compensating larger dimensions of the surrounding head parts (snout, suborbital, and interorbital), are in line with the relative size of the orbit and postorbital brought out in more detail in Figure 9. Between species, however, a considerable number of differences are obvious. These differences have been largely noted in the analytical comparisons of the species (pp. 276-279).

ACKNOWLEDGMENTS

We are grateful to Mexican and American colleagues for the loan or gift of specimens of significant value for the completion of this revision, and for information pertinent to that end. Dr. José Alvarez del Villar, of the Escuela Nacional de Ciencias Biológicas (ENCB), Instituto Politécnico de México, provided paratypes and other specimens of *Notropis ipni* Alvarez and Navarro (which we treat herein as *Dionda ipni*) and information regarding the type locality of that species. Dr. Salvador Contreras-Balderas, of the Universidad Autónoma de Nuevo León (UANL), provided material of *D. ipni* and conferred extensively with us, regarding *Dionda mandibularis* Contreras-Balderas and Verduzco-Martínez, and other species.

Pertinent field work was supported by the National Science Foundation to Miller from 1957 through 1974, by grants from the John Simon Guggenheim Memorial Foundation to each of the authors, and from the Horace H. Rackham School of Graduate Studies of The University of Michigan to Miller. Mexican officials kindly provided the necessary collecting permits, and Mexican colleagues and local residents gave valuable information for our respective field operations, starting in the 1930's. Dr. Richard T. Gregg introduced us to the extraordinary spring aquifers and outflows of La Media Luna, where two of the six species of *Dionda* are readily observed and collected.

American curatorial colleagues provided loans and information from specimens in their care: Dr. William N. Eschmeyer of California Academy of Sciences, now holding the Stanford University collection (CAS-SU); Loren P. Woods of Field Museum of Natural History (FMNH); Dr. John Michael Fitzsimons of Louisiana State University Museum of Zoology (LSUMZ); Dr. W. Ralph Taylor of National Museum of Natural History, Washington, D.C. (USNM); and Dr. Carter R. Gilbert of the Florida State Museum (UF).

Information regarding the status of the genus *Hybognathus* was provided by Dr. William L. Pflieger, University of Missouri, and Dr. Franklin F. Snelson, Florida Technological University, shared with us his findings and interpretations regarding intestinal coiling in minnows, including the species here treated.

Technical help has been provided by several of our respective staff members. Louis P. Martonyi took all of the fish photographs except the one (Fig. 8) done by David Bay. Mark Orsen prepared the final draft of the distributional map (Fig. 1) and the drawings of the pharyngeals (Figs. 2-3). Robert L. Wisner redrew the one graph (Fig. 9) and drafted the pencil sketches of the cephalic canals and pores (Figs. 6-7), and generously assisted in other ways. Elizabeth Noble Shor provided extensive clerical and other assistance. As usual in our studies, indispensable aid in laboratory and field has been provided by our respective wives, Laura Clark Hubbs and Frances Hubbs Miller.

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