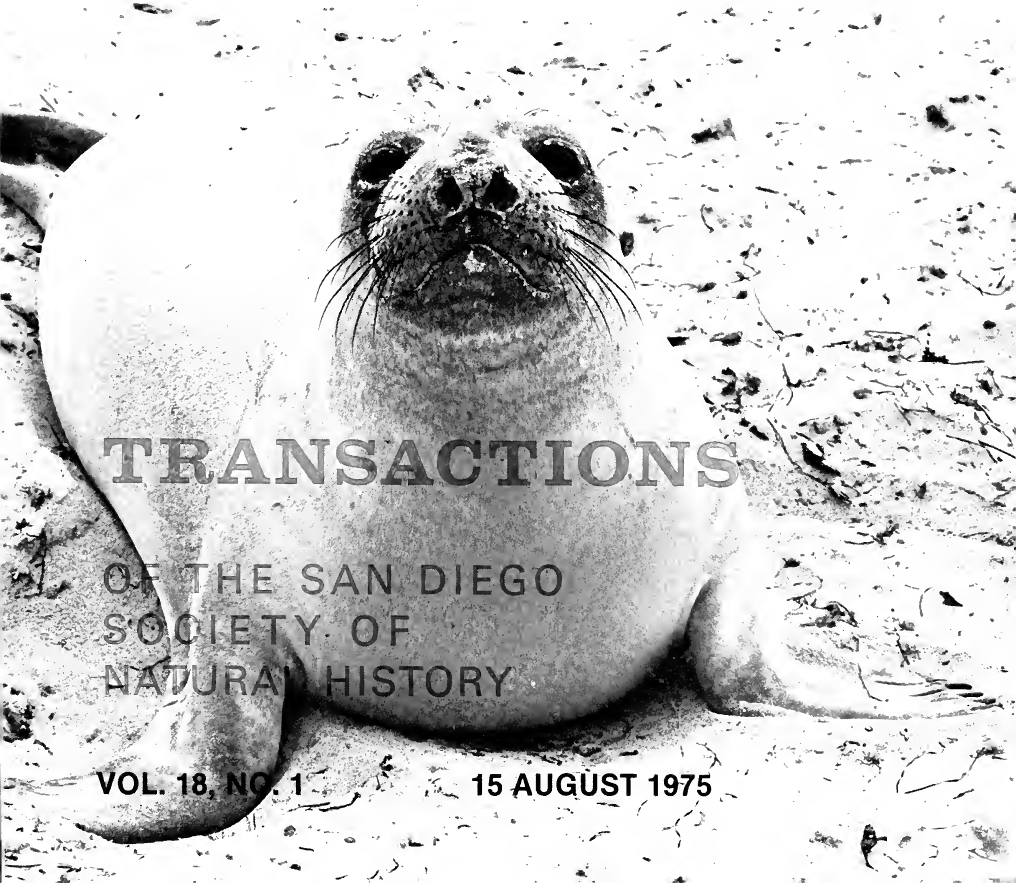
RECORDS OF ELEPHANT SEALS, *MIROUNGA ANGUSTIROSTRIS*, ON LOS CORONADOS ISLANDS, BAJA CALIFORNIA, MEXICO, WITH RECENT ANALYSES OF THE BREEDING POPULATION

Burney J. Le Boeuf, Donald A. Countryman, and
Carl L. Hubbs

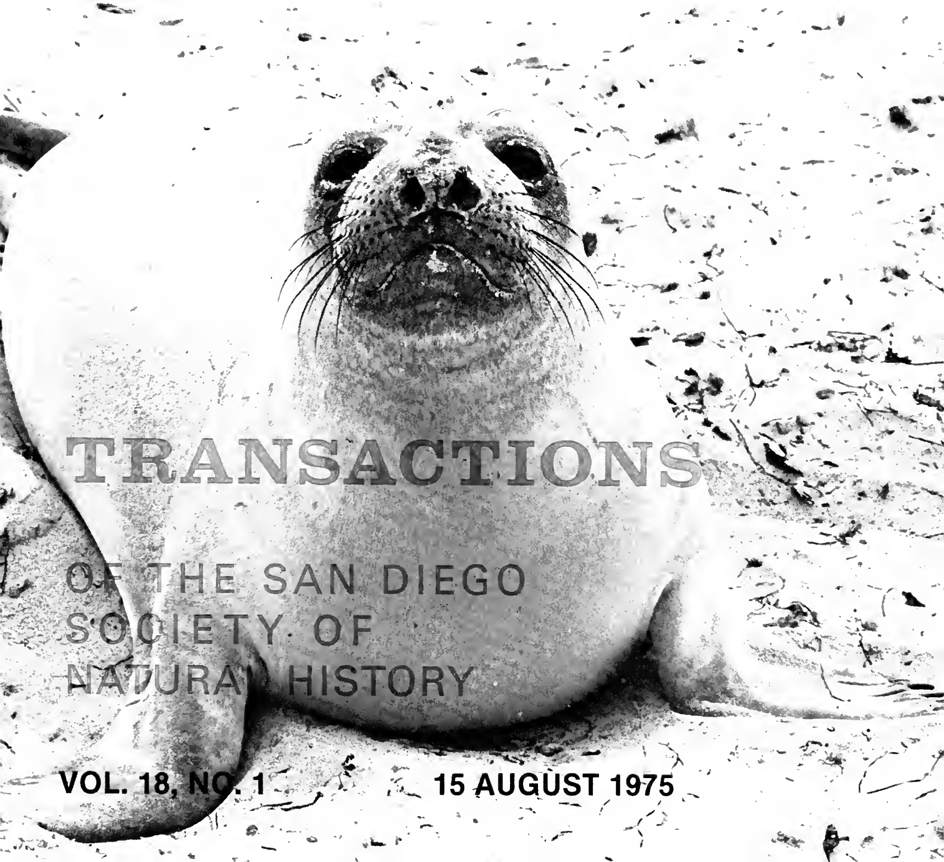


TRANSACTIONS
OF THE SAN DIEGO
SOCIETY OF
NATURAL HISTORY

VOL. 18, NO. 1 15 AUGUST 1975

RECORDS OF ELEPHANT SEALS, *MIROUNGA ANGUSTIROSTRIS*, ON LOS CORONADOS ISLANDS, BAJA CALIFORNIA, MEXICO, WITH RECENT ANALYSES OF THE BREEDING POPULATION

Burney J. Le Boeuf, Donald A. Countryman, and
Carl L. Hubbs



TRANSACTIONS

OF THE SAN DIEGO
SOCIETY OF
NATURAL HISTORY

VOL. 18, NO. 1 15 AUGUST 1975

Records of Elephant Seals, *Mirounga angustirostris*, on Los Coronados Islands, Baja California, Mexico, with recent analyses of the breeding population

Burney J. Le Boeuf, Donald A. Countryman, and
Carl L. Hubbs

ABSTRACT.—Northern elephant seals, *Mirounga angustirostris*, have been observed on Los Coronados Islands, Baja California, Mexico, on many occasions in recent decades, once in 1936 and often from 1949 to the present. Pups have been recorded on South Island in summer at least since 1950 and in winter since 1971. The composition of the breeding colony was tallied in 1974 and 1975. The colony is small (28 pups were born in 1974, 37 in 1975) and will probably not become much larger, due to the limited breeding space and to the exposure of the breeding beach. Pup mortality prior to weaning was at least 18 per cent in 1974 and 19 per cent in 1975. The colony receives immigrants from Isla de Guadalupe, Baja California.

RESUMEN.—Los elefantes marinos del norte, *Mirounga angustirostris*, se han observado muchas veces durante las últimas décadas en Las Islas Coronados, Baja California, México—una vez en 1936 y con frecuencia desde 1949 hasta ahora. Cachorros se han observado en la Isla Coronado del sur, en el verano, por lo menos, desde 1950 y en el invierno desde 1971. La composición de la colonia fue contada en 1974 y 1975. La colonia es muy pequeña (28 cachorros nacieron en 1974 y 37 en 1975) y probablemente no puede aumentar más porque falta espacio para reproducir y la zona de cría está espuesta a la marejada. La mortalidad de los cachorros antes del destete se calcula a por lo menos 18% in 1974 y 19% en 1975. La colonia recibe inmigrantes de la Isla de Guadalupe, Baja California.

The northern elephant seal population continues to increase since it was reduced to near extinction by sealers in the last century (Bartholomew and Hubbs, 1960; Radford, Orr, and Hubbs, 1965; Le Boeuf, Ainley, and Lewis, 1974). At present, the species has been reported to breed on islas Cedros, San Benitos, and Guadalupe, in northwestern Baja California, México; on San Nicolas, Santa Barbara, and San Miguel islands in southern California; and on Año Nuevo and Southeast Farallon islands in central California. Marine mammalogists in the area recognize that breeding also occurs on Los Coronados (small islands close to the northern border of Baja California). Elephant seals were rediscovered there more than 30 years ago (Bartholomew, 1950) and have been observed regularly since 1948, chiefly in the cove on South Island; also several biologists have seen young pups there. However, since none of the early censuses were made during the height of the breeding season in late January (Table 1), and few of these have been published, the precise composition and size of the colony has not been determined.

Observations on marine mammals in southern California and adjacent Baja California had been scanty for some time prior to the mid-1940's, but elephant seals may well have occurred earlier about Los Coronados. An item in the then current news notes of Scripps Institution of Oceanography reported that Mr. Robert Scripps had seen seven or eight there on 21 September 1936.

Reports of very young animals in the aggregation at West Cove of South Coronado Island (Table 1) — nine on 17 January 1971, six on 8 December 1972, and five on 22 February 1973 — indicated that pupping was occurring there (the eleven pups reported on 19 June 1950 and the two noted for 17 June 1966 may have wandered into the area instead of being born there). To determine whether elephant seals were actually breeding in this cove, and in what numbers, we circumnavigated the four islands six times in 1974 and 1975 (Figure 1). Two trips were made near the peak of the breeding season (on 31 January 1974 and 27

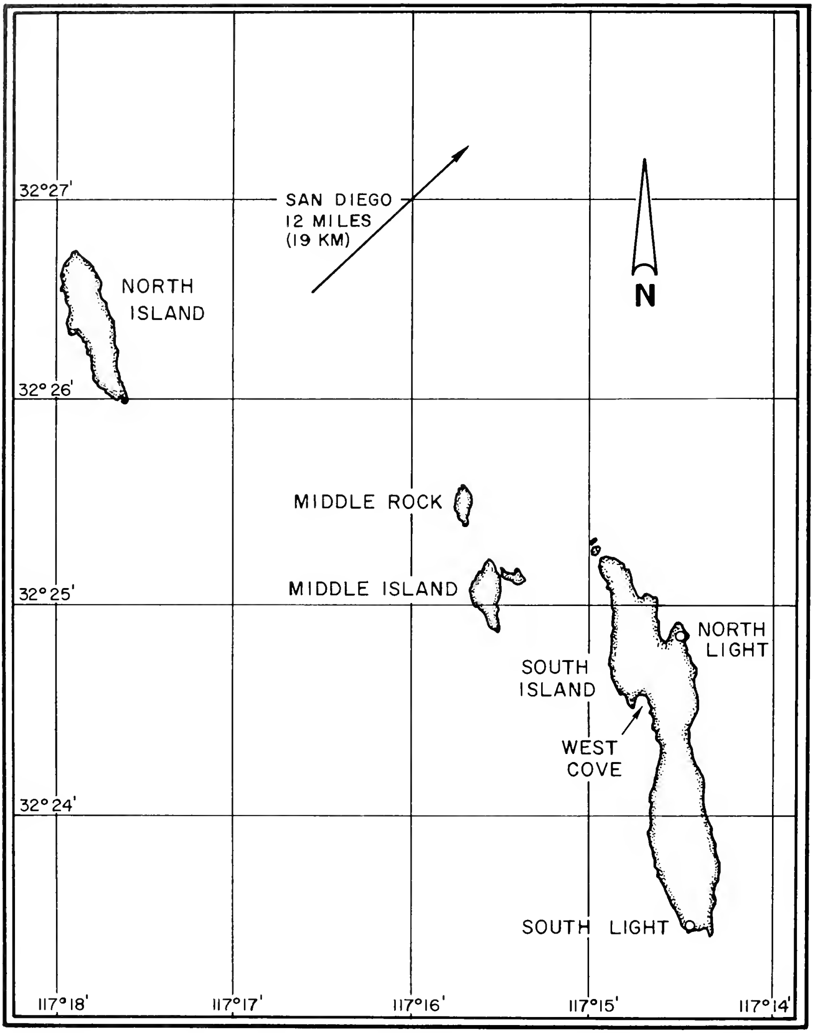


Figure 1. A diagram of Los Coronados. The breeding aggregation is located in West Cove on the South Island.

January 1975), when the number of breeding females is at a maximum (Le Boeuf, 1972). Other trips were made on 11 March 1974 and 13 March 1975, at the end of the breeding season, when all pups had been born but had not yet left the rookery. One census, on 8 May 1974, was made when molting juveniles predominate and when the total population reaches an annual peak in rookeries to the north; another census was made in the fall (4 October 1974) when yearlings and young juveniles are present. Our census dates were predetermined to coincide with key points in the annual cycle of northern elephant seals on other rookeries (Le Boeuf, Ainley, and Lewis, 1974; Odell, 1974).

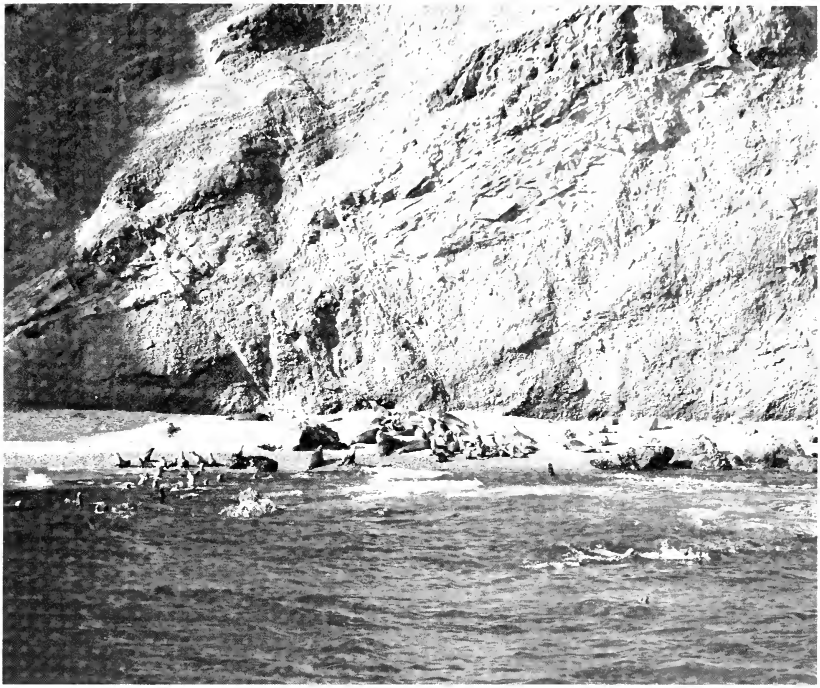


Figure 2. Elephant seals (22) and California sea lions on the beach of West Cove, South Coronado Island, photographed by Conrad Limbaugh, 11 June 1952.

Virtually all elephant seals counted in January 1974 and 1975 (Table 2) were associated with a breeding aggregation in West Cove on South Island (Fig. 1 and 2). Here we went ashore to count and observe the animals more closely. The composition of the breeding colony and the activities observed were typical of rookeries of this size at this time of year. The harem was overseen by one adult male who prevented other males from approaching females, and he no doubt was responsible for all or virtually all of the breeding (Le Boeuf, 1974). The beach is composed of small pebbles and measures approximately 50m long and 5 to 12m wide at a tide of about +1m. The only other beach on Los Coronados that could possibly accommodate a small colony of elephant seals is on the north side of a cove on the east side of Middle Island; this beach is of approximately the same depth as the other but is less than half as long.

In January, 1974, three pups in natal pelage died in the rookery, one from apparent starvation, one from drowning, and one from wounds inflicted by adult seals. Two other pups were dying; one was an orphaned newborn and the other was an unusually large newly-weaned pup that was irretrievably stuck in a crevice (it was dead when we returned on 11 March 1974). Thus, pup mortality in this colony in 1974 was at least 5/28 or 17.9 per cent. The following year, three dead pups in natal pelage were counted in January and four additional carcasses were censused on 13 March 1975, for a minimum pup mortality of 7/37 or 18.9 per cent. Three of the mortalities in 1975 were weaned and newly-molted pups.

As expected from March observations elsewhere, few breeding males were observed, all breeding females had departed, the majority of animals in residence were weaned pups of the year, and yearlings and juveniles had begun to arrive for the spring molt. In both years, slightly fewer weaners were observed than was expected. The others may have been swimming or they may have died and were washed out to sea.

The total number of elephant seals on 8 May 1974 was approximately double that on 31 January 1974, the peak of the breeding season. A similar relationship has been observed on Año Nuevo Island (Le Boeuf, Ainley, and Lewis, 1974) and on San Nicolas Island (Odell, 1974), which suggests to us that the temporal

TABLE 1. Censuses of Northern Elephant Seals on Los Coronados (in addition to those recorded in Table 2).

Date	Total Animals	Sex or Age Estimates	Location	Type of Census	Observer
21 Sept. 1936	7-8	Not specified	North Is.	Boat	R. Scripps (1936)
June 1948-1949	Individuals	Juveniles or subadults	Coronado Is.	?	"Lighthouse Keepers" (Bartholomew, 1950)
Last week of April 1949	73	Juveniles or subadults	Cove, South Is.	Land	G. A. Bartholomew (1950, 1952)
30 May 1949	3	Juveniles in kelp	North Is.	Boat?	L. W. Walker[1]
14-16 Aug. 1949	5		Cove, South Is.	Boat?	R. W. Lindberg (Bartholomew, 1951)
27 Nov. 1949	<5		South Is.	Boat?	C. L. Hubbs and G. A. Bartholomew (Bartholomew, 1951)
19 June 1950	38	4 adult males, 10 subadult males 13 females, 11 pups	Cove, South Is.	Boat?	A. Allanson[1]
16 Nov. 1950	Several	In water	North of North Is.	Boat?	C. L. Hubbs
14 Oct. 1951	7	3 females and 4 juveniles	Cove, South Is.	Boat?	C. Limbaugh[1]
11 May 1952	22	No large adult males	Cove, South Is.	Boat?	C. Limbaugh[1]
12 July 1952	7		Cove, South Is.	Boat?	C. Limbaugh[1]
20 July 1952	30		Cove, South Is.	Boat?	C. Limbaugh[1]
6 June 1953	20	Subadult males	Cove, South Is.	Land	J. Fisher, R. T. Peterson, and C. L. Hubbs (Peterson and Fisher, 1955)
30 May 1957	21		Cove, South Is.	Boat?	A. L. Kelly[1]
2 Aug. 1961	9	3 adult males, 1 yearling	Cove, South Is.	Boat?	A. L. Kelly[1]
12 Jan. 1964	5		Cove, South Is.	Air	C. L. Hubbs
15 Mar. 1965	1		Los Coronados	Boat?	D. W. Rice (Rice, Kenyon, and Lluch, 1965)
30 Sept. 1965	7[2]		Cove, South Is.	Boat?	D. Lluch[1]
17 June 1966	20	18 females or young males, 2 pups	Cove, South Is.	Land	C. L. Hubbs
1 June 1968	7		Cove, South Is.	Boat?	C. L. Hubbs
8 Mar. 1969	3+		Cove, South Is.	Boat	J. R. Jehl, Jr.[1]
7 June 1969	30		Cove, South Is.	Boat	J. R. Jehl, Jr.[1]
5 Aug. 1969	4	2 males, 2 females	Cove, South Is.	Boat	J. R. Jehl, Jr.[1]
14 Sept. 1969	2		Cove, South Is.	Boat	J. R. Jehl, Jr.[1]
6 Apr. 1970	79		South Is.	Boat	S. Bowen[1]
17 Jan. 1971	48	2 males, 33 females, 9 pups, 4 yearlings	Cove, South Is.	Boat	J. R. Jehl, Jr.[1]
2 May 1971	50		Cove, South Is.	Boat	J. R. Jehl, Jr.[1]
24 Oct. 1971	3		Cove, South Is.	Boat	A. L. Pentis[1]
18 Jan. 1972	35		Cove, South Is.	Air	S. Leatherwood (Odell, Leatherwood and Antonelli, manuscript)
2 Feb. 1972	32		Cove, South Is.	Air	L. Tsumoda[1]
7 Apr. 1972	85	30 very young animals	Cove, South Is.	Boat	J. R. Jehl, Jr.[1]
8 Dec. 1972	39	6 males, 27 females and subadults, 6 pups	Cove, South Is.	Land	S. Leatherwood (Odell, Leatherwood and Antonelli, manuscript)

TABLE 1. Continued

Date	Total Animals	Sex or Age Estimates	Location	Type of Census	Observer
22 Feb. 1973	25	7 males, 13 females and subadults, 5 pups	Cove, South Is.	Boat	D. Odell (Odell Leatherwood and Antonelli, manuscript)
10 Mar. 1973	4		Cove, South Is.	Boat	J. R. Jehl, Jr.[1]
	3		North Is.	Boat	
10 Mar. 1973	8		Cove, South Is.	Boat	A. L. Pentis[1]
13 May 1973	93	5 weaners 6 immatures	Cove, South Is. North Is.	Boat	J. R. Jehl, Jr.[1]
1 June 1973	99		Cove, South Is.	Land	A. L. Pentis[1]
7 Aug. 1973	8	2 males, 4 females, 2 weaners	Cove, South Is.	Land	J. R. Jehl, Jr.[1]
17 Mar. 1974	3	weaners	North Is.	Boat	A. L. Pentis[1]
	1	weaner	Middle Is.		
	8		Cove, South Is.		
23 July 1974	14		Cove, South Is.	Land	F. Todd and J. R. Jehl, Jr.[1]
15 Mar. 1975	38	Including 4 large males	Cove, South Is.	Boat	A. L. Pentis[1]
16 Mar. 1975	34		Cove, South Is.	Boat	A. L. Pentis[1]
22 Mar. 1975	43		Cove, South Is.	Boat	A. L. Pentis[1]
23 Mar. 1975	16		Cove, South Is.	Boat	A. L. Pentis[1]

---

[1] Personal communication

[2] Seven young animals caught on Isla de Guadalupe were released in the water near the cove on South Island.

aspects of the annual cycle are essentially identical in each of these colonies. The animals censused on South Island on 8 May 1974 consisted of molting and recently molted juveniles of both sexes two to four years old, one possibly adult female, and a few pups that had been born in January. Juveniles predominated in the 4 October 1974 census, which also included a few yearlings and pubertal males. Thus, our censuses and those of previous observers (Table 1) reveal that key points in the annual cycle on South Island, as well as the composition of groups at various times of the year parallel those found on other rookeries (Allanson's census on 19 June 1950 may seem out of line with this statement, since the group composition he reports suggests a breeding colony. No doubt, the pups he observed were born in the previous winter and the females were juveniles. The "pups" were not necessarily born on Los Coronados).

The elephant seals of South Coronado Island are usually roughly associated with California sea lions *(Zalophus californianus)*. The seals concentrate on the sandier part of the beach, leaving the cobbly areas or rocks to the moderate to large numbers of sea lions. The association between individuals of the two species varies from nearly complete segregation to close intermixing. Here, as elsewhere, the elephant seals are much the less wary, as is shown in Figure 2, taken at a time when nearly all of the sea lions had been frightened off the cobbles on the northern (left) part of the beach.

An eight-year tagging program confirms that the Coronados colony receives immigrants from the virtually saturated population at Isla de Guadalupe, 201 nautical miles (324 km) south and slightly west of Los Coronados. Since 1967, Le Boeuf and collaborators have tagged more than 8,000 elephant seals on the seven principal islands where the species breeds (Le Boeuf, Ainley, and Lewis, 1974); the majority were tagged as newly weaned pups. In recent years, seven seals tagged on Guadalupe have been seen on Los Coronados (Table 3). Six of these were tagged as pups and without question were born on Guadalupe; all six were in their second year of life when sighted on Los Coronados; all sightings were in winter or spring, and all animals were in apparent good health. Several other

TABLE 2. Six shore censuses of northern elephant seals in the west cove of South Island, Los Coronados, made in 1974 and 1975.

Date	Adult Males	Subadult Males	Females	Pups: Suckling	Pups: Weaned	Pups: Orphaned	Pups: Dead	Yearlings	Juveniles	Total Living	Total All Islands
31 Jan. 1974	5[1]	3[1]	29	13	11	1	3	1	0	63	67
11 Mar. 1974	2	2[2]	0	0	20	0	1	4	5	33	34
8 May 1974	0	0	0	0	4	0	0	0	126	130	130
4 Oct. 1974	0	4	0	0	0	0	0	5	30	39	39
27 Jan. 1975	3	5[3]	40	13	8	1	3	1	1	72	73
13 Mar. 1975	0	2	0	0	30	0	4	4	4	40	40

[1] Four males were observed elsewhere on the islands: one adult on the north point of South Island, one adult and one subadult about ½ mile south of the village on the east side of South Island, and one subadult in the east cove of Middle Island.

[2] One subadult was observed on the south end of South Island.

[3] One subadult was observed on the east side of South Island ½ mile north of the south end.

tagged animals have been seen on Los Coronados in recent years (Ronald R. McConnaughey, pers. comm.) but their age and sex was not determined.

The number of Guadalupe animals that migrate to Los Coronados appears to be small. Over 2200 elephant seals were tagged on Isla de Guadalupe during 1969, 1970, 1971, and 1973, but only two of 800 animals tagged there in 1973 were observed on Los Coronados. Seals born on Isla de Guadalupe also disperse to the San Benitos, San Nicolas, San Miguel, and Año Nuevo islands (Le Boeuf, unpubl. obs.).

Apparently the Coronados colony seldom if ever recruits from other colonies since none of 6,000 seals tagged on the San Benitos, Cedros, San Miguel, San Nicolas, Año Nuevo, and Southeast Farallon islands have been observed there.

In conclusion, elephant seals breed on Los Coronados but it is unclear when breeding began. Although the species has been observed on these islands since 1936, most of the early censuses were made during the non-breeding season. The appearance of elephant seals during the non-breeding season is no indication that a breeding colony is present in winter. Seals hauled out on Año Nuevo and Southeast Farallon islands in the spring and fall for several years before they began breeding there (Le Boeuf, Ainley, and Lewis, 1974). Not until 1964 were elephant seals censused during the breeding season on Los Coronados, and not until 1971 were females and pups reported (Table 1). Judging from the census figures, we speculate that breeding may have started on Los Coronados as early as 1950, certainly by 1964.

The present colony is small and precariously located. With tides of 2+ meters and moderate surf, much of the breeding beach, except for a few high spots next to the bluff, is flooded. On 27 January 1975 we observed the rookery from 0700 to 1000. There was a 10 to 15 knot wind, 2 to 4 ft swell from the south, and a tide of +7.3 ft at 0830. High water divided the single harem of females and their pups into two approximately equal groups that took refuge from the surf on two high spots approximately 10m apart at the base of the cliff. Density among females was so much higher than usual that most of them were in contact, female aggression was frequent and intense, and several pups were bitten. The group nearest the center of the beach was most vulnerable to wave action. For over an hour young pups were continuously being washed out to sea, struggling and swimming frantically, and then slammed back into the cliff by the pounding surf. This sort

TABLE 3. Tagged elephant seals observed on Los Coronados (all tagged on Isla de Guadalupe).

Tagging Information					Recovery Information			
Tag No.	Age Category	Sex	Date	Beach Where Tagged on Isla de Guadalupe	Location	Date	Age in Months	Observer
Blue 30	pup	M	15 Feb. 1969	South Barracks	South Is.	5 Apr. 1970	15	S. L. Bowen
Blue 31	adult	M	15 Feb. 1969	North Barracks	South Is.	15 & 29 Apr. 1969	?	D. Hunsaker
Blue 182	pup	F	15 Feb. 1969	North Barracks	North Is.	29 Jan. 1970	12	C. L. Hubbs
Blue 369	pup	M	16 Feb. 1969	Pilot Rock	North Is.	29 Jan. 1970	12	C. L. Hubbs
UC 5198	pup	F	19 Feb. 1969	South Barracks	South Is.	21 Mar. 1970	14	S. L. Bowen
Blue 2068	pup	?	14 Feb. 1973	Pilot Rock	South Is.	8 May 1974	16	B. J. Le Boeuf
Blue 2096	pup	?	14 Feb. 1973	Pilot Rock	South Is.	8 May 1974	16	B. J. Le Boeuf

of periodic engulfing of the beach area, combined with the lack of other suitable breeding areas, has clearly set limits to the growth of the Coronados colony in the past and may be expected to continue to do so in the future.

ACKNOWLEDGEMENTS

We thank Sea World of San Diego for providing and operating M/V *Shamu;* Scripps Institution of Oceanography for providing a support vessel and personnel; Dr. Amín Zarur Ménes of the San Diego office of the Mexican government fisheries department for the permits needed to land on Los Coronados and for his active interest in the project; and Mrs. Elizabeth Noble Shor for bringing to our attention the observation of several elephant seals at the Coronados Islands in 1936.

This study has been supported in part by NSF grants GB-16321X and GB-414487X to B. J. L.

LITERATURE CITED

BARTHOLOMEW, G. A., 1950. Reoccupation by the elephant seal of Los Coronados Islands, Baja California, Mexico. Journal of Mammalogy 31: 98.

BARTHOLOMEW, G. A., 1951. Spring, summer, and fall censuses of the pinnipeds on San Nicolas Island, California. Journal of Mammalogy 32: 15-21.

BARTHOLOMEW, G. A., 1952. Reproductive and social behavior of the northern elephant seal. University of California Publications in Zoology 47: 369-471.

BARTHOLOMEW, G. A., and C. L. HUBBS, 1960. Population growth and seasonal movements of the northern elephant seal, *Mirounga angustirostris.* Mammalia 24: 313-324.

LE BOEUF, B. J., 1972. Sexual behavior in the northern elephant seal, *Mirounga angustirostris.* Behavior 41: 1-26.

LE BOEUF, B. J., 1974. Male-male competition and reproductive success in elephant seals. American Zoologist 14: 163-176.

LE BOEUF, B. J., D. G. AINLEY, and T. J. LEWIS, 1974. Elephant seals on the Farallones: Population structure of an incipient breeding colony. Journal of Mammalogy 55: 370-385.

ODELL, D. K., 1974. Studies on the biology of the California Sea Lion and the Northern Elephant Seal on San Nicolas Island, California. Journal of Mammalogy 55: 81-98.

PETERSON, R. T., and J. FISHER, 1955. Wild America. Houghton Mifflin Co., Boston. 434 p.

RADFORD, K. W., R. T. ORR, and C. L. HUBBS, 1965. Reestablishment of the northern elephant seal *(Mirounga angustirostris)* off central California. Proceedings of the California Academy of Sciences 31: 601-612.

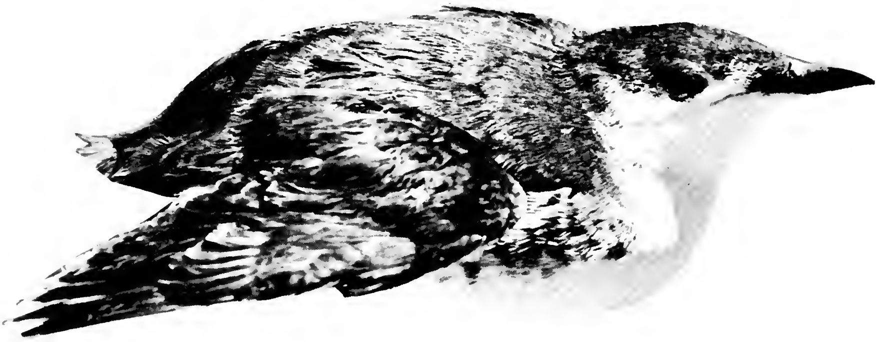
RICE, D. W., K. W. KENYON, and D. B. LLUCH, 1965. Pinniped populations at Islas Guadalupe, San Benito and Cedros, Baja California, in 1965. Transactions of the San Diego Society of Natural History 14: 73-84.

SCRIPPS, R., 1936. Scripps Institution notes. Scripps Institution of Oceanography: History in the News.

Le Boeuf: Crown College, University of California, Santa Cruz, Ca., 95064. Countryman: Department of Biology, University of California, San Diego, La Jolla, Ca., 92037. Hubbs: Scripps Institution of Oceanography, La Jolla, Ca., 92037.

MORPHOLOGICAL VARIATION AND SPECIES LIMITS IN MURRELETS OF THE GENUS *ENDOMYCHURA*

Joseph R. Jehl, Jr. and Suzanne I. Bond



TRANSACTIONS

OF THE SAN DIEGO
SOCIETY OF
NATURAL HISTORY

VOL. 18, NO. 2 23 OCTOBER 1975

Erratum: For Synthiloboramphus read Synthliboramphus

Morphological variation and species limits in Murrelets of the genus *Endomychura*

Joseph R. Jehl, Jr. and Suzanne I. Bond

ABSTRACT.—Species limits in *Endomychura* have been a matter of dispute. Recent field studies in Baja California have shown that the probable breeding ranges of two of the three currently recognized taxa are more extensive than has been realized, and that all three taxa occur on the San Benito Islands during the nesting season. Morphological data indicate that Craveri's Murrelet *(E. craveri)* is acting as a distinct species with respect to both forms of Xantus' Murrelet *(E. hypoleuca)*. *Endomychura h. hypoleuca* and *E. h. scrippsi* are exceptionally well-marked forms and differ significantly in size and plumage characters. They apparently hybridize on the San Benitos, but the limited data suggest that interbreeding is not random, that gene flow between the two is reduced, and that isolating mechanisms are being tested. Face pattern and bill shape may be the most effective isolating mechanisms as they are sufficient to provide a rapid means of species recognition. Differences in face pattern and bill shape among the several populations may constitute a complex case of character displacement. Further studies in the area of overlap are needed to determine the extent of hybridization and whether a third species of *Endomychura* should be recognized. Color patterns of the downy young support the view that *Endomychura* is most closely allied to *Synthiloboramphus.*

The beginning of ornithological explorations in Baja California in the mid-1850's resulted in the description of many taxa, including two new species of alcids. Xantus' Murrelet *(Endomychura hypoleuca)* was described by Xantus in 1859 from a specimen taken off Cabo San Lucas. Shortly thereafter, in 1865, Salvadori described a similar species, Craveri's Murrelet *(Endomychura craveri)*, from Natividad Island on the west side of the Baja California peninsula. (Although the A. O. U. [1957] has recognized Isla Raza in the Gulf of California as the type locality of *craveri*, DeLong and Crossin [MS] argue convincingly that the Natividad Island designation is correct.)

The taxonomic ranking of *craveri* soon came under fire. Coues (1884) thought it "questionably distinct" from *hypoleuca.* Ogilvie-Grant (1898) suggested that it might be the breeding plumage of *hypoleuca*, Ridgway (*in* Anthony, 1900) speculated that the forms represented different sexes or color phases of the same species. Anthony (1900) effectively refuted these views but speculated, in turn, that *craveri* might be the immature plumage of *hypoleuca*, a position supported by Grinnell (1915) after "a hasty glance at the material in the Museum of Vertebrate Zoology."

Van Rossem (1926) made the first critical study of the problem. He showed that *craveri* was not an age variant of *hypoleuca* but was a "perfectly distinct" form, whose breeding range was confined, so far as known, to the Gulf of California; *hypoleuca* breeds on islands of the Pacific coast. Grinnell (1928) relented, writing; "The systematic status of the Craveri Murrelet has been much discussed . . .; the last and seemingly final word is by van Rossem (1926a, p. 80)."

Grinnell's hopes, however, were in vain, for van Rossem (1939) changed his mind. Early in 1939, Green and Arnold showed that *E. hypoleuca* was divisible into two well-marked subspecies, *E. h. hypoleuca*, from Guadalupe Island, and *E. h. scrippsi,* from the near-shore islands of California and northern Baja California. For his 1926 paper, van Rossem had examined only one specimen from Guadalupe. He now (1939) examined specimens from the San Benito Islands — another area which he had ignored in his earlier paper — and after a cursory study described a new form, *E. h. pontilus,* that seemed intermediate between *craveri* and *hypoleuca (sensu lato).* This convinced him (1939: 442) that "there is no longer the slightest reason to consider the two supposed species as other than geographic races. Further evidence of intergradation is provided by a specimen . . . from Natividad Island . . . that is exactly intermediate in all particulars."

San Diego Soc. Nat. Hist., Trans. 18 (2): 9-24, 23 October 1975

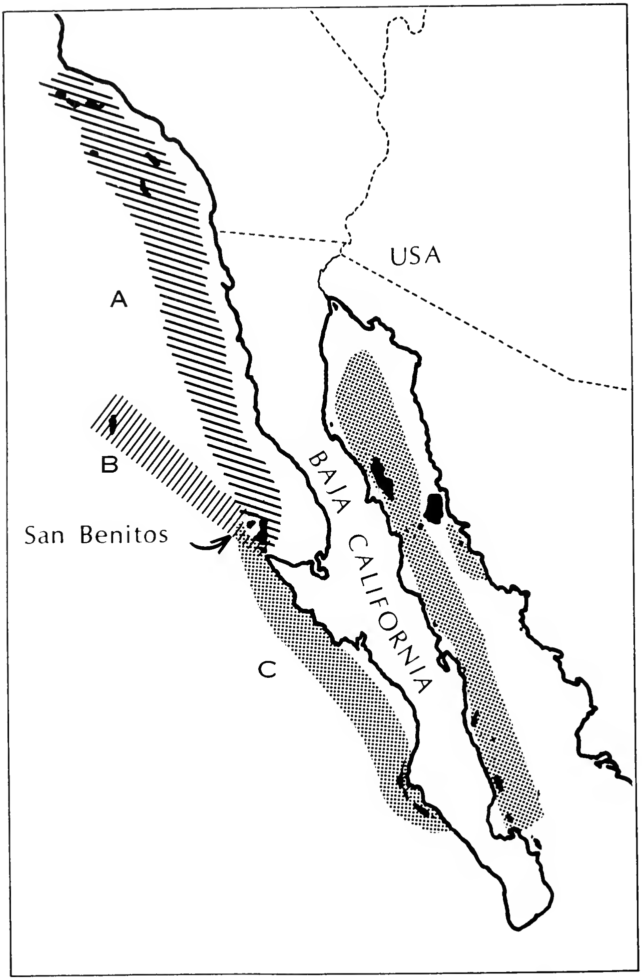


Figure 1. Probable breeding distribution of *Endomychura* murrelets: *E. h. scrippsi* (A); *E. h. hypoleuca* (B); *E. craveri* (C). The three forms are sympatric on the San Benito Islands.

At this point, one might have expected the case to be closed and that taxonomists would have adopted a consistent treatment of variation in *Endomychura*. That was not the case. The A. O. U. Check-List committee (Wetmore, et al., 1944) took no action, then or subsequently, on van Rossem's new race but accepted that proposed by Green and Arnold. This was surprising, for van Rossem was a member of the committee, and it is hard to believe that he would have forgotten to request formal consideration for one of his own creations. Confusion resulted. By ignoring van Rossem (1939), the A. O. U. was forced to continue to recognize two species of *Endomychura*. On the other hand, the compilers of the Mexican Check-List (Friedmann, Griscom, and Moore, 1957) followed van Rossem and recognized one polytypic species. But, inexplicably, they did not recognize, comment on, or even synonymize *E. h. pontilus*, the supposed connecting link!

The early taxonomists were severely limited by a fragmentary knowledge of the breeding range of the several forms and by extremely limited specimen collections of *hypoleuca* from Baja California. That the mid-peninsula islands of the west coast might prove critical in understanding relationships in *Endomychura* was anticipated by Bancroft (*in* Dawson, 1923), who speculated that "intergradation . . . probably occurs . . . in the vicinity of Cedros Island." Recent field work in this area, by ourselves and others, has resulted in the collection of new material from Guadalupe Island and the San Benitos Islands. We now recognize that birds of the *craveri* type occur along the southern half of the west coast of Baja California during the breeding season, and furthermore that all three forms, *craveri*, *h. hypoleuca*, and *h. scrippsi*, occur synchronously on the San Benito Islands in spring. These discoveries have led us to review morphological variation in the several populations, with special reference to the San Benitos.

DISTRIBUTION DURING THE BREEDING SEASON: EVIDENCE OF SYMPATRY

Endomychura hypoleuca presumably once nested on all of the islands along the coast of Southern California and Baja California, from San Miguel in the north to the San Benitos in the south. We know of breeding records for the following islands[1]: Prince Islet, San Miguel Island (specimens USNM); Anacapa Island (specimens SDSNH; eggs collected, Peyton, 1913; Wright and Snyder, 1913); Santa Barbara Island (specimens LACMNH; eggs collected, Willet, 1912; G. Hunt, pers. comm.); San Clemente Island (Jehl and G. McCaskie, adult and downy chick in waters adjacent to island in 1968); Los Coronados (specimens SDNHM; Lamb, 1909; Howell, 1917; pers. obs.); Todos Santos Islands ("on and about" island, Kaeding, 1905; broken egg, birds eaten by cats, Van Denburgh, 1924); San Martín Island ("on and about" island, Kaeding, 1905); San Benito Islands (specimens Carnegie Mus., SDNHM; Kaeding, 1905; pers. obs.); and islets at Guadalupe Island (specimens SDNHM, USNM; Green and Arnold, 1939: pers. obs.). Populations on some islands, (Todos Santos, San Geronimo, San Martín, the main island of Guadalupe) have apparently been extermined by rats or feral cats (e.g., Howell, 1912; Van Denburgh, 1924). The current status of populations on most islands is not known.

Various authorities (e.g., A. O. U., 1957) list Natividad Island as a breeding station; this presumption is based on Lamb's (1927) *winter* observations of "pairs" of murrelets alleged to be *hypoleuca* at sea near the island. Murrelets (species?) probably have nested there, but there is no evidence of that event. Natividad is currently infested with feral cats and we doubt that nesting murrelets could survive. We know of no sight records or specimens of *hypoleuca* during the breeding season south of Turtle Bay. Studies between Natividad and Magdalena Bay and especially on Islas San Roque and Asuncion are needed.

Endomychura craveri has been generally thought to breed only in the Gulf of California (see DeWeese and Anderson MS for a review of nesting areas) but evidence is accumulating that its range is not so restricted. Anthony (1900) reported "a number of family parties" of murrelets off Magdalena Bay in June 1897; although he presumed these were *hypoleuca*, his only specimen was of a flightless adult *craveri*! (It was this specimen [now Carnegie Mus. no. 22973], which he identified as a juvenile *hypoleuca*, that led to his speculation that *craveri* was the juvenile of *hypoleuca*). More recent observations also suggest breeding in the Magdalena Bay area. On a transect between Cabo San Lucas and San Diego in mid-June 1974, we saw 12 murrelets, including several pairs, between Cabo San Lucas and the San Benitos; the eight that could be identified were *craveri*. On a southward transect through the same area, in early April 1975 Jehl and K. E. Stager saw five murrelets off Turtle Bay on 5 April and the several that could be identified were *craveri*. On 6 April they saw 7 pairs of murrelets, all *craveri*, 5 to 8 miles off Santa Margarita Island, Magdalena Bay.

[1] Listed here are selected primary references that substantiate breeding at a particular locality.

There are also records of *craveri* off northern Baja California during the breeding season. Jehl saw a single bird 4 mi S of Los Coronados on 20 February 1972, and another 4 mi S of Point Loma, San Diego, on 6 June 1969. On a transect between San Diego and the San Benito Islands in early April 1974, Jehl saw a pair of *craveri* (but no other murrelets) 21 mi S of San Martín Island on 4 April. On 8 April he saw 30 murrelets in the northeast corner of Vizcaino Bay; these included 6 pairs and 1 single *craveri*, 1 pair of *hypoleuca*, and 15 unidentified. Specimens from this area, all of which were taken aboard ship, are: NW end Cedros Island, 27 February 1941 (LACMNH 50594); Cabo Colnett, 2 March 1949 (LACMNH 51845); and San Martín Island, 13 April 1951, largest ovum 4 mm (LACMNH 51879).

The most convincing evidence that *craveri* breeds along the west coast of Baja California comes from the San Benito Islands. In late April 1968, members of the Smithsonian Institution's Pacific Ocean Biological Survey Program collected 19 murrelets, all with enlarged gonads, from many that flew aboard their ship at night: seven were *craveri* and 12 *hypoleuca*, including *E. h. hypoleuca* and *E. h. scrippsi*. In late May 1971 Jehl examined 27 murrelets that flew aboard at West Benito Island; five were *craveri*, and both races of *hypoleuca* were present among the remainder. A total of ten individuals of the three forms were collected; their gonads were enlarged.

In summary, observations of Craveri's Murrelets, some obviously paired, along the west coast of Baja California during the breeding season provide presumptive evidence of nesting north to the San Benitos-Cedros area and perhaps beyond. The population at the San Benitos may comprise 20–30% *craveri*, and also includes both forms of *hypoleuca*. Limited field observations suggest that where *craveri* comes into contact with *hypoleuca* pairing is assortative. Finally, Anthony's 1897 observations indicate that the presence of *craveri* on the west coast of Baja California is not the result of a recent range expansion.

The probable breeding ranges of the several forms are shown in Figure 1.

GEOGRAPHIC VARIATION

We examined approximately 370 specimens of *Endomychura* from the following institutions: San Diego Natural History Museum; California Academy of Sciences; University of California, Los Angeles; American Museum of Natural History; Museum of Vertebrate Zoology, University of California; Los Angeles County Museum of Natural History; United States National Museum; Burke Memorial Museum, University of Washington. These collections include much new material from the San Benito Islands and Guadalupe Island that has not been analyzed previously.

Specimens were sorted according to the criteria of van Rossem (1926) and Green and Arnold (1939). Briefly, *E. craveri* may be characterized as a small black-and-white murrelet with a long, slender bill; the underwing is usually grayish, but varies from whitish (though never pure white) to dark sooty gray: the inner vane of the outer primaries is brownish. Birds in fresh plumage have a brownish cast to the black back feathers, which is often evident even in worn nesting birds. The dark feathers extend onto the sides of the neck forming a partial collar. Flank feathers are uniformly dark.

E. hypoleuca is slightly larger, with a shorter, stouter bill; the underwing is whitish, sometimes flecked with a few dark feathers; the inner vane of the outer primaries is whitish. Freshly-plumaged birds have a blue or blue-gray tinge to the back, and the flank feathers may be tipped with white. The face pattern varies geographically (see below).

For each species samples were separated into probable breeding and nonbreeding subsamples. We have no data on how far murrelets may range from their nesting area and assume that specimens taken in the vicinity of a known breeding island in the breeding period (roughly February through June) are representative of the local population.

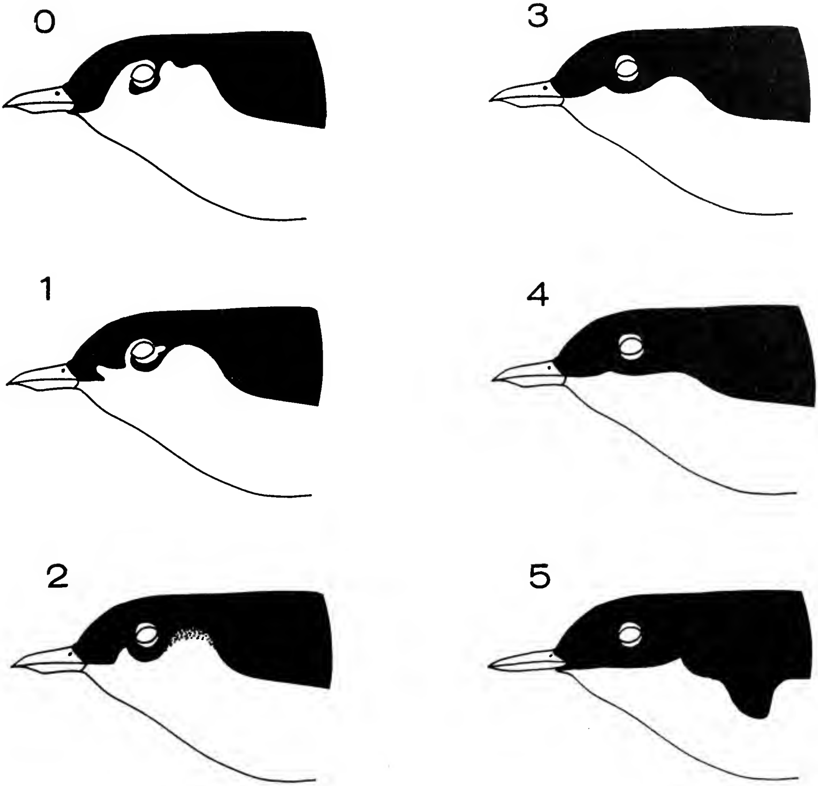


Figure 2. Face and throat pattern variation in *Endomychura hypoleuca* (0-4) and *E. craveri* (5), drawn from specimens collected on the San Benito Islands, 26 May 1971.

We emphasize that localities given on specimen labels are too often imprecise. Murrelets are notorious for landing on ships, but labels rarely indicate whether a specimen collected, say, at "Guadalupe Island" was taken at sea near the island, from a nesting burrow, or flew aboard at night. Future workers are cautioned to record these data precisely.

The following measurements were taken: exposed culmen; bill depth at gonys, chord of wing, and length of tarsus. Variation in face pattern was coded as shown in Figure 2. The ratio of bill depth to bill length was calculated. Mensural characters were not recorded from all specimens, due to time limitations, but all specimens were carefully checked for evidence of intergradation.

Endomychura hypoleuca

Measurements of Xantus' Murrelet are given in Table 1. Size varies clinally in this species, birds from northern colonies having shorter and deeper bills but longer wings and tarsi than those from farther south. Weight data, though few, also suggest that northern birds are bigger. In northern populations (Channel Islands, Los Coronados) the face pattern is exclusively dark (Classes "3" and "4", Figure 2), whereas whiter patterns (Classes "0" and "1") characterize the

TABLE 1. Measurements of Xantus' Murrelet *(Endomychura hypoleuca)*

	Male				Female			
Area	No.	Range, mean and S.E.	S.D.	C.V.	No.	Range, mean and S.E.	S.D.	C.V.
		Exposed Culmen						
1. Northern Channel Islands	10	15.6–19.3(17.05) ± 0.33	1.05	6.15	7	16.8–19.0(18.04) ± .44	1.17	6.48
2. Southern Channel Islands	1	16.5			2	18.3–18.7(18.5)		
3. Los Coronados	41	16.3–19.2(17.98) ± .10	0.69	3.83	36	16.5–20.3(18.21) ± .13	0.83	4.55
4. San Benito Is.	11	16.8–21.4(18.58) ± .42	1.41	7.58	12	16.0–20.5(18.25) ± .40	1.40	7.67
5. Guadalupe Is.	27	17.4–21.2(19.32) ± .19	1.00	5.17	22	18.4–21.3(19.85) ± .16	0.77	3.87
		Bill Depth						
1. Northern Channel Islands	10	5.8-6.4(6.17) ± .09	0.28	4.53	8	5.4–6.5(5.92) ± .11	0.31	5.23
2. Southern Channel Islands	1	5.9			2	5.9, 5.9		
3. Los Coronados	41	5.6–6.5(6.09) ± .03	0.24	3.94	37	5.5–6.4(5.97) ± .03	0.23	3.85
4. San Benito Is.	12	5.3–6.1(5.75) ± .08	0.29	5.04	12	5.3–6.3(5.73) ± .08	0.28	4.88
5. Guadalupe Is.	28	5.2–6.1(5.78) ± .05	0.27	4.67	22	5.2–6.3(5.64) ± .05	0.27	4.78
		Bill Ratio						
1. Northern Channel Islands	10	.31–.42(.35) ± .01	0.04	11.4	7	.26–.37(.33) ± .01	0.03	9.09
2. Southern Channel Islands	1	.36			2	.32–.37(.34)		
3. Los Coronados**	37	.31–.38(.34) ± .003	0.01	2.94	36	.30–.36(.32) ± .002	0.01	3.12
4. San Benito Is.	11	.26–.36(.31) ± .02	0.02	6.45	12	.28–.41(.31) ± .01	0.03	10.71
5. Guadalupe Is.**	26	.26–.34(.29) ± .003	0.01	3.44	21	.25–.32(.28) ± .003	0.01	3.57
		Wing						
1. Northern Channel Islands	10	115–124(120.3) ± .94	3.00	2.49	8	119–126(122.5) ± .68	1.93	1.57
2. Southern Channel Islands	1	110			2	115–117(116)		
3. Los Coronados	44	115–125(119.1) ± .41	2.66	2.23	37	115–127(120.0) ± .53	3.20	2.66
4. San Benito Is.	13	111–123(118.5) ± .87	3.15	2.65	12	115–125(120.5) ± .84	2.91	2.41
5. Guadalupe Is.	29	114–128(119.3) ± .72	3.87	3.24	23	115–127(120.5) ± .66	3.18	2.63
		Tarsus						
1. Northern Channel Islands	10	23.4–25.5(24.5) ± .21	0.67	2.73	8	23.8–26.0(24.9) ± .28	0.75	3.01
2. Southern Channel Islands	1	23.8			2	23.5–25.8(24.6)		
3. Los Coronados	40	22.9–25.3(24.2) ± .08	0.52	2.14	37	22.3–25.5(24.4) ± .11	0.67	2.74
4. San Benito Is.	13	22.4–25.2(23.6) ± .26	0.93	3.94	12	22.0–26.9(23.9) ± .34	1.17	4.89
5. Guadalupe Is.	29	21.2–25.4(23.5) ± .15	0.85	3.61	23	21.8–27.5(23.8) ± .27	1.32	5.54
		Weight						
1. Northern Channel Islands	8	150–185(166.1)			5	156–184(173.2)		
4. San Benito Is.	9	134–161.5(148.0)			8	130–162.5(148.4)		
5. Guadalupe Is.	8	138–177(153.4)			8	148–185(168.1)		

**Sexual size differences significant at $P < 0.01$

Guadalupe population. The situation on the San Benitos is discussed below.

Northern populations.—Plumage characters do not allow separation of Channel Islands and Los Coronados birds. However, males from Los Coronados have significantly longer and thinner bills; significant size differences are not demonstrable among females, although the general trends noted above persist (Table 2).

TABLE 2. A statistical comparison (t-test) of size characters among several populations of Xantus' Murrelet *(Endomychura hypoleuca)*. Values for males are given to the top and right, for females to the bottom and left.

		Channel Is.	Los Coronados	San Benitos	Guadalupe
	Bill Length		P<.001	P<.001	P<.001
	Bill Depth		NS	.01>P>.001	P<.001
Channel Is.	Ratio		.01>P>.001	P<.001	P<.001
	Wing		NS	NS	NS
	Tarsus		NS	.05>P>.02	.02>P>.01
	Bill Length	NS		.1>P>.05	P<.001
	Bill Depth	NS		.01>P>.001	P<.001
Los Coronados	Ratio	NS		P<.001	P<.001
	Wing	NS		NS	NS
	Tarsus	NS		.02>P>.01	P<.001
	Bill Length	NS	NS		.1>P>.05
	Bill Depth	.02>P>.01	.01>P>.001		NS
San Benitos	Ratio	NS	NS		.02>P>.01
	Wing	NS	NS		NS
	Tarsus	NS	NS		NS
	Bill Length	P<.001	P<.001	P<.001	
	Bill Depth	.02>P>.01	P<.001	NS	
Guadalupe	Ratio	P<.001	P<.001	.01>P>.001	
	NS	NS	NS		
	NS	NS	NS		

Guadalupe Island.—As Green and Arnold (1939) reported, face pattern distinguishes the Guadalupe Island population *(hypoleuca)* from populations on more northern islands *(scrippsi)*. In Guadalupe birds the white of the face extends up in front of (and occasionally over) the eye, and onto the ear coverts; this condition is also present in the downy young. All but one of the specimens we examined had a face pattern of Class "0" or "1", the exception being a female that "had laid" taken by the POBSP in April 1968. Jehl has examined over 80 living murrelets at Guadalupe, either taken from nesting burrows or captured aboard ship, and all were "white-faced." Guadalupe birds also have longer, thinner bills than other populations of Xantus' Murrelet, and in bill size and proportions more closely resemble *craveri*.

Mensural differences alone are sufficient to distinguish the Guadalupe population. Males differ significantly from Channel Islands and Los Coronados birds in bill length, bill depth, bill ratio, and tarsus length, and females differ in bill length, bill depth, and bill ratio. As would be expected, the Guadalupe population shows fewer differences from the mixed San Benitos population; nevertheless, bill depth of Guadalupe males is significantly less, and females are significantly longer and thinner billed (Tables 1, 2).

The San Benitos.—The situation on the San Benitos is complicated in that birds typical of both *scrippsi* and *hypoleuca*, as well as intermediates, are present and apparently breeding. Van Rossem (1939) failed to appreciate the mixed nature of this population and described it as a new race, *pontilus*, which he said differed from *scrippsi* "in having the inner webs of the outer primaries with a light brown area next to the shaft; neck outline between dorsal and ventral areas very close to that of *Brachyramphus hypoleucus craveri* (Salvadori); bill shape intermediate between *scrippsae* (sic) and *craveri*, but perhaps closer to the former."

San Benitos birds are, on the average, thinner billed than those from more northern populations (Table 1), but are stouter billed than Guadalupe birds. However, we are unable to confirm the other differences alleged by van Rossem. Our

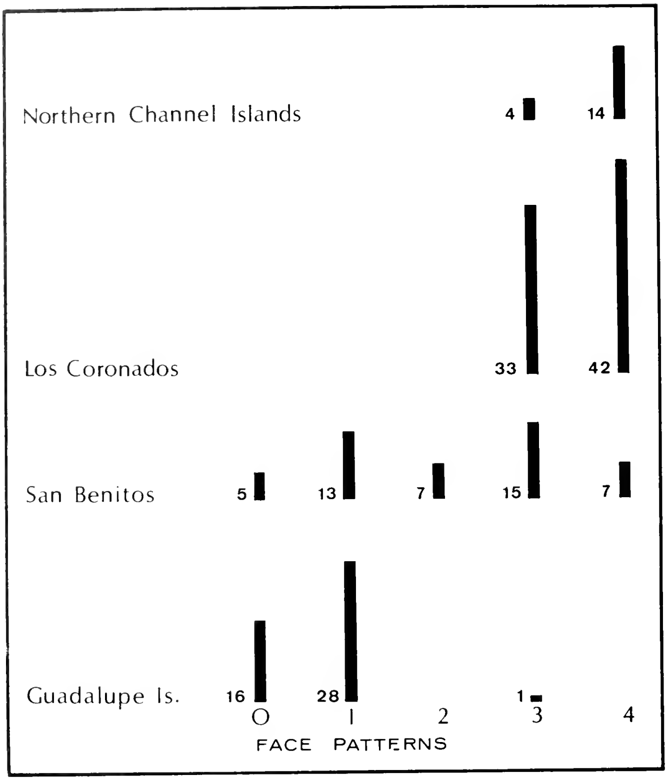


Figure 3. Geographic variation in face patterns among breeding populations of *Endomychura hypoleuca*. Character states (0-4) are illustrated in Figure 2.

sample included 7 of the 10 specimens on which he based his new race (type not examined), and from these it is clear that the alleged ventral extension of the dark collar is due to the make of the skins — in this case with the neck highly compressed. We can determine no differences in primary pattern among birds of any of the several populations.

San Benitos birds average intermediate in size between the Los Coronados and Guadalupe Island Populations, yet in several characters differ significantly from those populations (Table 2). Note, also, that variation in most characters is higher than elsewhere — which is further evidence of the composite origin of this population. Perhaps the greatest variability is shown in face pattern, which encompasses the entire range of variation in the species (Figs. 3, 4).

Sexual dimorphism.—Females of *E. hypoleuca* tend to have longer bills, wings, and tarsi than males but the differences are not significant. Bill depth of males averages greater, and in the Guadalupe and Los Coronados populations males are significantly heavier-billed ($P<.01$) than females. There are no sexual differences in coloration (Table 1).

Endomychura craveri

Measurements of Craveri's Murrelets are given in Table 3. The sample was subdivided into specimens from three probable breeding areas: Northern Gulf of

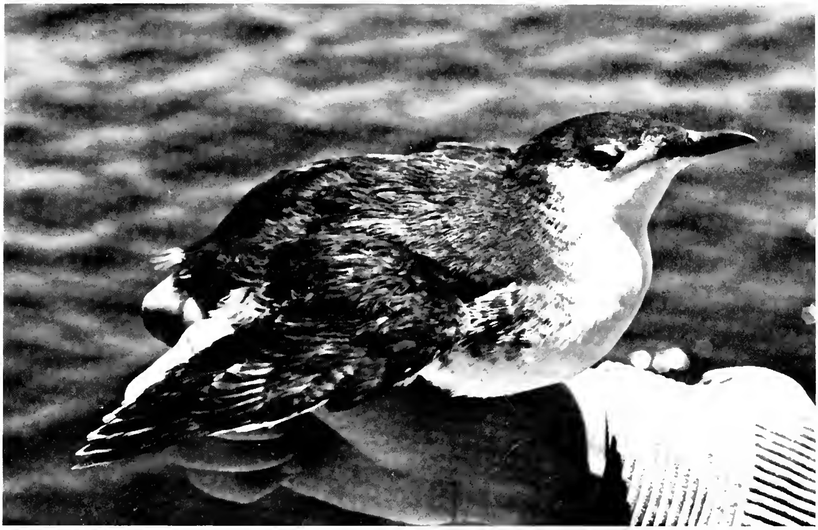


Figure 4. An example of *Endomychura hypoleuca* with an intermediate face pattern ("2"), captured aboard ship at the San Benito Islands, 26 May 1971.

California (islands off Baja California Norte), Southern Gulf of California (islands off Baja California Sur), west coast of Baja California (Magdalena Bay to Cabo Colnett). A fourth sample comprises birds collected off northern Baja California and California following the breeding season.

No statistical differences or trends in mensural characters could be demonstrated among the three putative breeding populations, and the data from all areas were combined. No plumage differences are evident. The face pattern is uniform (Class "5") in all populations. There is considerable variation in underwing coloration, but because of the make of the skins this character could not be analyzed in detail — it does not seem to vary geographically.

Post-breeding birds from northern Baja California and California differ significantly from breeding populations: 1) males and females average longer-billed ($P<.001$); 2) the bill depth of males averages smaller ($.01>P>.001$); 3) the bill ratio is smaller in both sexes ($P<.001$); 4) and post-breeding birds tend to have longer wings (males, $.1>P>.05$; females, $.05>P>.02$). The vast majority of these birds were collected in Monterey Bay in the autumns of 1907 and 1909. Since it is untenable to suggest that they were derived from a morphologically distinct but unknown breeding population, the differences could reflect a) selection for larger birds to disperse more widely (Monterey is near the northern limit of the species' range), or b) differences in the age composition of the post-breeding sample. The second alternative seems likely, as the Monterey population doubtless includes immatures as well as adults. We attribute the relatively shallow bill of the Monterey sample to the presence of juveniles, whole bill growth was incomplete. Longer wings probably result from a recent molt. The relatively long bill is less easy to explain. Breeding birds suffer extensive wear of the body plumage and, probably, bill tip as well, as they scramble among rocks and into their nest crevices. We suspect that the "increased" bill length is merely a return to unworn dimensions. Bill lengths of birds taken in September off Monterey average 0.4 mm longer than those taken in August.

Sexual dimorphism.—As in *E. hypoleuca*, bill length and tarsus length average

TABLE 3. Measurements of Craveri's Murrelet *(Endomychura craveri)*

	Male				Female			
Area	No.	Range, mean and S.E.	S.D.	C.V.	No.	Range, mean and S.E.	S.D.	C.V.
				Exposed Culmen				
1. Northern Gulf of California	11	18.6-21.3(19.95) ± 0.23	0.78	3.90	11	18.2-21.9(19.80) ± 0.30	1.02	5.15
2. Southern Gulf of California	21	18.0-22.5(19.77) ± 0.22	1.04	5.26	10	18.6-21.8(19.99) ± 0.33	1.04	5.20
3. West Coast of Baja California	10	19.0-21.0(19.67) ± 0.24	0.73	3.70	8	18.7-21.2(19.72)		
Areas 1-3	42	18.0-22.5(19.80) ± 0.14	0.92	4.64	29	18.2-21.9(19.86) ± 0.19	1.00	5.03
4. California and Northern Baja California	34	18.0-21.7(20.87) ± 0.10	0.78	3.73	21	19.1-22.4(20.99) ± 0.17	0.81	3.85
				Bill Depth				
1. Northern Gulf of California	11	5.3-5.9(5.56) ± 0.05	0.19	3.41	10	5.2-5.7(5.43) ± 0.04	0.14	2.57
2. Southern Gulf of California	22	4.9-5.8(5.39) ± 0.05	0.23	4.26	10	5.0-5.6(5.27) ± 0.18	0.18	3.41
3. West Coast of Baja California	9	5.1-5.6(5.37) ± 0.04	0.14	2.61	8	4.9-5.7(5.31)		
Areas 1-3*	43	4.9-5.9(5.43) ± 0.03	0.22	4.05	28	4.9-5.7(5.34) ± 0.03	0.18	3.38
4. California and Northern Baja California	35	4.7-5.7(5.28) ± 0.03	0.23	4.35	24	4.6-5.7(5.25) ± 0.05	0.26	4.95
				Bill Ratio				
1. Northern Gulf of California	11	0.25-0.31(0.27) ± 0.005	0.01	3.70	11	0.25-0.30(0.27) ± 0.004	0.01	3.70
2. Southern Gulf of California	21	0.24-0.30(0.27) ± 0.003	0.01	3.70	10	0.25-0.29(0.26) ± 0.004	0.01	3.84
3. West Coast of Baja California	10	0.24-0.29(0.27) ± 0.004	0.01	3.70	8	0.25-0.30(0.27)		
Areas 1-3	42	0.24-0.31(0.27) ± 0.002	0.01	3.70	29	0.25-0.30(0.27) ± 0.002	0.01	3.84
4. California and Northern Baja California	34	0.21-0.29(0.25) ± 0.002	0.01	4.00	22	0.23-0.27(0.25) ± 0.002	0.01	4.00
				Wing				
1. Northern Gulf of California	11	112-123(116.6) ± 0.98	3.28	2.81	12	115-122(118.7) ± 0.60	2.02	1.70
2. Southern Gulf of California	21	107-119(115.4) ± 0.74	1.43	1.24	10	111-123(117.8) ± 1.11	3.51	2.97
3. West Coast of Baja California	9	111-121(116.5) ± 1.11	3.15	2.71	8	116-119(117.5)		
Areas 1-3*	41	107-123(116.1) ± 0.49	3.08	2.65	30	111-123(117.8) ± 0.49	2.59	2.18
4. California and Northern Baja California	36	111-122(117.4) ± 0.43	2.63	2.24	26	114-124(118.9) ± 0.56	2.85	2.39
				Tarsus				
1. Northern Gulf of California	11	21.9-23.5(22.67) ± 0.15	0.51	2.25	11	22.4-23.8(22.88) ± 0.13	0.43	1.88
2. Southern Gulf of California	22	21.0-24.4(22.95) ± 0.17	0.82	2.78	10	22.0-24.1(22.96) ± 0.22	0.71	3.09
3. West Coast of Baja California	10	21.8-24.4(23.29) ± 0.27	0.82	3.53	8	22.6-24.4(23.27)		
Areas 1-3	43	21.0-24.4(22.93) ± 0.12	0.78	3.40	29	22.0-24.4(23.01) ± 0.11	0.60	2.60
4. California and Northern Baja California	34	21.4-24.4(23.04) ± 0.11	0.66	2.86	26	22.2-24.5(23.24) ± 0.11	0.57	2.45
				Weight				
Area 3 (San Benito Is. April-May)	6	128-149(137.1)			5	131-137(134.8)		

*Sexual size differences significant at P<0.05

greater in females, and wing length is significantly greater (.05>P>.01). Among breeding populations bill depth of males is greater (.05>P>.02), and there is a tendency for the bill ratio to be larger as well. There are no sexual differences in coloration (Table 3).

DISCUSSION

As shown above, size varies clinally in *E. hypoleuca*, birds in the southern part of the range having longer and thinner bills but shorter wings and tarsi. These trends are, in all cases, toward the condition shown by *E. craveri* (cf. Tables 1, 3). On the other hand, *craveri* shows no geographic variation in size, and specifically *does not* show trends toward *hypoleuca (sensu lato)* as it approaches the zone of contact. This fact, plus the absence of intergradation in face pattern or underwing coloration in the mid-peninsula region, indicates that *hypoleuca* and *craveri* are behaving as distinct species — a conclusion that gains support from field observations of assortatively mated pairs in this area.

If hybridization between *hypoleuca* and *craveri* is occurring, it seems to be extremely rare. Van Rossem (1939) considered an unsexed specimen from Natividad Island, collected on 9 April 1897, (now Carnegie Mus. 22965) "exactly intermediate in all particulars . . ." Unaware of van Rossem's opinion, we independently discovered this specimen and noted its unusual combination of characters. Its measurements (exposed culmen 19.4 mm; bill depth 5.1 mm; bill ratio 0.26; wing 111 mm; tarsus 22.2 mm), with one exception, are within the range of either species, though much closer to the mean values for *craveri;* bill depth is smaller than that of any *hypoleuca* examined. Its face pattern and brownish tinge to the back are also like that of *craveri* and the undersides of the outer primaries are dark. However, the ventral extension of the collar seems less pronounced than in most examples of *craveri* and the underwing is mainly white, with only a few grayish feathers, as in *hypoleuca.* The specimen is certainly closer to *craveri*, but we suspect that it is of hybrid origin.

The taxonomic status of Xantus' Murrelet populations is less clear. *E. h. hypoleuca* and *E. h. scrippsi* are as distinct from each other morphologically as either is from *E. craveri* and on that basis two species of "Xantus'" murrelets might be recognized. However, these forms evidently interbreed where they come in contact, because intermediate face patterns (Class "2") occur only in the San Benitos. Although the categorization of face patterns is subjective, it is evident that the distribution of face pattern character states is strongly bimodal, with parental types (Classes "0" and "1" vs. "3" and "4") predominating (Figure 3). (In this population bill length, bill depth, and bill ratio are strongly correlated with face pattern [$P \cong .01$; $.05 > P > .01$; and $P > .01$ respectively] but bimodality cannot be demonstrated in those characters because of extensive overlap in dimensions between the parental populations). This indicates non-random mating and suggests that some isolating mechanisms between these populations are operating. Whether interbreeding will lead to strengthening of the isolating mechanisms or to swamping of populational differences is uncertain. For the time being, we consider it preferable to continue to recognize *hypoleuca* and *scrippsi* as well-marked races of Xantus' Murrelet, realizing that the divergence may have already passed that stage.

One difficulty in analyzing the San Benitos situation is the lack of historical information. Birds with intermediate face patterns were present in the 1890's, but the earliest collection of *E. h. hypoleuca* there was in 1968, and this form now comprises a large fraction of that population (Fig. 3). Green and Arnold (1939) and DeLong and Crossin (MS) both mention that breeding colonies on islets at Guadalupe Island appear overcrowded, and it may be that birds have shifted to the San Benitos — the nearest alternate breeding site — very recently.

Isolating Mechanisms

If *E. craveri* and *E. hypoleuca* are distinct species what isolating mechanisms are fuctioning to restrict interbreeding? We know very little about the breeding behavior of these birds, but the following might be involved.

Voice.—Murrelets are vocal at sea during the breeding season, especially at night when singing birds congregate on the water near breeding colonies. The "song" is a trilling whistle given on one pitch which to Jehl's ear is slightly drier and less musical in *craveri.* These songs are so similar that we doubt they play any role in species recognition, but further analysis is warranted.

Timing of the breeding season.—Straggering of the breeding seasons is a potentially useful mechanism for reducing the potential for interbreeding among closely related, sympatric species. In the Gulf of California Craveri's Murrelets apparently begin to pair in late December; chicks have been reported as early as March and large young as late as June. The peak of hatching in most years probably occurs in April (DeWeese and Anderson, MS). Xantus' Murrelets in California nest much later. Egg dates (376 sets) on Los Coronados range from 4 April to 6 July, with the peak of laying from 15 to 20 May. Similar periods have been recorded for the Channel Islands. At Guadalupe, nesting is slightly earlier, the peak of laying occurring between mid-April and early May.

Breeding phenology on the San Benitos is less clear. We know of seven sets of eggs taken between 10 March and 26 April; Kaeding (1905) also reported nests in late March. Presumably these records all pertain to *hypoleuca,* as all of the specimens that we have examined from these islands taken prior to 1968 were collected in March and all were Xantus'. Further, Kaeding specifically stated that none of the birds he saw had characters of *craveri.* In the winters of 1971-1973, staff members of the San Diego Natural History Museum made weekly visits to the San Benitos from mid-January to mid-March. Casual observations indicated that singing murrelets had congregated near the islands by January, but all that were captured aboard ship or identified in the ship's lights were reported as Xantus'. Our earliest record of *craveri* is a bird found dead in a life boat on 4 April 1971. By late April and May however, *craveri* seems to comprise 20–30% of the population. These data are insufficient to prove asynchronous nesting. But if *craveri* does nest on the San Benitos, its nesting period seems retarded as compared to the Gulf population, and later than that of *hypoleuca* in the area of overlap.

Face pattern and bill shape.—Although *Endomychura* murrelets lack the facial plumes and bill ornamentation that are highly developed in many other alcids, differences in face pattern and bill shape are sufficient to allow rapid species identification and to function as isolating mechanisms. *E. craveri* and *E. h. scrippsi* have similar face patterns but distinct bill shapes. Bill shapes of *craveri* and *E. h. hypoleuca* are similar, but these taxa differ completely in face pattern. A combination of face and bill characters distinguishes *E. h. hypoleuca* from *E. h. scrippsi.* The ranges of these three taxa are essentially parapatric, and it is conceivable that the differences among the several populations constitute a complex pattern of character displacement.

Relationships of *Endomychura*

Many authors have treated *Endomychura* as a synonym of *Brachyramphus,* and that merging has recently been re-advanced, without justification, by Mayr and Short (1970). Yet, as long ago as 1945, Storer showed that morphology, plumage, and nesting habits clearly separated the Marbled and Kittlitz' murrelets *(B. marmoratus* and *B. brevirostris)* from other murrelets including *Endomychura,* and that *Endomychura* was more closely allied to *Synthiloboramphus* than to other alcid genera. Storer's position is further confirmed by the color patterns of the downy young, which form an almost perfectly graded series from *Synthilobor-*

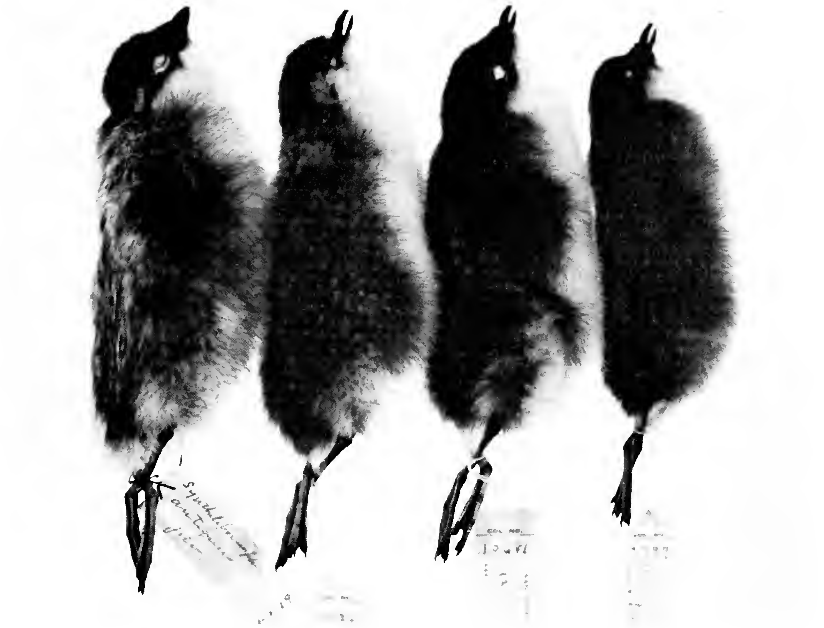


Figure 5. The downy young of *Synthiloboramphus antiquus*, *Endomychura hypoleuca hypoleuca*, *E. h. scrippsi*, and *E. craveri*.

amphus to *craveri* (Fig. 5), and which differ markedly from the color patterns of *Brachyramphus* chicks (Thompson, Hines, and Williamson, 1966; Singer and Verardo, 1975). In *Synthiloboramphus* chicks the dorsum is extensively reduced with gray, resulting in a frosty appearance; the frosting is progressively reduced in *E. h. hypoleuca* and *E. h. scrippsi* and is lost in *E. craveri.* A similar cline is evident in face pattern: *Synthiloboramphus* shows a white postocular spot that is separated from the whitish venter by a thin dark line; in *E. h. hypoleuca* the line is absent but the white of the underparts extends up behind the eye; in *E. h. scrippsi* and *E. craveri* the post-orbital spot has been lost.[2]

Perhaps of greater interest is that the adult morphology of *Synthiloboramphus* also fits the general pattern of geographic variation in *Endomychura.* Considering *Synthiloboramphus-Endomychura* as an evolutionary unit, we find a rough cline from a relatively large (long-winged, long-legged) but short and deep-billed murrelet in the north *(Synthiloboramphus)* to a smaller (shorter wings and tarsi) but longer and thinner-billed southern form *(craveri;* Table 4).

Recently, Cody (1973) has attempted to analyze the structure of alcid communities in ecological terms (see Bedard, in press, for a critique of Cody's approach). It should be obvious that success in modeling community structure depends upon knowledge of the *biology* of the component species and a firm understanding of their evolutionary histories. In the present case, the reasons for the pattern of clinal variation shown in *Synthiloboramphus-Endomychura* remain to be determined. While they might involve the effects of selection from potential competitors, it seems more likely that they reflect the operation of the well-known (if controversial) "Ecogeographic Rules" of Bergmann and Allen.

---

[2] In a paper received while this paper was in galleys, Binford, Elliott, and Singer (1975, Wilson Bulletin, 87: 303-319) described the young of *Brachyramphus marmoratus* and compared it with chicks of *Synthiloboramphus* and *Endomychura.* The taxonomic conclusions they reached are identical to ours.

TABLE 4. Patterns of Morphological Variation in *Synthiloboramphus-Endomychura*

	Mean dimensions (mm)[1]				
Taxon	**Culmen**	**Bill Depth**	**Bill Ratio**	**Wing**	**Tarsus**
S. antiquus	13.2	6.55	.49	135	26.5
E. h. scrippsi	17.0	6.17	.35	120.3	24.5
E. h. hypoleuca	19.3	5.78	.31	118.5	23.5
E. craveri	19.8	5.43	.27	116.1	22.9

[1] Dimensions for *Synthiloboramphus* based on Ridgway (1919) and specimens in San Diego Natural History Museum; for *Endomychura* data are abstracted from Tables 1 and 2 (males only).

ACKNOWLEDGMENTS

We are indebted to L. C. Binford, T. R. Howell, W. E. Lanyon, N. K. Johnson, I. McT. Cowan, K. C. Parkes, S. Rowher, K. E. Stager, and R. L. Zusi for allowing us to examine specimens in their care. Transportation and field work in Baja California was provided by: Thomas P. Hearne; Scripps Institution of Oceanography, through Carl L. Hubbs; and the Los Angeles County Museum of Natural History, through K. E. Stager. Philip Unitt assisted in the calculations. Miss Gail Culver prepared Figures 1 and 3, and Ken Goldman executed Figure 2. Extensive information on the breeding seasons of murrelets was kindly made available through Lloyd F. Kiff from the collections of the Western Foundation of Vertebrate Zoology. D. W. Anderson and R. W. Storer commented on a draft of the manuscript.

LITERATURE CITED

American Ornithologists' Union, 1957. Check-List of North American Birds. Fifth Ed., Lord Baltimore Press, Baltimore, Md.

Anthony, A. W., 1900. Notes on the genus Micruria. Auk 17: 168-169.

Bedard, J. [MS.]. Coexistence, coevolution and convergent evolution in seabird communities. Ecology, in press.

Cody, M. L., 1973. Coexistence, coevolution and convergent evolution in seabird communities. Ecology 54: 31-44.

Coues, E., 1884. Key to North American Birds. Estes and Lauriat, Boston.

Cowan, I. MC T., and P. W. Martin, 1954. A new northern record of Xanthus [sic] Murrelet, *Brachyramphus* [sic] *hypoleuca*. Murrelet 35: 50.

Dawson, W. L., 1923. The birds of California. South Moulton Co., San Diego.

De Long, R. L., and R. S. Crossin, [MS.]. Status of seabirds in Islas de Guadalupe, Natividad, Cedros, San Benitos, and Los Coronados.

De Weese, L., and D. W. Anderson, [MS.]. Distribution and breeding biology of Craveri's Murrelet. Trans. San Diego Soc. Nat. Hist., in press.

Feinstein, B., 1958. Xantus' Murrelet *(Endomychura hypoleuca scrippsi)* from the State of Washington. Auk 75: 90-91.

Freidmann, H., L. Griscom, and R. T. Moore, 1950. Distributional Check-List of the birds of Mexico. Part I. Pacific Coast Avifauna No. 29.

Green, J. E., and L. W. Arnold, 1939. An unrecognized race of murrelet on the Pacific coast of North America. Condor 41: 25-29.

Grinnell, J., 1915. A distributional list of the birds of California. Pacific Coast Avifauna No. 11.

Grinnell, J. 1928. A distributional summation of the ornithology of Lower California. University of California Publications in Zoology 32: 1-300.

Howell, A. B., 1912. Notes from Todos Santos Islands. Condor 14: 187-191.

Howell, A. B., 1917. Birds of the islands off the coast of Southern California. Pacific Coast Avifauna No. 12.

Jehl, J. R., Jr., 1974. The near-shore avifauna of the Middle American west coast. Auk 91: 681-699.

Jehl, J. R., Jr. [MS.]. A Craveri's Murrelet from Oregon. Western Birds, in press.

Kaeding, H. B., 1905. Birds from the west coast of Lower California and adjacent islands. Condor 7: 105-138.

Lamb, C. C., 1909. Nesting of the Xantus Murrelet as observed on Los Coronados Islands, Lower California. Condor 11: 8-9.

Lamb, C. C., 1927. The birds of Natividad Island, Lower California. Condor 29: 67-70.

Mayr, E., and L. L. Short, 1970. Species taxa of North American birds. Publications of the Nuttall Ornithological Club. No. 9. Cambridge, Mass.

Ogilvie-Grant, W. R., 1898. Catalogue of birds in the collection of the British Museum, Vol. 26. British Museum (Natural History), London.

Peyton, S. B., 1913. A collecting trip to Anacapa Island. Oologist 30: 78.

Ridgway, R., 1919. The birds of North and Middle America, Part VIII. United States National Museum Bulletin 50.

Sanger, G., 1973. New northern record for Xantus' Murrelet. Condor 75: 253.

Scott, J. M., J. Butler, W. G. Pearcy, and G. A. Bertrand, 1971. Occurrence of the Xantus' Murrelet off the Oregon coast. Condor 73: 254.

Singer, S. W., and D. R. Verardo, 1975. The murrelet's nest discovered. Pacific Discovery

28: 18-21.

Storer, R. W., 1945. The systematic position of the murrelet genus *Endomychura*. Condor 47: 154-160.

Thompson, M. C., J. Q. Hines, and F. S. L. Williamson, 1966. Discovery of the downy young of Kittlitz' Murrelet. Auk 83: 349-351.

Van Denburgh, J., 1924. The birds of the Todos Santos Islands. Condor 26: 67-71.

van Rossem, A. J., 1926. The Craveri Murrelet in California. Condor 28: 80-83.

van Rossem, A. J., 1939. Some new races of birds from Mexico. Annals and Magazine of Natural History, ser. 2, 4: 439-443.

Wetmore, A., et. al., 1944. Nineteenth supplement to the American Ornithologists Union Check-List of North American Birds. Auk 61: 441-464.

Willet, G., Birds of the Pacific slope of southern California. Pacific Coast Avifauna No. 7.

Wright, H., and G. K. Snyder, 1913. Birds observed in the summer of 1912 among the Santa Barbara Islands. Condor 15: 86-92.

APPENDIX I

Specimens examined

Endomychura craveri

Northern Gulf of California: Tiburon Island and vicinity-12; Partida Island-3; Bahía de los Angeles-3; San Esteban Island-1; Pond Island-3. Dates: 8 March - 20 April.

Southern Gulf of California: Ildefonso Island and vicinity-17; San Francisco Island-5; San José Island-16; Roca El Cayo-1; Puerto San Carlos, Sonora-1. Dates: 6 February - 1 May.

West Coast of Baja California: Bahía San Juanico-1; Magdalena Bay-1; San Benito Islands-12; Pequina Point (near San Ignacio Lagoon)-1; Cedros Island-1; Cabo Colnett-1; San Martín Island-1. Dates: 8 February - 13 June.

California and Northern Baja California (post-breeding): Oregon-1; Monterey Bay, Ca.-29; Catalina Channel, Ca.-1; Off San Diego and Los Coronados-2; Off San Pedro, Ca.-1; Los Angeles County, Ca.-1; Off Pta. San Ysidro, B. C.,-1; San Martín Island, B. C-1. Dates: 4 August - 6 October.

Endomychura hypoleuca

California: Prince Islet, San Miguel Island-13; Anacapa Island-5. 6 May - 4 June.

Baja California: Los Coronados-87; San Benito Islands-25 (plus 22 banded); Guadalupe Island-54. 11 February - 13 July.

Non-breeding birds. Off Washington State-1. California: Monterey Bay-24; Santa Cruz Island-1; Santa Barbara Island-2; Off San Luis Obispo-1; Santa Catalina Island-2; Catalina Channel-2; Los Angeles County-7; Orange County-1; Off San Diego-8. Baja California: Off Northern Baja California-1; 150 mi NW Guadalupe Island-1. Dates: Entire year, but mainly late summer-early spring.

APPENDIX II

Distribution of *Endomychura* murrelets

Endomychura craveri.—Breeds on islands in the Gulf of California from Consag Rock to Isla del Espiritu Santo (DeWeese and Anderson, MS). Probably breeds on islands along the west coast of Baja California from Magdalena Bay (Sta. Margarita Island) to the San Benitos (this paper), and perhaps slightly farther northward. Post-breeding birds wander northward, irregularly, to Monterey, California; one Oregon record (Jehl, in press). April sight record off Guatemala (Jehl, 1974).

Endomychura hypoleuca hypoleuca.—Breeds on Guadalupe Island, Baja California, and presumably on the San Benitos, where it hybridizes with *E. h. scrippsi.* Post-breeding distribution poorly known. Type specimen taken off Cabo San Lucas, B. C. in mid-July. Apparently wanders regularly to southern California (specimen 150 mi NW Guadalupe Island; 2 juveniles from Catalina Channel, Ca.) and perhaps well beyond. Two birds (mated pair?) taken well off Cape Flaherty, Wash. (Cowan and Martin, 1954) are referable to this race (racial identity determined by us).

Endomychura hypoleuca scrippsi.—Breeds or formerly bred on near-shore island, of California and Baja California, from Prince Islet, San Miguel Island, to the San Benitos. Apparently extirpated on the Todos Santos Islands and San Martín and perhaps elsewhere. May have formerly bred on Natividad Island. After breeding, ranges to northern California, occasionally to Oregon and Washington (Scott et al., 1971; Sanger, 1973 [specimen examined by us]; Feinstein, 1958 [specimen examined by us]).

Department of Birds and Mammals, Natural History Museum, San Diego, California 92112.

PLUVIANELLUS SOCIALIS: BIOLOGY, ECOLOGY, AND RELATIONSHIPS OF AN ENIGMATIC PATAGONIAN SHOREBIRD.

Joseph R. Jehl, Jr.

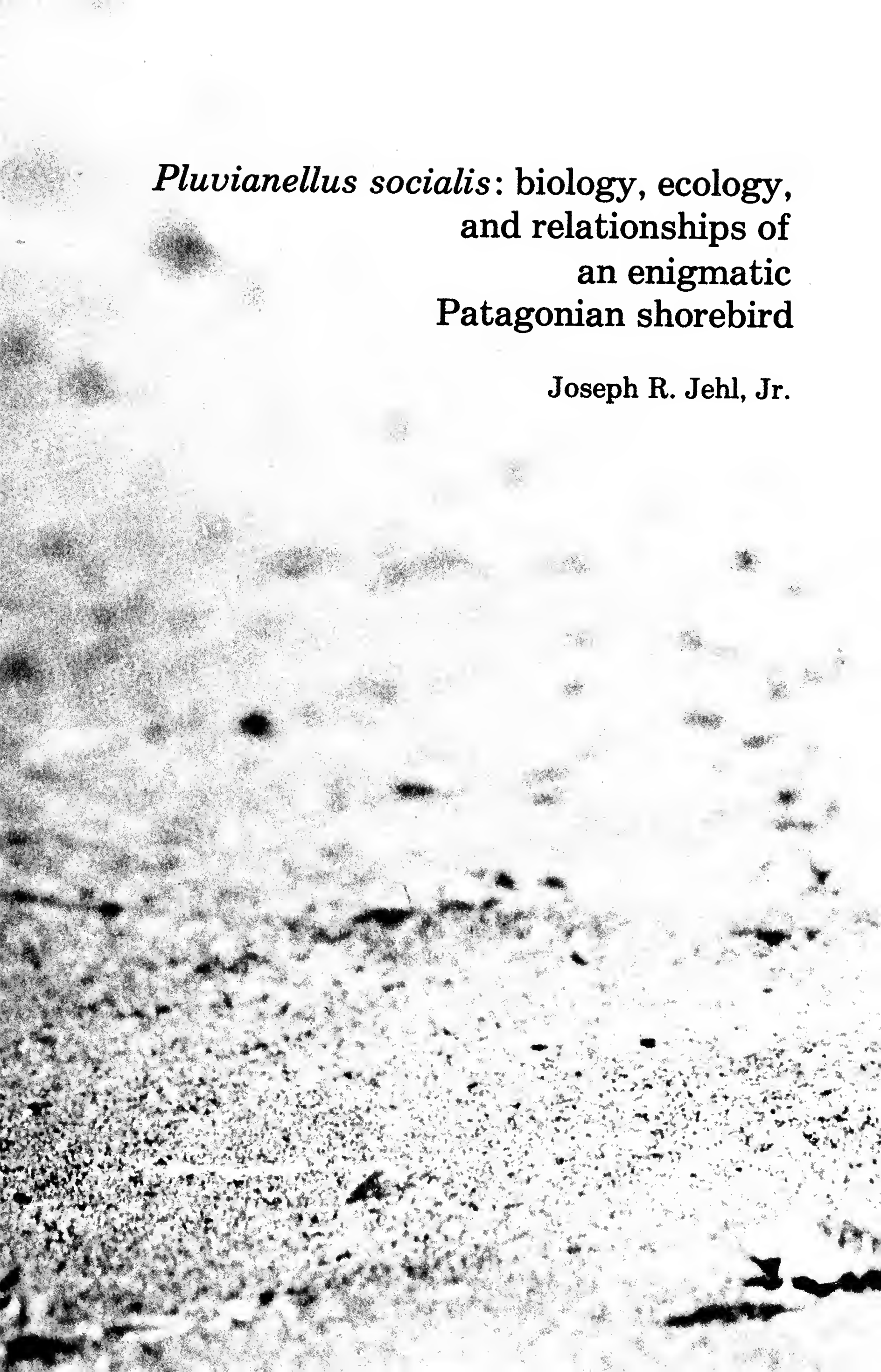
TRANSACTIONS

OF THE SAN DIEGO
SOCIETY OF
NATURAL HISTORY

VOL. 18, NO. 3 5 DECEMBER 1975

Pluvianellus socialis: biology, ecology, and relationships of an enigmatic Patagonian shorebird

Joseph R. Jehl, Jr.



Transactions of the San Diego Society of Natural History
Volume 18, number 3, pages 25-74
Issued December 5, 1975

Figure 1. *Pluvianellus socialis*, photographed at Laguna de los Cisnes, Isla Grande, Tierra del Fuego, Argentina.

CONTENTS

The windswept tip of South America had been of great interest to biologists even before Darwin, aboard H. M. S. *Beagle*, explored its waters in the early 1830's. The botanical findings by Joseph Banks on Capt. Cook's first voyage in 1769, the zoological observations of Quoy and Gaimard during the French "Voyage around the World" led by M. Freycinet from 1817-1820, and the discoveries of the British expedition to Patagonia and Tierra del Fuego (1826-1830) under Capt. Philip King, among others, alerted the western world to many undiscovered forms of life at the end of the continent.

In recent years, biological studies in the southern hemisphere have taken on added significance. Geological confirmation of plate tectonics theories has stimulated biologists to re-examine their data to determine whether the distributional patterns of some organisms might be better explained in light of past, rather than present, distribution of land masses. Indeed, it is now evident that even for such mobile creatures as birds events in the Mesozoic and Cenozoic must be taken into consideration in accounting for the present day distribution and evolution of some taxa (Cracraft, 1973; Rich, 1975).

The shorebird (Charadrii) fauna of southern South America and the nearby antarctic islands poses a special challenge to ornithologists, for it contains a high percentage of endemic taxa whose relationships are largely unresolved. These include: two families (Chionididae, Thinocoridae); four species of plovers *(Charadrius falklandicus, Charadrius [Zonibyx] modestus, Oreopholus ruficollis, Pluvianellus socialis),* three of which have been placed in monotypic genera; and a distinctive oystercatcher *(Haematopus leucopodus).*

The most interesting of these Fuegian shorebirds is *Pluvianellus socialis,* the so-called Magellanic Plover, a rare species whose breeding range was thought to be restricted to Tierra del Fuego (Peters, 1934; Olrog, 1948; Johnson and Goodall, 1965; Humphrey et al., 1970). Because of its rarity, limited distribution, and inconspicuousness, practically nothing has been recorded about its biology (see Humphrey et al., 1970, and references therein). In fact, the species itself escaped description until 1848.

Since its discovery, *Pluvianellus* has usually been considered a plover (Seebohm, 1887; Sharpe, 1896), even though no substantive reasons for that classification have been presented. Seebohm's opinion may have been influenced by Young's erroneous statement (*in* Seebohm, 1887) that its habits "closely resemble those of the Ringed Plover." Lowe (1931) included *Pluvianellus* in the Charadriidae, but admitted that he had not dissected the species and that its placement was open to question. In his review of the plovers, Bock (1958) called it a "nondescript and rather strange plover" and considered it "allied to the *Charadrius* group on the basis of past usage rather than on any strong evidence." Bock commented on the species' turnstone-like bill, and Jehl (1968) speculated that it might be more closely related to turnstones (Scolopacidae) than to plovers. Burton (1974), however, noted anatomical similarities to the plovers, but also showed that it differed from typical plovers in having a highly rhynchokinetic upper jaw.

None of the taxonomists who had hazarded opinions on *Pluvianellus* had ever seen the species in life, and on the basis of preserved material there seemed to be little reason to question its traditional placement among the plovers. Biological, behavioral, and ecological data from the present study, however, show that *Pluvianellus*[1] is a remarkably singular species, and they also suggest that its relationships are far less obvious than is currently supposed.

In 1971 and 1972 I studied wintering flocks of *Pluvianellus* at Golfo San José, Chubut Province, Argentina. Additional observations were made at Puerto Madryn, Chubut Province, and at Bahía de los Nodales, Santa Cruz Province. Details are

---

[1] In this paper I refer to *Pluvianellus* by its scientific rather than vernacular name, because in my view its affinities to the plovers have not been demonstrated.

Figure 2. *Pluvianellus socialis* (center) blends inconspicuously among a resting flock of Two-banded Plovers *(Charadrius falklandicus)*.

given under Winter Biology. In 1972 I was assisted by Jon P. Winter and by Maurice A. E. Rumboll, Naturalista de Campaña, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires. From 24 October to 13 November 1973, in the austral summer, again with the assistance of Sr. Rumboll, I studied the breeding biology of this species in Argentine Tierra del Fuego. Most of our observations were made at three localities: Laguna de los Cisnes, a fresh water lake immediately north of the airport at Rio Grande, where four pairs nested; a gravel pit along the highway 10 km north of Rio Grande (1 pair); and at Ea. Los Flamencos, 35m WNW of Rio Grande, where we found single pairs at each of two adjacent lakes. In addition, we surveyed a wide area of the island, from the Strait of Magellan to Ushuaia, to determine its breeding distribution and abundance. After leaving Tierra del Fuego we worked northward along Rte. 3, the major north-south highway in Argentina, as far as Bahía Blanca, investigating areas of suitable habitat.

GENERAL OBSERVATIONS

Despite its common name of Magellanic Plover, *Pluvianellus* is remarkably unploverlike (Fig. 1). It is a squat, short-legged bird with a small rounded head; its thick tarsi and stout, blunt toes and nails differ from those of typical plovers; and it has a well developed hind toe. In general, it is more reminiscent of a turnstone than a plover, and the resemblance is heightened by similar bill shapes and, in part, foraging behavior. It also resembles the small ground doves, such as *Columbigallina picui,* to an astonishing degree in coloration, morphology, and its flat-footed waddling gait.

The colors of its soft parts are unusual for a plover. The iris is bright coral pink and in excited breeding adults, at least, the inner rim is yellow. The legs and toes are also highly colored, varying from bright pink to orange-pink in adults and from orange to orange-yellow in juveniles. In adults the bill is black except for a small spot 1-2 mm long at the base of the culmen and another at the lateral base of the mandibular rami; these spots are yellowish in winter (pers. obs.), pinkish in summer (Reynolds, MS, cited by Humphrey et al., 1970), but they are so inconspicuous that I did not notice them even when watching nesting birds from a distance of several meters. In immatures the spots are yellowish-horn and are larger than in the adults. Their function, if any, remains to be determined.

As earlier writers have noted, *Pluvianellus* is extremely inconspicuous. Despite its broad white wing stripe, it is difficult to pick out among a mixed flock of flying shorebirds. On the ground its pale gray back and white underparts blend remarkably with a wide variety of beach substrates including muds, sands, and gravel, and careful observation is required to detect birds resting among flocks of Two-banded Plovers (Fig. 2). On several occasions I first realized the species' presence by noting the bright pink legs that were attached to an otherwise unnoticed gray lump. Active birds are easily picked out by their unique feeding behavior and leisurely but direct rolling walk, which distinguishes them at once from the erratically dashing plovers. When they stop, however, birds can seemingly vanish, even though they may be only a few meters away on an unobstructed mudflat. *Pluvianellus* also tends to be wary, especially on the wintering grounds, and often cannot be approached closer than 50 m without its taking flight. For these reasons, it is not an easy species to study. The necessity of making observations from a distance, while trying to find shelter from the ever-present Patagonian winds, makes it probable that many details of behavior and vocalization went unobserved.

External sexual differences are very slight, and most museum specimens cannot be sexed by differences in size or plumage. I made no attempt to distinguish sexes on the wintering grounds, but in observing mated pairs I found that one member was slightly larger and more intensely colored than its mate; its lores were blacker, the lower border of its chest band darker, and in some cases its legs were more brightly colored. Males average larger and heavier than females (Table 1), and I believe that the darker bird in each pair was the male; in one pair this was confirmed behaviorally. In any event, the intra-pair differences, though slight, were sufficient that I could usually determine the identity, if not the sex, of a particular individual.

TABLE 1. Dimensions of *Pluvianellus socialis*[1]

	Bill		**Wing**		**Tarsus**
N	Range and mean SD	N	Range and mean SD	N	Range and mean SD
♂11	14.2-16.4 (15.61) ± 0.66mm	11	131-140 (136.3) ± 2.59mm	11	19.9-22.2 (21.19) ± 0.69mm
♀13	14.0-15.1 (14.63) ± 0.33mm	14	131-140 (133.8) ± 2.48mm	12	18.9-22.0 (20.14) ± 0.78mm
	Tail		**Weight**		
♂10	59-67 (63.2) ± 2.0mm	5	79-102 (89.1)g.		
♀12	59-66 (62.8) ± 2.2mm	8	69.5-87.3 (79.5) ± 5.58g.		

[1] Based on specimens in the American Museum of Natural History, San Diego Natural History Museum, and Museo de Ciencias Naturales, Buenos Aires.

HABITAT AND DISTRIBUTION

Prior to this study *Pluvianellus* was known to nest only on Isla Grande, Tierra del Fuego. However, as Johnson and Goodall (1965) surmised, its breeding range is not so sharply restricted. It nests on the shores of shallow ponds, lagoons, and lakes, mostly of glacial origin, in the steppe regions of northern Tierra del

Figure 3. Typical nesting localities in Tierra del Fuego are on the shores of shallow lakes. In the top photograph the nest site is at the lower left; in the bottom photograph the position of the nest is indicated by a small pile of stones to the left of the blind.

Fuego and southern Patagonia (Fig. 3). Rumboll and I discovered nesting or apparently-nesting pairs in the vicinity of Rte. 3, between Cabo Peñas, Tierra del Fuego, and El Salado, Santa Cruz Province (Table 2).

The literature suggests that *Pluvianellus* breeds mainly in areas of brackish water. We found it on fresh water lakes as well as those that were slightly brackish; none had any outlet to the sea. We did not find it along the banks of rivers or streams, and searches along ocean beaches immediately adjacent to inland nesting areas failed to reveal even single, nonbreeding birds. Not all lakes are suitable for nesting. Beaches of intermixed small stones and mud with adjacent stretches of open shoreline are obvious requisites. Shallow lakes that dry rapidly in the summer are avoided, as are lakes with vegetation extending to the waterline. In Tierra del Fuego, where prevailing winds are strong northerlies and westerlies, gravel tends to accumulate along the south and east shores of the lakes. Since nesting territories require at least a small area of stony beach, residents could usually be found by searching carefully there. The size of the water body does not seem important: pairs occurred on small ponds of about an acre as well as on lakes several kilometers in length. At most lakes, however, areas of stony beach were quite limited, and as a result occupancy by more than one or two pairs—even at the largest lakes—seemed precluded by habitat limitations and by *Pluvianellus*' territorial requirements.

Physiographic features, however, are not the only criteria for occupancy, for *Pluvianellus* only occurred on lakes that were frequented by other shorebirds such as Two-banded Plover *(Charadrius falklandicus)*, Baird's Sandpiper *(Calidris bairdii)*, White-rumped Sandpiper *(Calidris fuscicollis)*, Wilson's Phalarope *(Phalaropus tricolor)*, Hudsonian Godwit *(Limosa haemastica)*, and Magellanic Oystercatcher *(Haematopus leucopodus)*. The underlying ecological basis for the general attractiveness of these ponds is unknown.

TABLE 2. Localities where *Pluvianellus socialis* was observed in October and November 1973. All are in Argentina unless noted otherwise.

Locality	Dates	Remarks
TIERRA DEL FUEGO		
Rio Grande, Laguna de los Cisnes	24 Oct.-13 Nov.	4 pairs nesting.
Rio Grande, gravel pit 10 km N of town	24 Oct.-13 Nov.	1 pair nesting.
Ea. Los Flamencos, Lago Cerro Conico	31 Oct.-13 Nov.	1 pair nesting; 1 additional pair (?)
Ea. Los Flamencos, lake 2 km W Lago Cerro Conico	31 Oct.-4 Nov.	1 pair nesting.
Laguna Cabo Peñas	30 Oct.	1 bird, nesting?
Chile, 10 km W San Sebastián	14 Nov.	1 bird in grassy pasture pond.
Chile, 30 km N San Sebastián	14 Nov.	1 bird on shore of shallow pond.
SANTA CRUZ PROVINCE		
Ea. Tres de Enero, 33 km S Rio Gallegos	14 Nov.	3 pairs and one partly-grown flying juvenile.
20 km S Ea. Coy Aike	15 Nov.	1 bird apparently on territory.
"Hotel Lemarchand"	15 Nov.	2 pairs defending territories.
35 km S Ea. Monte León	15 Nov.	1 bird on territory.
10 km W Cmte. Luis Piedrabuena	16 Nov.	1 pair on territory.
51 km S access road to San Julián on Rte. 3	17 Nov.	1 pair nesting.
31 km N San Julián	18 Nov.	1 pair plus 1 adult, territorial defense.
11 km S El Salado	18 Nov.	3 adults, 1 flying juvenile.

With an understanding of *Pluvianellus'* specialized requirements, one can fairly confidently infer the limits of its breeding range (Fig. 4).

Distribution in Tierra del Fuego.—*Pluvianellus* is not widespread on Isla Grande. On the Argentine side of the island its southernmost breeding site is probably Laguna Cabo Peñas. We found no nesting habitat south of that locality and Mr. Len Bridges of Ea. Viamonte confirmed that it did not nest farther south. (Reynolds' [1953] report of nesting at Cabo Viamonte, 20 km S. of Cabo Peñas is not fully convincing; see below). There appear to be no nesting ponds between Cabo Peñas and Rio Grande. Slightly north of Rio Grande a glacial morraine parallels the coast, behind which, extending up to 20 km inland, are a series of small lakes (including Laguna de los Cisnes). *Pluvianellus* nests on a few, but not a majority, of these inland to at least Ea. Los Flamencos. It is absent from the low, rolling hill country east of Rte. 3 between Rio Grande and Bahía San Sebastián. C. C. Olrog (pers. comm. to M. Rumboll) found birds nesting in the San Sebastián area, but we did not; all of the ponds we investigated there had low but steep sandy banks and lacked rocks. However, we saw two single birds at ponds a few kilometers inland from San Sebastián that were probably nesting nearby. Inland on the Chilean side as well as along the northern edge of Isla Grande the land is higher and provides few if any nesting areas. On the coast near Porvenir, however, there are a few small lagoons where *Pluvianellus* apparently nests fairly commonly (Olrog, 1948).

Distribution in Patagonia.—The mainland bordering the north shore of the Strait of Magellan is flat and dry, offering no nesting habitat. Beginning slightly farther north, maps show that the steppe grassland that extends inland for over 100 km between Rio Gallegos and Puerto Santa Cruz is dotted with hundreds of small lakes. This may be *Pluvianellus'* major breeding area, for we found pairs at about half of the ponds we investigated, as much as 40 km inland, along Rte. 3. North of Puerto Santa Cruz the land is much higher and ponds are scarce, but *Pluvianellus* occurs where conditions are suitable. Our northernmost sighting was at El Salado. Farther north there is practically no habitat, at least near the coast, and I doubt that the breeding range extends north of Puerto Deseado. Rumboll found four adults and two juveniles on a small pond near Puerto Deseado in April 1974.

Distribution in winter.—*Pluvianellus* winters exclusively in coastal localities, from the Strait of Magellan to the Valdes Peninsula and perhaps beyond. Its distribution is discontinuous, for it seems to prefer sheltered areas (river mouths, bays) and to avoid the exposed outer coast.

Humphrey et al. (1970) gave no records for Tierra del Fuego between May and August and speculated that *Pluvianellus* might leave the island in winter. However, Rumboll (pers. comm.) found groups of 7, 8, 15, and 15 at Bahía San Sebastián on 3 May 1975; Johnson and Goodall (1965) reported "small flocks" as late as June; and R. H. Beck collected several specimens on the mainland side of the Strait of Magellan on 23 July 1914 (specimens in American Museum of Natural History). In Santa Cruz Province there are winter records from Rio Gallegos (May, June; Beck, specimens in AMNH) and Bahía de los Nodales (August, this study), and in Chubut Province from Tova Harbor (August, specimen AMNH), Puerto Madryn (July; this study), and Golfo San José (July, August; this study). There is also an undocumented (and presumably winter) report from the Falkland Islands (Anon, 1935). In the summer of 1973, Rumboll and I found potential wintering localities at Rio Gallegos, San Julián, and Puerto Santa Cruz. North of the Valdes Peninsula there seems to be little or no habitat for the species. Olrog has informed me (pers. comm.) of a recent sight record from Buenos Aires Province, but details are not available. *Pluvianellus* has

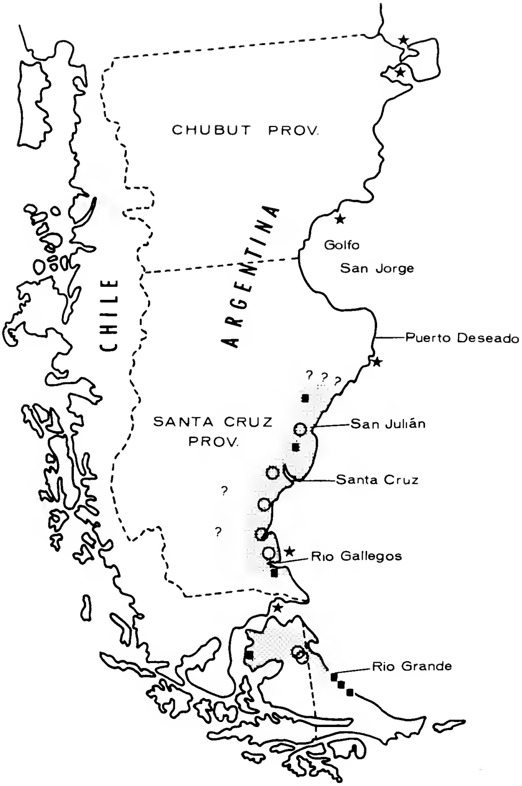


Figure 4. Distribution of *Pluvianellus socialis.* The breeding range (stippled) extends from Tierra del Fuego through southern Patagonia. Nesting localities including those in the literature, are shown by a square. Circles represent observations of probable breeding birds. Stars indicate wintering localities, determined from this study and from the literature.

not been reported along the Pacific coast of Chile, and probably does not winter there. That coast is entirely rocky and offers no suitable beach habitats.

Abundance.—Virtually all of the nesting habitat in Argentine Isla Grande is confined to the small area between Cabo Peñas, Ea. Los Flamencos, and Bahía San Sebastián. We found only nine pairs there (four at one lake) plus two other birds near San Sebastián. Olrog (1948) reported 20 pairs near Porvenir, where several nests have been found (Johnson and Goodall, 1965), but maps show that nesting habitat there is also sparse. I suspect that no more than 75 pairs nest on all of Isla Grande, and that estimate may be very generous.

Potential breeding habitat in southern Patagonia is much more extensive, but since about half of the lakes we investigated near the coast were not suitable, the region is probably less productive than a glance at the maps would indicate and may only support a few hundred pairs. The winter range, though extending from 55–42°S, is also small, since few coastal areas meet its habitat requirements. The small winter flocks (see below) also suggest a small population.

Although it is hazardous to evaluate the abundance of an inconspicuous species after a brief and obviously incomplete survey, it is evident that *Pluvianellus* is very rare. I suspect that the total population may not exceed 1000 individuals.

VOCALIZATIONS

Pluvianellus has an unusually wide variety of calls for a shorebird. Many are similar, and some appear to be used in more than one context. The following catalog is almost certainly incomplete; most notable is the absence of any vocalization that might be considered a true song (pairs had already formed by the time of our arrival).

Whée-you.—A soft contact note, used by the adults to inform each other and the chick of their location; sometimes only the last syllable is given in response. This is the most frequent vocalization and is given commonly by nesting birds. A variation that I have recorded as *whee* or *quee* is sometimes given by wintering birds as they take flight. I have heard the *whee-you* note directed to pipping chicks by the incubating parent.

Wheet.—A sharp note signalling mild alarm, sometimes drawn out to *oo-eet.* Chicks give a similar call when they are hungry or after they have been captured.

Pip-whéet (also transcribed as *pi-dée*).—An alarm note given by adults that instructs the chick to hide or to remain concealed. For example, an adult that had been feeding away from the territory for two hours returned to the vicinity of its chick. Alarmed by my presence, it gave the *pip-whéet* call frequently as it walked around—passing at times within 3 cm of the hiding chick. Chicks give a similar note when captured.

Pi-deedle-dée.—Used by the adults to call the chick from hiding, usually to be fed.

Pip-whéet, whée-you.—Apparently a high intensity threat note, perhaps sometimes indicating frustration, directed at other species. It was used to attack and drive White-rumped Sandpipers away from feeding areas.

Ti-ti-ti-ti. . . .—A series of rapidly run-on notes (almost a trill) that signals a low level of aggression. It is the first call to be given in threat displays toward conspecifics or in territorial defense. Given from the hunchbacked and upright postures.

Pi-pedée, pi-pedée. . . .—A high intensity aggressive call, delivered rapidly and repeated many times. It is given from an upright posture and is used in threat displays and territorial defense. This call seems to grade into another, *péek-a-ta, péek-a-ta . . .*, which is also given rapidly in series and signals a higher degree of concern. I have heard that call during the Attack Glide, in territorial displays, and from a flying pair that may have been establishing a territory.

Coo-coo-róo.—This low dove-like note announces an extreme stage of agitation. Given many times in succession, and from an extreme upright posture, it is used in incipient and actual fight situations. Rumboll believed that it may be given only by one sex (male?), with the mate delivering an "asthmatic wheeze" in situations of great stress.

Kuk-kuk-kuk.—A quiet call, signifying that the adult is ready to feed a chick.

Pupupupupu . . ., péek-a-ta, péek-a-ta . . . .—The *pupupu . . .* call, delivered as a rapid trill and followed by a series of fast and insistent *péek-a-ta* calls is given by the adult to the chick and means "follow me."

The chicks have a variety of peeping notes. I did not record at what age they begin to give the *whee-you* call.

ARRIVAL, TERRITORIALITY, PRE-NESTING ACTIVITIES

Pluvianellus returns to breeding grounds in Tierra del Fuego by early September. By the time we arrived (24 October) some pairs had chicks as much as 20 days old (estimated); the adults must have arrived no later than the first week of September, allowing 24 days for incubation and several more for territory and

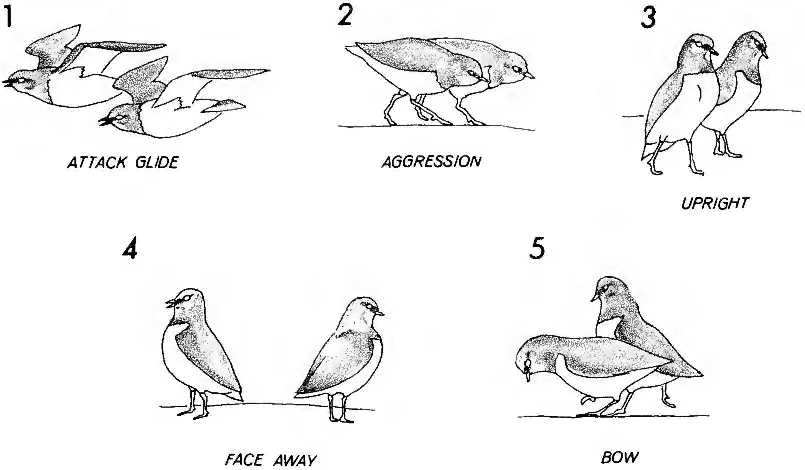


Figure 5. Important components of territorial defense.

pair formation. Some birds may return even earlier, as circumstantial evidence indicates that departure from wintering areas begins in August.

Because nesting was well along, we were unable to observe pair formation or the establishment of a nesting territory. However, near Rio Gallegos on 14 November we saw a display that we had not seen farther south. Three pairs and a flying juvenile were present at a small lake. Two groups of two, each presumably consisting of a mated pair, were performing prolonged aerial chases, flying along 1000 m or more of the shore at elevations of 2 to 20 m, giving the aggressive *pee-pidee* call repeatedly. A similar behavior involving a pair chasing a single bird was seen near San Julián on 18 November. The display began with birds flying low over the pond and continued as they climbed erratically to 80 m and flew out of sight; I could not determine if any vocalizations were used. Similar aggressive chases over a wide area are often performed by other shorebirds while establishing territories; however, the context in which *Pluvianellus* performed its chases could not be determined.

Territoriality.—Pluvianellus maintains a territory for nesting, much of the feeding, and raising the chick, presumably from the time it arrives at the nesting lakes until well after the chick fledges; one pair continued to defend its boundaries even though its 40-day old chick had departed and was feeding at a nearby pond.

Territory shape is essentially linear, conflicts beginning and being resolved on land within a few feet of shore. Birds walking into the area are attacked at once; those flying past are usually ignored. At Laguna de los Cisnes each of four adjacent pairs defended 300 to 500 m of shoreline, and a pair at Los Flamencos approximately 500 m.

Displays used in territorial defense are complicated (Fig. 5, 6). They are also unusual in that they are often performed by both members of the pair together, *as a unit.* In these respects they differ sharply from territorial displays of typical plovers but are remarkably reminiscent of piping displays of oystercatchers. When an intruder enters a defended beach the residents immediately run toward it side by side, in an aggressive posture—head low, bill pointed forward—calling ti-ti-ti. . . . If the intruder enters the far end of the territory, the residents may fly there fast and low; shortly before landing they set their wings at a 20–30° angle

Figure 6. Aggressive postures used in territorial defense. Top, Extreme Upright posture by pair directed toward an intruding neighbor (right); note that the chest of the defending pair is inflated and expanded laterally. Middle, from a Facing Away position the male (center) has adopted an Extreme Upright posture directed at the intruder (not visible to right); note the inflated chest and nape, and that the bird is standing on tip-toe. Bottom, pair in a modified Upright posture chases off an intruder; the inflated nape shows clearly. Note the prominence of the brightly colored iris in these displays.

above the horizontal and glide in (Attack Glide) giving the *pi-pedee*, or *peek-a-ta* attack calls. On nearing the intruder, residents adopt an Upright posture—head high, chest inflated, and bill pointed at the ground. As they run forward, one or both members of the pair will perform stiff stereotyped Bows, with the bill nearly reaching the ground; all the while they continue their vocalizations, which vary with their state of anxiety. Details of the Bowing display are not clear. Often they are performed by one bird and then the other; simultaneous bowing does occur but may be fortuitous. After running a few meters, the pair suddenly stops and Faces Away from each other at an angle of perhaps 120°. After a brief pause, and perhaps another Bow, the chase is resumed. Most disputes are resolved within a few seconds and end when the intruder walks away.

Territorial clashes increase in number and intensity as the chicks become more mobile. One, at Laguna de los Cisnes on 12 November, lasted over five minutes. Pair 3 and their large, flying chick (est. age 32 days) wandered into Pair 4's territory. They were immediately challenged by the *pi-pedee* call and Pair 4 charged in an Upright posture. For several minutes both pairs swerved back and forth across the beach like little clockwork toys. In each chase Pair 4 would run a few steps, stop, bow, and face away. After each pause, the mates spun away from each other before returning to the side-by-side formation; and in resuming the attack their paths crossed (Fig. 7). (Because of the intensity of this display, I could not determine whether the intruding pair was performing identical displays). When Pair 3 would not leave, the residents adopted an Extreme Upright posture, in which the birds stood on tip-toe (Fig. 6), inflated the back of the neck, fully expanded the chest forward and laterally, and shifted to the *coo-coo-roo* call. After two minutes of frantic chasing Pair 3 retreated, leaving the chick behind (Fig. 8). Male 4 attempted to feed it, which caused the immediate return of the parents and another brief bout of agitated chasing before the chick was led away.

When one member of the pair is off the territory displays are given by the remaining bird. I once watched a male chase away the male of an intruding pair. However, instead of chasing the female, he positioned himself in front of her, Bowing stiffly, with his head to the substrate; she flew off. Similar displays are used in courtship. When the absent mate returns to the territory, the resident adopts an Upright posture until the returning bird establishes its identity by approaching and Bowing several times. Possibly this constitutes a "greeting ceremony" distinct from territorial behavior.

In addition to nesting territories, birds at Laguna de los Cisnes also established temporary feeding territories at the south end of the lake where rows of rotting algae lay partly buried in the sand (Fig. 9). Birds foraged there by digging up extensive areas of shore (see Foraging behavior, below). This was the only area of such habitat on the lake and, though not included within the nesting territory of any pair (small rocks were lacking), it provided an important and contested supply of food. At least three and probably all four pairs fed there regularly, perhaps sequentially. Members of a pair might feed in close proximity, though never at the same dig, but other conspecifics, including flightless chicks, were vigorously excluded from areas within 30 to 50 m of the dig sites. Digs were also defended against other species *(Charadrius falklandicus, Sicalis lebruni)* that searched for food on the freshly-turned beach. A brief threat or chase usually sufficed to discourage their investigations.

Birds at Laguna de los Cisnes also seemed to defend temporary feeding areas at a nearby pond, but critical observations were not made there. The shore of that pond lacked areas of buried vegetation suitable for digging.

Within its nesting territory, *Pluvianellus* gives the impression of being a placid and non-aggressive species. It pays little attention to White-rumped and

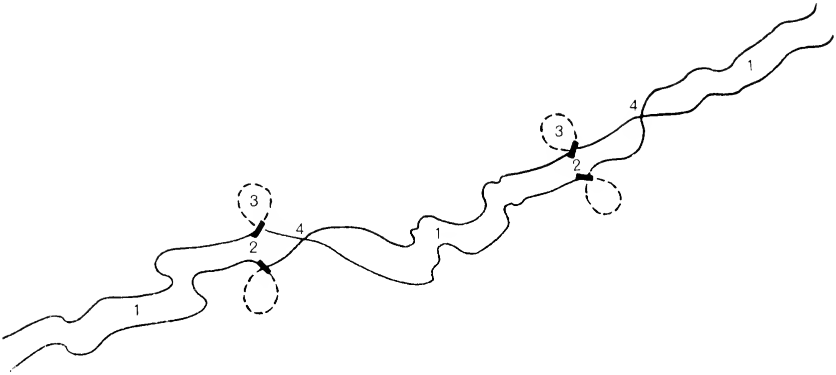


Figure 7. Approximate path of Pair 4 in an aggressive display against Pair 3: 1) Aggressive chasing; 2) Bow and Face Away; 3) Spin Away; 4) Cross-over and resume chase (see text for details).

Baird's sandpipers feeding nearby, which give way immediately at its approach. At a pond in Santa Cruz Province, Wilson's Phalaropes *(Phalaropus tricolor)* seemed to be defending temporary feeding territories along small stretches of shore, driving off intruding "peep" and Two-banded Plovers; one also charged a *Pluvianellus*, but was itself repulsed after sustaining several hard pecks to the head.

Pre-nesting activities.—Since breeding had commenced before our arrival, it was only by luck that we observed some of the displays associated with the early stages of nesting. On 28 October I collected a 3-day old chick at the gravel pit. The adults disappeared the next day, but were present and preparing to re-nest on 31 October. In two hours we saw precopulatory and scrape displays several times, which I assume were identical to those used in the original nesting.

Figure 8. Conflict involving two pairs and a large chick. The female (?) of Pair 4 escorts away the chick of Pair 3 (partly hidden), while her mate (center), in an Extreme Upright posture, displays toward Pair 3.

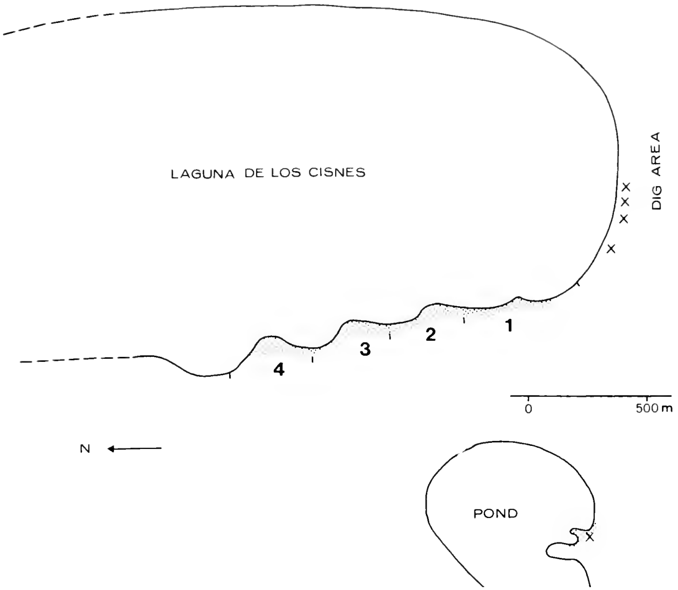


Figure 9. Sketch map of Laguna de Los Cisnes showing relationship of nesting territories (numbered) to areas of mixed gravel and mud substrate (stippled). All pairs foraged in the Dig Area at the south end of the lake, and along a stretch of rocky shore (X) at a nearby pond.

When rediscovered, the pair was feeding at the edge of a small pool. Suddenly, with no apparent signal, they ran in a crouched posture (Hunchbacked Run) to the top of a small pile of gravel, the female in the lead (Fig. 10). They then adopted the Upright posture, ran side by side for a few feet, then stopped abruptly and Faced Away (120–180°). The female remained motionless, perhaps slightly crouched, but the male resumed turning away from the female, coming to rest about a foot behind her. With a series of short, shuffling steps he Back-Stepped a few inches, then began the Arc Dance. In this display he sidestepped until perpendicular to her side, then reversed course until he faced her opposite flank; during this performance his head was directed at the female. After eight or nine 180° arcs he stopped directly behind her; she crouched, he ran forward and mounted. After two minutes of flapping his wings and shuffling his feet, he achieved a stable position; she raised her tail and copulation was quickly achieved.

After copulating the pair walked back to the pond, where they bathed and preened for 20 minutes. Suddenly they became alert and ran side-by-side to the site of copulation, but returned immediately to the pond and resumed feeding. Ten minutes later they began to run together along the shore. Initially they adopted an Upright posture, but this gave way to a Hunchbacked Run. After 20 m they stopped, faced each other and Bowed, pointing their bills at a common spot on the gravel. I presumed that this indicated the choice of a nest site, but that was not the case. Almost at once they flew 50 m to a flat ridge of gravel, where the male (?) began spinning and digging, while its mate stood motionless, slightly crouched, a few feet away. This behavior continued for 15 minutes, and later investigation revealed many small digs that could have served as nest scrapes.

The pair returned to the pond but after feeding quietly for 10 minutes came

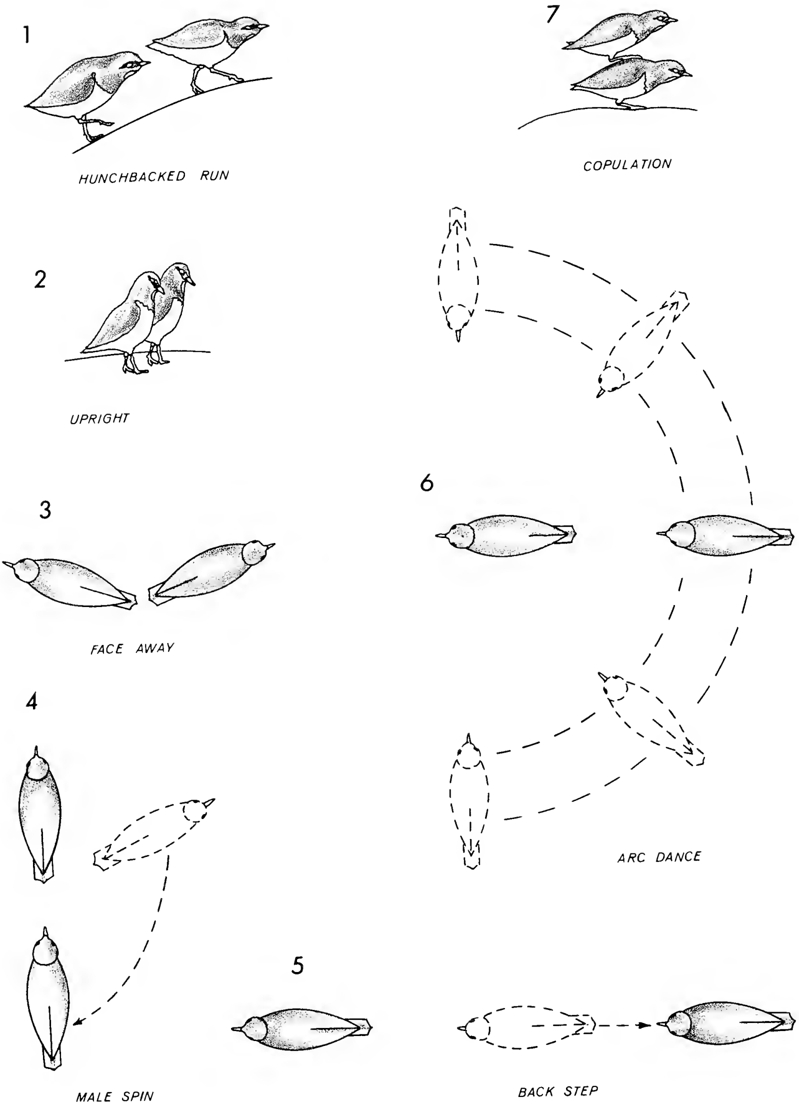


Figure 10. Components of the precopulatory display.

together in an Upright posture and once more ran to the copulation site. The precopulatory display was repeated, but this time the male's Arc Dance involved only one 180° sweep. The female did not crouch and when he attempted to mount she flew to the pond. Twenty minutes later they again returned to the copulation site, but from a new vantage point we could not see what happened. Whether the repeated return to the site of the original copulation is characteristic of the species' behavior or resulted from the unusual territory of this pair remains to be

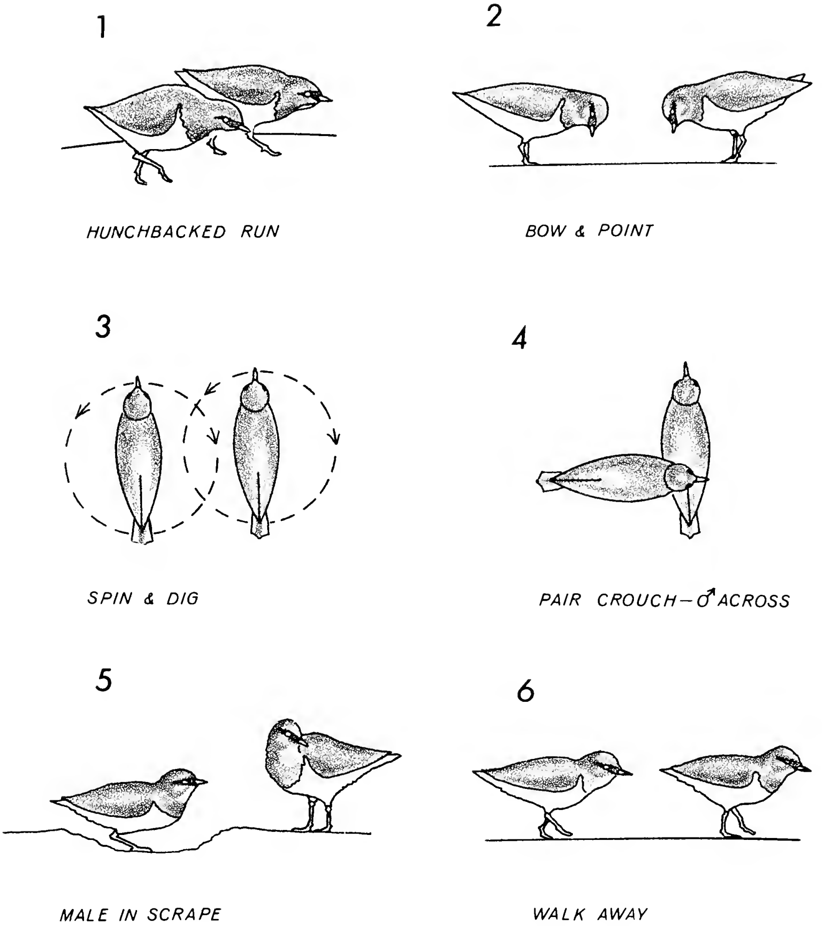


Figure 11. Components of the scrape displays.

determined. If normal, it represents a behavior pattern unique among monogamous shorebirds.

Ten minutes later the birds began to make a scrape (Fig. 11). Side-by-side they ran away from the pond in a Hunchbacked Run. After a few feet they stopped and both began to dig, each spinning in a tight circle. When the female (?) crouched in her scrape the male (?) left his and crouched at a right angle to her, placing his bill across her rump. After several seconds she shuffled from the scrape and he entered. She paid no attention and stood nearby for a few seconds preening her scapulars (a ritualized preening?), after which they returned to the pond and fed. A half hour later they walked from the pond and again began to dig. When the female (?) settled in her scrape, the male crouched across her. This time she did not move. After a few seconds he placed his bill under her flank, shoved her out, and settled. Scrape displays were apparently continued for the rest of the day, perhaps longer, for when we returned three days later we found 20 or more scrapes, each approximately 20 cm in diameter and five cm deep.

On 3 November, six days after the chick was collected, the adults fed along the shore of a small pond for about an hour, then flew to the pond nearest the copulation site. One bird ran excitedly back and forth to the copulation site several times and once the mate followed, but we could not see their subsequent behavior. By this time the female appeared bulky and was probably gravid. The pair returned to the pond, and the male courtship fed the female 11 times in 8 minutes, lowering his head almost to the ground and rotating it 90°, so that the commisure of his bill was perpendicular to hers. Foods presented were presumably tiny, as I saw nothing in his bill. The birds then disappeared, and when found a half-hour later were resting in a small hollow. Disturbed, they arose and began feeding in the gravel. Soon the female settled in an old scrape but the male pushed her out and entered. As she walked away, he followed and began to court. His Arc Dance included two 180° arcs, but when he approached to copulate she flew to a pond.

For most of the next hour the pair fed together while making a leisurely circle of the pond. Occasionally the male fed the female, and together they investigated several old scrapes. Once he picked up but quickly dropped a small pebble of the size used in lining the nest. When he made a scrape the female pushed him out, almost immediately. Shortly afterward the male crouched with his neck extended and remained motionless while the female walked alongside and began to dig, but when she had finished they walked away. In the next hour the pair made or investigated 10 more scrapes.

By 5 November their behavior had changed markedly. They were wary and no longer preoccupied with scrape making; courtship feeding had ceased. I think they had begun to lay a second clutch. By 9 November their activities were largely confined to an area 150 m from the presumed location of their first nest. Almost certainly they were nesting there, but lacking a concealed vantage point we could not find the nest. Two *Charadrius modestus* in an aerial display nearby were chased off by the male.

Pluvianellus' vivid iris coloration is featured prominently in courtship and territorial displays. In these displays (Fig. 6), or when a bird is excited (Fig. 1), the eye is opened wide and the pupil contracts, giving added prominence and brightness to the expanded coral iris. At these times the inner rim of the iris is yellow, which intensifies the eye-head contrast pattern. Leg coloration does not seem to be important in any display.

NESTING

Nests are placed on the open shores of fresh or slightly brackish ponds, usually within a few feet of the waterline (L. Bridges, pers. comm.). We found nests 0.7, 20, and 25 m from the water, in fully exposed situations where the substrate included small rocks, shingle, or gravel intermixed with mud. The importance of a substrate containing small rocks or gravel to the location of a nest site—implicit in the literature (Reynolds, 1953; Johnson and Goodall, 1965)—was obvious. The four pairs at Laguna de los Cisnes occupied the only 1500 m of shore that included small stones and mud; the remaining lake shore consisted largely of mudflats. Similar nesting habitat was used at Los Flamencos and in Patagonia. The gravel pit pair occupied an atypical situation; their nest was almost certainly built on a large flat pile of gravel that had been dredged from the adjacent ponds; the shores of these ponds were so steep and narrow that it would have been impossible to place a nest there.

As noted *Pluvianellus* excavates its scrapes by digging. The nests are lined with small bits of gravel (Fig. 12).

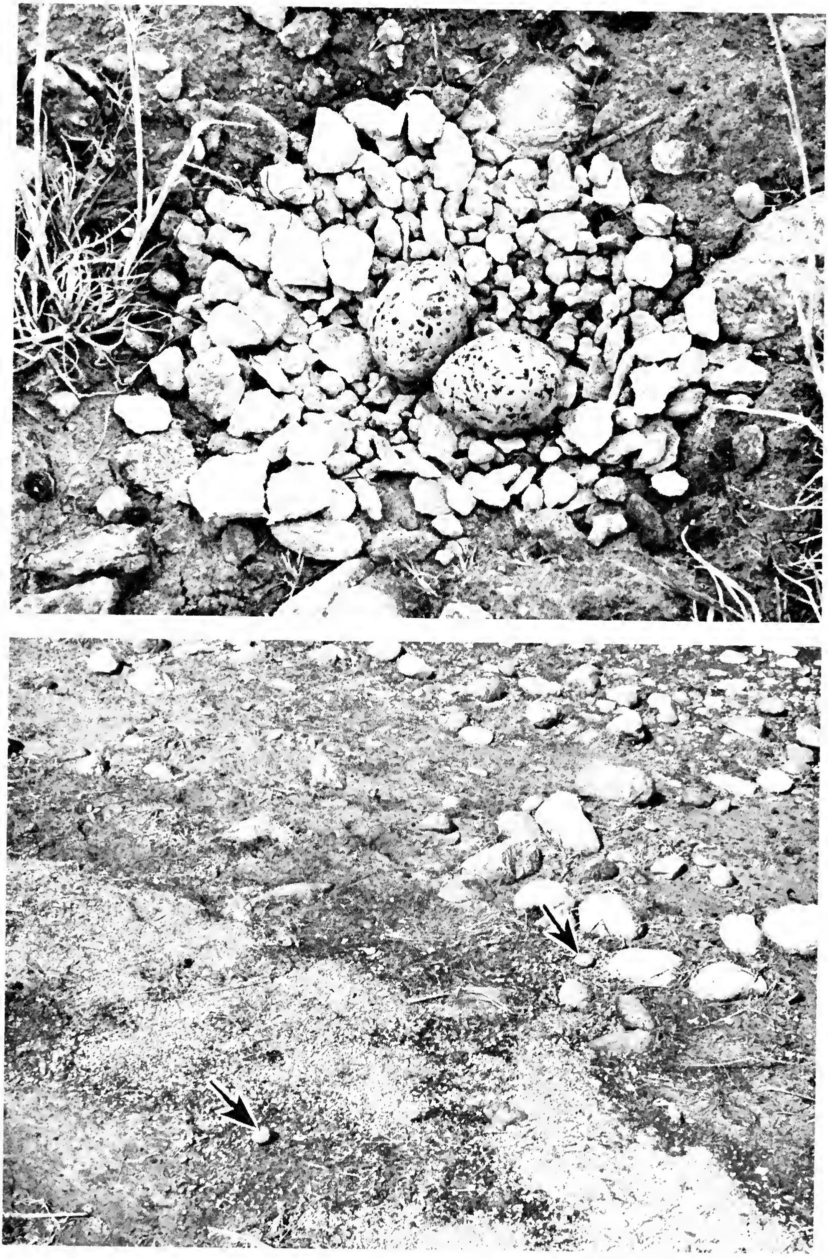


Figure 12. Top, nest lined with small pebbles at Laguna Cerro Conico, Tierra del Fuego. Bottom, nest site at Ea. Los Flamencos showing typical nesting habitat of intermixed rocks, muds, and gravel. One egg (lower left) has been washed from the nest (right center).

Laying, clutch size, eggs.—The few egg dates for Tierra del Fuego extend from 4 September (inferred; this study) to 13 November (Johnson and Goodall, (1965), and for Patagonia from 8 September (inferred, this study) to 17 November (this study). I suspect that most pairs begin laying in September. Birds at Laguna de los Cisnes and two pairs with flying chicks in Patagonia (Table 2) must have completed laying by 14 September. In view of the potentially high rate of egg or nest loss (see Productivity), late dates may represent replacement clutches. Egg dates for the renesting gravel pit pair would have extended from ca. 9 November to 3 December.

The normal clutch is two (Johnson and Goodall, 1965; Maclean, 1972; L. Bridges, pers. comm.), which was true of the three clutches we examined. Three one-egg nests found by Mr. Mac Lennan (Johnson and Goodall, 1965) may have represented incomplete clutches, or more likely one egg had been lost. A nest at Los Flamencos that was 0.7 m from the shore contained two eggs when discovered but only one several days later; the second egg was found 0.7 m farther inland, apparently having been washed there by high waves (Fig. 12). Reynolds (1953) photographed a one-egg nest at Cabo Viamonte that he claimed contained four eggs when the clutch was completed. If this report is accurate, it almost certainly represents laying by two females.

Eggs vary in ground color from grayish tan to pale grayish green; brownish black markings, which range from a series of fine dots to thin lines, are scattered rather uniformly over the surface. In three of the four clutches that we examined (including one in the collection of Mr. Bridges) the eggs were strongly dissimilar. In the nest the eggs are positioned about 30 mm apart, rather than being grouped as in shorebirds with larger clutches, and each is brooded in a lateral incubation patch.

Dimensions of 9 eggs (5 measured by me, 2 listed by Johnson and Goodall, 1965, and 2 in the Western Foundation of Vertebrate Zoology) are: length, 32.8-34.8(34.0) ± 0.79 mm; width, 25.0-26.3(25.7) ± 0.44 mm. Weights of two eggs 8 days prior to hatching were 10.5 and 10.5 g; one day prior to hatching 9.6, and

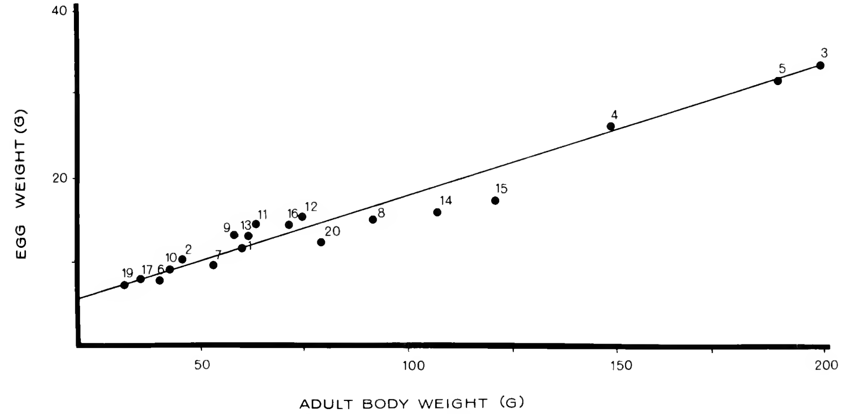


Figure 13. Relationship of egg weight to adult body weight in plovers. The equation for the regression line is Y = 2.93 + 0.14X. Data largely from Graul, 1973. Species: 1. *Charadrius hiaticula*, 2. *C. semipalmatus*, 3. *Pluvialis apricaria*, 4. *P. dominica*, 5. *P. squatarola*, 6. *C. dubius*, 7. *C. melodus*, 8. *C. vociferus*, 9. *C. wilsonia*, 10. *C. alexandrinus*, 11. *C. asiaticus*, 12. *C. leschenaultii*, 13. *C. mongolus*, 14. *C. montanus*, 15. *C. (Eudromius) morinellus*, 16. *C. falklandicus*, 17. *C. tricollaris*, 18. *C. (Zonibyx) modestus*, 19. *C. collaris*, 20. *Pluvianellus socialis*.

Figure 14. *Pluvianellus socialis* incubating. The bird is slightly alarmed and the yellow inner rim of the iris is visible. Note that wing molt is in progress and that the outer remiges have not yet been replaced.

9.7 g; two eggs at an unknown stage of incubation were 10.6 and 10.9 g. I estimate the weight of a fresh egg at 12.0 g.

Pluvianellus' clutch size is smaller than that of most plovers. Moreover, each egg comprises only about 15% of the adult body weight, which is small for a plover, especially when compared with species that also lay two eggs: *Charadrius tricollaris,* 21.4%; *C. modestus,* 27.6%, and *C. collaris,* 22% (Fig. 13; cf. Graul, 1973). *Pluvianellus* feeds on small prey, and one gets the impression that nearly all of its time is spent searching for food. As a result, the effort required to produce an egg may be greater in *Pluvianellus* than in other species. If so, the interval between successive eggs might be as much as several days.

Behavior during incubation.—At three nests (one containing apparently fresh eggs, one observed over the last half of the incubation period, and one at an unknown stage) the parents alternated incubation, seemingly equally, through the entire period (Fig. 14). All of the incubation stints we saw were exceptionally brief, averaging about 15 minutes. Typically, the relieving bird flies to within 20 to 40 m of the nest and walks in a leisurely and sometimes circuitous fashion. When it is within 5 m of the nest, the incubating bird moves off quietly and rapidly. There are no change-over displays. Sometimes the mates feed together for a few minutes, but more frequently the new bird begins to incubate at once. The relieved partner may rest and preen nearby, but soon retreats to the water's edge and spends nearly all of its time feeding.

Incubating birds show no overt reaction to gulls or skuas flying overhead, or to sheep grazing nearby, but will leave the nest to feed briefly or to join in territorial defense when an intruder appears on the territory. One, probably disturbed by my presence, repeatedly chased a female *Lessonia rufa* feeding nearby. Another, hesitant to approach the nest, tossed several feathers and pieces of grass over its shoulder. Most gave the impression of being totally unconcerned when forced from the nest.

Distraction displays.—Unlike typical plovers, *Pluvianellus* shows no distraction displays, either during incubation or when caring for chicks of any age. Adults rely on their cryptic coloration and vacate the nest area before such displays become necessary. When I approached within 50 m, the incubating bird walked off a few meters and then either flew away or stood quietly and began mock preening or feeding motions. Neither member of the pair showed any anxiety or made any vocalizations as I examined the clutch, and the non-incubating parent never returned to the vicinity to observe my actions.

I tried to elicit a distraction display from a bird whose eggs were pipped. It shuffled off the nest in a crouched posture, perhaps with back feathers slightly ruffled. When I charged, it flew 3 m, landed, and calmly walked away; several additional chases all produced the same result.

Incubation period.—The incubation period is unknown, but presumably approximates 24–26 days as in similarly sized Chardrii.

GROWTH AND CARE OF THE YOUNG

Hatching.—Late on 11 November a nest at Ea. Los Flamencos contained one pipped egg; the other was intact but the chick was calling loudly. As in earlier stages of incubation the parents continued to alternate short stinits at the nest. Once the male arrived with a distended crop and carrying food; he pointed his bill at the eggs, then made motions as if regurgitating (!) before starting to brood.

By noon on 12 November one egg had hatched and the other was pipped. The male brooded for the next hour, until the female appeared carrying food; I could not determine whether she fed the chick. She brooded quietly for 45 minutes, occasionally giving soft purring calls as well as the *whee-you* note, then suddenly became restless. Reaching into the nest she removed an eggshell and flew off a short distance before dropping it; she landed, ate bits of shell, returned to the nest for the other half and repeated the performance. The shells had been transported 7 and 2 m. She resumed brooding, and the male, though nearby, did not relieve her until 45 minutes later, when I left the blind and flushed the female. He was still brooding 30 minutes later, when observations ceased.

At 1000 on 13 November the nest was empty, but the chicks had moved only 5 m. In the next hour they were alternately fed and brooded by the female, who sometimes foraged on the upper beach, mainly by gleaning from the leaves of grasses and by flipping stones with her bill. She delivered food to the nearest chick, then made motions as if trying to regurgitate more. The male mostly remained near the edge of the territory. Several times he approached carrying food, but did not feed the chicks.

The most striking characteristic of the chicks at this time is their general weakness: they are far less agile than plover or sandpiper chicks of the same age. For example, Chick 2, at the age of 22 hours, stumbled into the 4-cm deep hoofprint of a horse and for 20 minutes lay flat on its back unable to right itself. After finally regaining its feet, it required another 20 minutes to climb from this minor depression—a task that would have proved no problem to a newly-hatched plover. During this incident the female occasionally walked back to look at the chick, but showed no anxiety, made no effort to assist, and continued to feed and brood the other chick.

The slight age difference between the chicks (8–14 hours) was sufficient to give Chick 1 a great advantage. Because of its greater strength, it was able to follow more closely, and as a result received 3 or 4 feedings to each one of its nest-mate's. This advantage was reflected in the weight of the chicks. At hatching each weighed 8.5 g. When Chick 1 was 30–36 hours old and Chick 2 22 hours, Chick 1 weighed a full gram more (9.5 vs. 8.5 g), and it seemed inevitable that differences in size and agility would continue to increase in its favor. The subsequent development of these chicks could not be followed. However, none of the five families that I studied with young 3-days old or older included more than one chick. I infer that the later-hatching chick is separated from its parents within a day or so of hatching and starves.

The crop; feeding the chick.—Pluvianellus has a well developed crop. In specimens I have examined it is a permanent structure (as in Figure 4C of Zisweiler and Farner, 1972) on the right side of the neck; its opening to the esophagus is continuous and its walls seem slightly thickened. The dimensions of an empty crop were 12.4×6.5 mm; a full crop measured 20×12 mm and contained a bolus weighing 1.5 g. Most shorebirds lack a well-defined crop. In *Pluvianellus,* in addition to serving as a storage organ, it is used in a function unique among the Chardrii—to transport and regurgitate food to the young.

When adults return to feed the chick, they carry small bits of food in the bill, and if they have been gone for a long time the crop is noticeably distended. After delivering the visible food (Fig. 15), adults make regurgitating motions and again present their bill to the chick. I was never able to see new food appear in the adult's bill, but the subsequent behavior of the chick left no doubt that food had been transferred. Several times I watched adults regurgitate up to three additional feedings. I saw no evidence that the chick was able to induce this behavior, for example by pecking at the rictus or at the bill, as has been described for doves and gulls.

Parental feeding of the young is extremely unusual among the Charadrii. It is known in the Haematopodidae, Dromadidae, and Chionididae, is rare in the Scolopacidae (e.g., *Scolopax minor,* Pettingill, 1939; *Gallinago gallinago,* Tuck, 1972), and is unreported in the Charadriidae. The occurrence of this behavior in *Pluvianellus* and the species' concomitant use of the crop to regurgitate food to the young differentiates it from not only the plovers but from all other shorebirds.

Behavior during the fledging period.—In their first two weeks *Pluvianellus* chicks are extremely difficult to observe. Apparently they remain concealed and largely stationary in the vicinity of the nest. A 3-day old chick discovered in a small depression that was rimmed with 20 fecal sacs had obviously been there for some time.

The adults spend nearly all of their time in foraging, either on the territory or on adjacent ponds. As a result the chicks may be deserted for two hours or more, even on cold wet days. The adults pay little attention to the chicks, except to feed them, and I never observed them brooding other than newly-hatched young. When adults return to the territory they immediately give a location note and wander slowly toward the area in which they left the chick. The chick remains immobile—even though the parents may walk within an inch of it—until it is called out from hiding.

Although day-old chicks peck at the ground and may obtain some nourishment from their efforts, virtually all of the food during the first two weeks is provided by the parents. After that time they begin to accompany the adults along the shore and to forage in part for themselves. Much of their foraging is done by pecking at the surface or investigating the areas under and around small rocks. But even as early as D-14 they exhibit the unique digging behavior that characterizes this species (see below).

Figure 15. Adult, with distended crop, feeding the chick. Foraging birds with distended crops are also shown in Figure 19.

Until nearly four weeks old, the chick relies almost entirely upon cryptic coloration for protection from predators. Both the natal down and juvenal plumage are extraordinarily effective in rendering the young bird nearly invisible against a wide variety of substrates—sparse grass, gravel banks, mudflats. Chicks freeze immediately when a human appears nearby, and discovering their hiding place usually requires the cooperation of two observers, one marking the spot through binoculars and the other searching the area; success is not invariable. Small chicks surprised in the open sometimes run for cover but direct evasive action was uncommon in chicks younger than D-24. Older chicks dash off, peeping and flailing their stubby wings. Chicks of all ages paid little attention to avian predators, often not even bothering to crouch when a gull or skua passed directly overhead.

As soon as the chicks fledge (ca. D-28) they begin to appear independently on the mudflats and soon begin to wander beyond the limits of the territory, or to adjacent ponds. Yet, they remain in at least loose association with the parents. One chick was still receiving some food at D-40 (est.), when my observations terminated.

Growth rate.—Because of their tendency to freeze when approached, chicks could be captured at irregular intervals after they began to forage in exposed areas at about two weeks of age. Since each of the pairs at Laguna de los Cisnes had only one chick, which remained on the territory until fledging, and since chicks of adjacent pairs were of slightly different ages, I could determine their identity and follow their development without marking them. Data were taken on dimensions, molt, and soft part coloration. Chicks were subsequently released at the spot at which they were caught and were watched until they were rejoined by the parents.

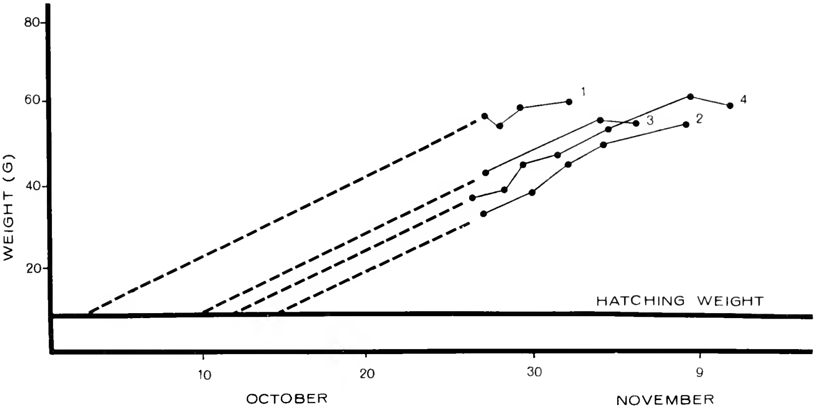


Figure 16. Growth patterns of four chicks at Laguna de los Cisnes. The last data point for chicks 1 and 4 was obtained on the day of their first flights; Chick 3 flew three days after its last weight was obtained, and chick 2 disappeared.

Growth patterns are similar for the three chicks (2, 3, and 4) that were studied for a reasonable period prior to fledging (Fig. 16). By assuming a linear growth rate one can extrapolate to hatching weight and thereby estimate hatching date, age of the chick, and duration of the fledging period. I infer that chicks 2, 3, and 4 hatched on 14, 10 and 12 October, respectively, and fledged 28½, 28, and 29 days later. (For chick 1, which was not caught until it was nearly fledged, a hatching date of 4 October and a fledging period of 28 days seem reasonable.) Of course, growth curves are not linear but sigmoid (Ricklefs, 1968, 1973; Fig. 17) and the

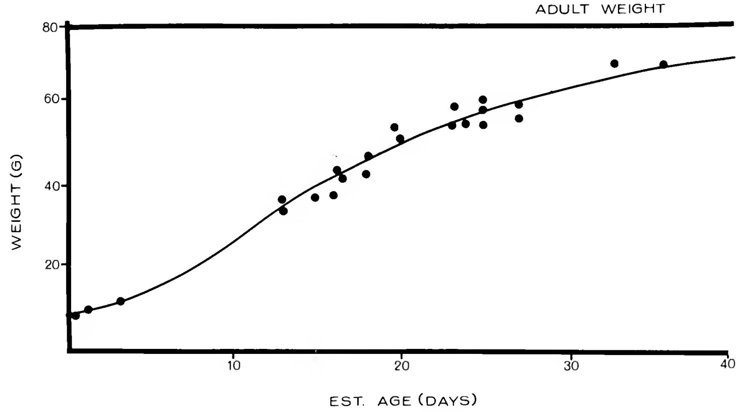


Figure 17. Combined growth curve for chicks of *Pluvianellus socialis,* based on two newly-hatched chicks, one three-day-old chick, four chicks at Laguna de los Cisnes, and one 35-40 day old chick.

assumption of linearity results in an underestimate of both hatching date and fledging period. A fleding period of 30-31 days may be more closely approximate to the actual condition, although shorter periods seem possible. The winter and spring of 1973 were exceptionally dry and the nesting ponds were drying rapidly by early November. In addition, strong but variable winds caused the position of the waterline to fluctuate daily. During westerlies, the shoreline shifted as much as 300 m "seaward," and on those days chicks grew very slowly because the adults had to forage more widely for food. I did not appreciate the significance of these "wind tides" early enough to make detailed observations of their effects. But even allowing for these conditions, which are a fact of life in Tierra del Fuego, it is clear that the fledging period for *Pluvianellus* chicks is much longer than that of similarly sized shorebirds that find their own food (Table 3).

TABLE 3. Age at fledging and adult weights of some Charadrii

Species	Adult weight(g)	Age at fledging (days)	Reference
Charadrius semipalmatus	40-43	25 (max.)	Parmelee, Stephens, and Schmidt, 1967
Calidris fuscicollis	43-46	15-17	Parmelee, Stephens, and Schmidt, 1967
Calidris himantopus	61	17-18	Jehl, 1973
Pluvianellus socialis	80	30	This paper
Gallinago gallinago	100	17-20	Tuck, 1972
Arenaria interpres	110-115	19	Parmelee et al., op. cit.
Pluvialis dominica	149-155	22	Parmelee et al., op. cit.
Pluvialis squatarola	190	23	Hussell and Page, Ms
Haematopus ostralegus	500-536	28-31	Harris, 1967
Chionis alba	580-680	50-60	James, 1963

Chicks fledge at a weight of approximately 56 g, or 70 per cent of the adult weight (Fig. 17). I have no data on when adult weight is attained; a flying juvenile, estimated age 35–40 days, weighed 68 g. Adult tarsus length is reached by the time the chicks are 16–17 days old. Bill growth is slower and adult dimensions had not yet been attained by a 35–40 day chick. At fledging wing length (chord) approximates 100 mm, or 74 per cent of adult dimensions, and the outer primary 65 mm (Fig. 18).

As I have noted above, newly-hatched chicks of this species are far less agile than those of sandpipers or plovers. Although nidifugous, they do not wander far from the nest and receive virtually all of their sustenance from the adults for several weeks. In this respect they are more similar to gulls than to plovers and are best considered as semi-precocial. Ricklefs (1973) found that growth rates of altricial and semi-precocial species were similar and greater than in precocial species. He presented data for only one plover, *Charadrius hiaticula*, whose growth rate (KG = .091) is greater than that of *Pluvianellus* (KG = .081). The significance of these differences is not clear, but growth rate of *Pluvianellus* seems exceptionally low even for a precocial species.

FORAGING AND FEEDING BEHAVIOR

Burton (1974) described the foraging behavior of a typical plover, *Pluvialis apricaria*, as follows: "They move by repeated runs of a few yards at a time, interrupted by pauses in a very upright attitude. These pauses frequently lead to feed-

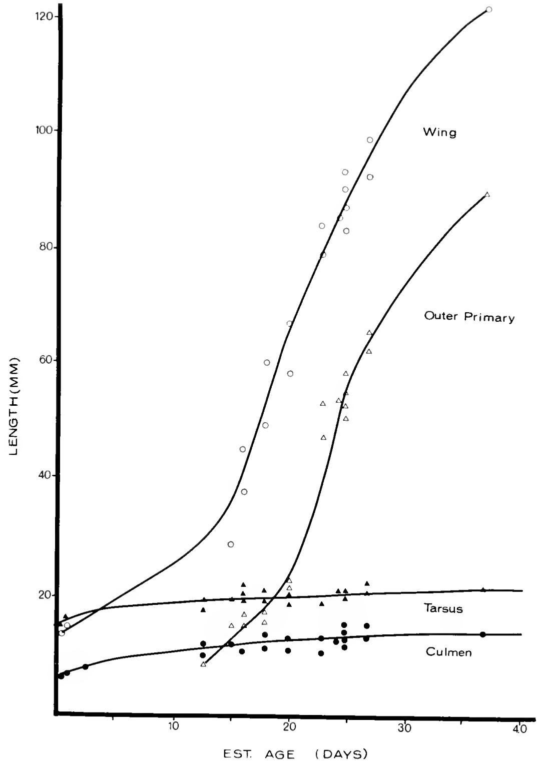


Figure 18. Growth of wing, outer primary, tarsus, and culmen in chicks of *Pluvianellus socialis*, based on chicks identified in Figure 17.

ing movement, either directly, or after a further pause with head lowered close to the ground and bill pointing ahead. This attitude is maintained for about a second, and a peck at the ground usually follows."

This "run, stop, and peck" behavior, which seems to characterize the Charadriidae, is absent in *Pluvianellus*. Birds foraging along the shore or on mudflats waddle along in a curious stoop-shouldered stance, head low and eyes constantly peering at the ground (Fig. 19). As they progress, more or less in a straight line, the head moves from side to side in a shallow arc and they peck rapidly and repeatedly at the substrate. They may stop and feed for a few seconds before moving on, but they rarely raise the head above the level of the back and, except when disturbed, do not assume a plover-like upright posture. Occasionally birds claw at the surface to expose more food. Unlike typical plovers, *Pluvianellus* does not usually peck perpendicularly but uses a slight twisting motion, so that the bill hits the ground at an angle. The result is a distinctive cocked-head feeding posture (Fig. 19, 20). Individuals peck preferentially in one direction for the tip of the rhamphotheca—but not the underlying bone—is slightly deflected laterally. In approximately 80 per cent of the specimens I have examined curvature is to the right.

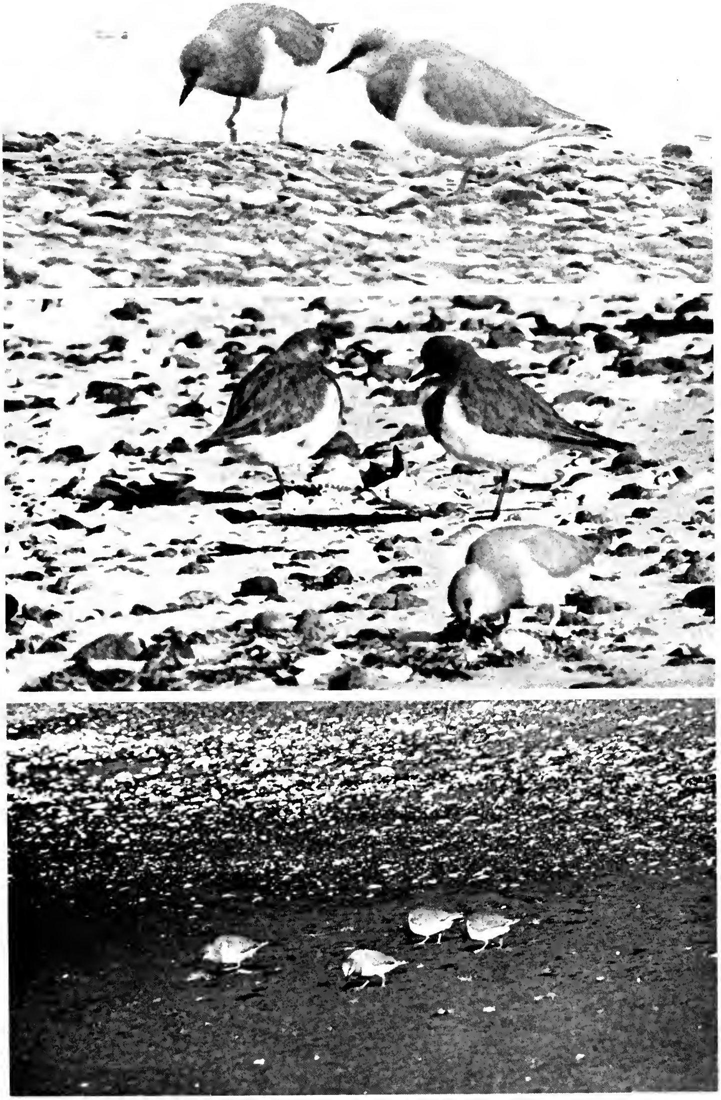


Figure 19. Foraging. Top, pair foraging along the shore at Laguna de los Cisnes, Tierra del Fuego (note distended crop). Middle, "Turnstoning" among shell and seaweed debris, Bahía de los Nodales, Santa Cruz Province. Bottom, birds feeding on upper beach, Golfo San José, Chubut Province. Note characteristic "stoop-shouldered" posture.

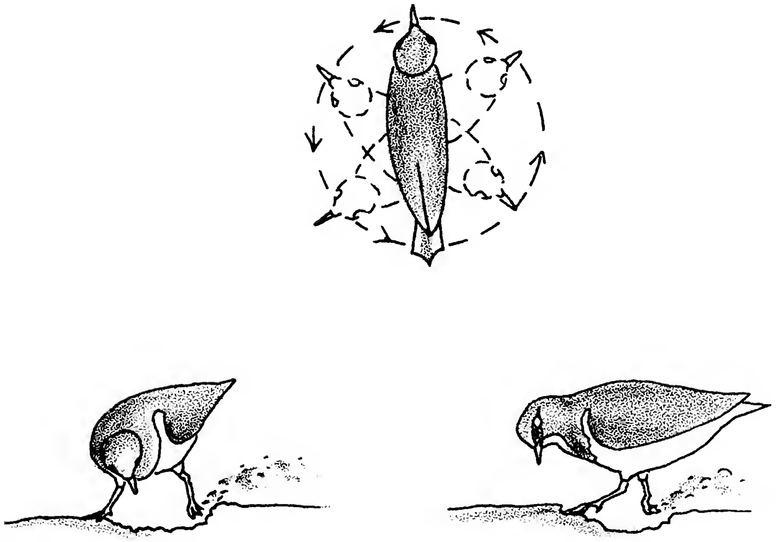


Figure 20. Diagrams of digging behavior.

In many respects *Pluvianellus'* foraging behavior parallels that of turnstones. Birds foraging on the upper beach search amid piles of seaweed or other debris, probe into crevices at the base of rocks, and even flip small stones or shells forward with the bill. However, their most distinctive and characteristic foraging behavior involves the use of their stout legs and blunt claws to *dig* for food. Digging is performed in many situations but is by far most common in areas where aquatic vegetation tossed up by the tides has been subsequently buried by shifting sand. These areas of decomposing matter form natural incubators for the eggs of kelp flies and other invertebrates, and seem to provide an important source of food in all seasons.

On arriving in a suitable area, a bird begins to dig by kicking alternate feet postero-laterally at a rate of 6–8 kicks per second. At the same time it pirouettes rapidly in place, and pecks rapidly at the substrate, as a phalarope might do in an aquatic situation. Small quantities of sand fly from beneath its feet, and one is reminded of a tiny dog trying to dig up a bone (Fig. 20). Digs tend to be circular, their size and depth varying with substrate conditions; at Laguna de los Cisnes, for example, where the sand beach was well compacted, they averaged 10–12 cm in diameter and 1–2 cm deep. The digs are easy to identify and provide an important clue to the presence of this inconspicuous species. In some areas large stretches of beach may be disrupted by digging activities (Fig. 21).

An important variation of the digging technique was observed at Golfo San José, where birds "dug" in shallow pools, utilizing the same movements as in terrestrial digging. Digging in aquatic situations was not seen on the breeding grounds.

Many charadriiform birds use foot-paddling behavior in foraging, but *Pluvianellus* is apparently the only one that digs for food. I think this behavior has been derived not from foot-paddling but from nest-making, for the parallels between the postero-lateral kicking, waddling gait, and pirouetting of a foraging bird and, respectively, the foot motions used by shorebirds in clearing a scrape,

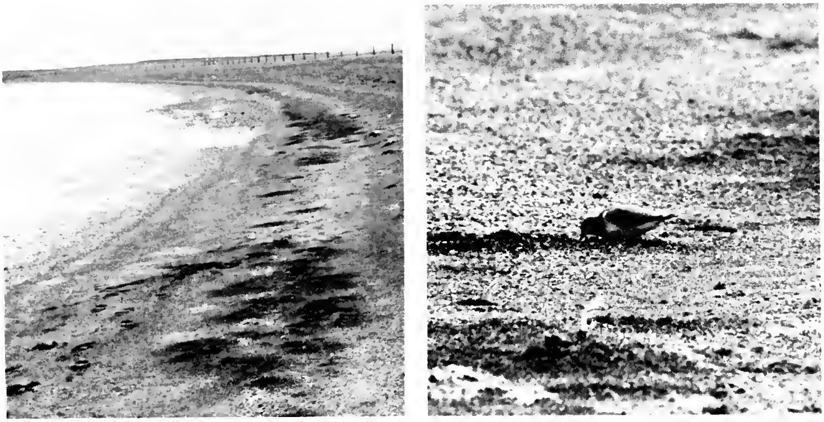


Figure 21. Left, portion of the Dig Area at Laguna de los Cisnes (see Figure 9) showing the broad area of beach that has been turned by digging birds. Right, a bird digging.

the rocking motion of a bird settling on eggs, and the movements used to mold the nest cup by rotating the breast against the earth are remarkably similar. Birds clearing a scrape must often uncover potential sources of food, and modifying this behavior into a foraging pattern would be simple.

On the breeding grounds, *Pluvianellus* forages primarily along the shore, usually within a meter of the waterline. From early in the season until well after the chicks are fledged foraging is the main activity and seems to require nearly the bird's entire time. For the most part birds forage singly, although members of a pair often feed in close proximity without interaction. Perhaps 70 per cent of the foraging occurs at the water's edge, where the birds peck small invertebrates from the mud and, occasionally, wade to belly depth to pluck tiny items (emerging insects?) from the surface. The extent to which birds feed along shingle beaches or mudflats or dig for food varies with the topography of the breeding territory. At the Gravel Pit and at Laguna de los Cisnes, for example, digging was relatively frequent, whereas at Los Flamencos it was not observed.

Food.—There is practically no information on the summer food of this species. Crawshay (1907: 122) stated that birds feed at inland lagoons "where the water is pink with the minute crustacea on which they feed;" those conditions were not encountered in this study. Visual inspection of actual feeding sites and digs in a variety of situations did not reveal any potential prey species other than fly larvae among the decomposing vegetation. In fact, most of the food taken is extremely small, which may account for the species' incessant search for food. Prey species seem to be largely scavenging insects that are attracted to areas of debris.

Only one specimen was collected in Tierra del Fuego; the stomach of a 3 day old chick at the gravel pit that was being fed by both parents contained approximately 30 dipteran (tipulid?) larvae 8–10 mm long, 1 larval dytiscid, and an adult hemipteran (Saldidae). A soil sample from the digging area at Laguna de los Cisnes contained several larvae and pupae of muscoid flies (suborder Cyclorrhapha), 8–10 mm long. A male of a mated pair collected at El Salado contained grit, unidentifiable animal remains, and 2 emerging muscoid flies (Anthomyiidae or Muscidae); the female contained grit and approximately 12 dipteran larvae (suborder Cylorrhapha) 9–10 mm long. At a pond near Rio Gallegos a pair and their flying chick, after being flushed from the edge of a lake, landed in a grassy pasture 100 m from the shore and began digging at the edge of a pile of sheep manure. The stomach of the young bird contained only the remains of seeds.

PRODUCTIVITY AND MORTALITY

Pluvianellus lays two eggs but apparently raises only one chick. As noted, the later-hatching chick is at a marked competitive disadvantage and is lost soon after hatching. This event, a normal consequence of asynchronous hatching, seems to be the major cause of chick mortality. Avian predators, mainly *Catharacta skua*, *Larus dominicanus*, and *Polyborus plancus*, are fairly common and may also account for some mortality. Yet, although gulls constantly patrolled the shorelines, I never saw them attempt to capture chicks, and the chicks usually paid them no attention.

There are few other data on productivity. One egg from a nest at Ea. Los Flamencos was apparently washed out by high waves; the other egg subsequently disappeared and was presumably eaten by a Patagonian fox *(Dusicyon culpaeus)* that hunted along the shore. Mac Lennan (in Johnson, 1965) reported finding several one-egg clutches. If these resulted from predation the entire clutch might have been destroyed. I suspect that trampling by sheep may be an important cause of egg loss. The shores of the ponds are paths for hordes of these animals, and hardly an inch of mud is devoid of their tracks. Since *Pluvianellus* makes no attempt to distract predators from its nest or chicks, it seems to have no defense against the meanderings of the sheep. One can only speculate whether the introduction of sheep into Tierra del Fuego 100 years ago may have affected the abundance of this species.

POST-BREEDING MOVEMENTS AND MIGRATION

There are no data on the extent or timing of post-breeding movements. Since the breeding lakes dry rapidly, in some years birds may move to nearby coastal areas as soon as the chicks become independent (early December?), although in wet years some might remain inland until the lakes freeze.

Also unknown is whether *Pluvianellus* undertakes extensive northward migrations in the austral autumn. The northernmost wintering area is only 600 km north of the northernmost breeding locality, and post-breeding birds might merely wander eastward to winter along the coast at the general latitude of their nesting grounds. On the other hand, there is indirect evidence for southward movement toward the breeding grounds in August. In July 1971 approximately 36 birds were wintering at Golfo San José and Golfo Nuevo, whereas we found only 10 birds at Golfo San José and none at Golfo Nuevo in a much more intensive survey in August 1972 (Jehl et al., 1973). Furthermore, the heaviest individuals I collected (93, 102 g) were taken in mid-August; the mean weight for midwinter and breeding birds approximates 80 g. The decreased population and an apparent weight increase only two weeks prior to *Pluvianellus*' inferred arrival time in Tierra del Fuego provide circumstantive evidence for an early August departure, and also suggest that some birds may undertake an extensive migration to reach the breeding grounds.

MISCELLANEOUS OBSERVATIONS

Timing of the breeding season.—The hatching period of birds has often been assumed to occur when food supplies for the young are maximum. I have no data on seasonal food availability in Tierra del Fuego, nor on diets of potentially competing species. However, it is interesting that *Pluvianellus*' nesting period begins up to several weeks prior to those of other Fuegian shorebirds (Humphrey et al.,

Figure 22. A pair of *Pluvianellus socialis* and their chick at Laguna de los Cisnes feeds along the shore, while large numbers of White-rumped (mainly) and Baird's sandpipers forage nearby.

1970; pers. obs.). By the time the first *Pluvianellus* chicks hatched in early October 1973, flocks of White-rumped and Baird's sandpipers had begun to take up winter residence on the nesting lakes, and by early November thousands were often present. These species feed along the shore and presumably compete with *Pluvianellus* for food (Fig. 22). Perhaps early nesting allows the species to fledge young before competition from North American migrants becomes intense. The extremely slow growth of the chick and the fact that only one chick is raised also suggest that food availability may be a limiting factor. On the other hand, it is hard to explain how *Pluvianellus* can accumulate enough energy to molt during incubation (see below) but does not seem able to provide food for a second chick.

Renesting.—Although some pairs may lay a replacement clutch after losing their eggs or small chicks, I doubt that successful breeders attempt a second clutch. The combination of two factors—the rapid drying of nesting lakes in early summer and the extremely long period in which chicks are dependent on the adults for food—is sufficient to preclude efforts to renest.

Age at first breeding.—Evidently some birds breed in their first year. A mated female at El Salado, collected on 18 November, had large brood patches and had retained some juvenile wing coverts.

Drinking.—I saw apparent drinking only once. An incubating female left the nest and walked to the shore. Inserting her bill into the water, she opened and closed it several times and appeared to make sucking motions, like those of a pigeon. This behavior took place so rapidly and was so unexpected that I was unable to make critical observations. No other member of the Charadrii is known to drink in this manner. Even the Pteroclidae, which may be closely allied to the shorebirds (Maclean 1967a) do not drink by sucking, contrary to early reports (Cade et al., 1966). Immelman (address, XVI Intern. Ornithol. Congr.) has argued that this behavior allows open-country species to drink rapidly and avoid predation at water holes, but that explanation is not applicable to *Pluvianellus,* which spends its whole life near water and in the open. The taxonomic implications of its drinking behavior remain to be determined, and further comment is unwarranted until confirmatory observations are made.

Defecation.—The gravel pit pair, which customarily fed in shallow water at the edge of the pond, invariably walked 2 to 4 m from the water to defecate. I did not record this behavior from other pairs.

Scratching.—Pluvianellus scratches "indirectly" or "over the wing." Indirect scratching is characteristic of the Charadriidae, Recurvirostridae, and Haematopodidae (Simmons, 1957). Direct scratching occurs in the Scolopacidae, including *Arenaria* and *Phalaropus tricolor* (Hohn, 1967), Burhinidae (Maclean, 1966, pers. obs.), Jacanidae (pers. obs.) Glareolidae (Maclean, 1967b), and Thinocoridae (Maclean, 1969), and Rostratulidae (J. P. Myers, pers. comm.).

WINTER BIOLOGY

Winter studies were made principally on the Valdes Peninsula, Chubut Province. At Golfo San José, I observed flocks of 20 and 10 birds on several days between 1 and 7 July 1971. Each flock contained adults and immatures, the former predominating, and was associated with wintering flocks of White-rumped and Baird's sandpipers and Two-banded Plovers; also present in the vicinity were wintering Magellanic Oystercatchers and smaller numbers of resident American *(Haematopus palliatus)* and Blackish *(H. ater)* oystercatchers. Although most other shorebirds were widely distributed, *Pluvianellus* was confined to the southwestern corner of the bay. On 12 July 1971, at Puerto Madryn at Golfo Nuevo, I studied six birds that fed along a 3 km stretch of sandy beach.

In 1972 I was unable to find *Pluvianellus* at Puerto Madryn on 3 August, and a thorough survey of 58 of Golfo San José's 80 miles of shoreline between 4 and 19 August (Jehl et al., 1973) revealed only 10 individuals, all in the area where flocks had wintered the previous year. On 27 August nine birds, including six immatures, were observed at Bahía de los Nodales (48°S), Santa Cruz Province. The topography of shore areas there was similar to that at Golfo San José.

Habitat.—Pluvianellus' major requirements in winter seem to be the presence of suitable restingas and, to a lesser degree, debris-covered sandy beaches, on which to feed. Such habitat is uncommon and irregularly distributed along the coast of Patagonia. In fact, except for a few sheltered bays and river mouths, the coast of Patagonia provides relatively little area for any wintering shorebirds other than oystercatchers and sheathbills. From the Strait of Magellan to Rio Deseado much of the coast is lined by steep sandstone cliffs, and beach areas are narrow or lacking. Farther north, from the Rio Deseado to the Rio Chubut:

> "The usual shore . . . is marked by three features: restinga, beach, and cliff. The restinga is a broad wave-cut platform in the country rock . . . and its level is between tides but nearer low tide. Its surface is broadly plane, but very rough in detail, with many pools in which fishes and other marine animals survive between tides. The rocky projections are usually covered with mussels. . . . The beach usually begins abruptly on the shoreward side of the restinga, and extends to the base of the cliff. It may be broad and nearly level, but more commonly is narrow and steep. . . . At the points and at some of the indentations the sea cliff is high and abrupt, and is cut in the native rock, like the restinga, the structure being that of a cut-notch or step, with debris, the beach, piled against its riser. Along the larger and older indentations, however . . . the true cut-cliff is low or absent, and the beach abuts against a series of older marine terraces" (Murphy 1936: 195).

This description is applicable to the coast at Golfo San José where the shoreline largely consists of steep, narrow, shell or sand beaches, interrupted by small

Figure 23: Feeding on the restingas at Golfo San José. Left, a bird clawing at the surface. Center and right, feeding on chironomid larvae on a small sand lens. Note the "cocked-head" feeding posture.

rocky outcrops or steep sandstone cliffs. Restingas of impenetrable claystone are widely distributed, but only in the southwestern corner of the gulf do they form a low, sloping terrace 30 cm or so above the low tide level.

Feeding.—At Golfo San José, *Pluvianellus* fed largely on restingas in the southwestern corner and to a lesser extent above the high-tide line on some sandy beaches. Similar habitats were used by the flock at Bahía de los Nodales. In sharp contrast to their summer preferences, wintering birds at all localities avoided the water's edge and only very rarely ventured onto mudflats.

Starting in well-drained areas high on the restingas, they foraged widely, working seaward as the falling tide exposed new feeding areas, but always remaining far from the water's edge. They were especially attracted to small sand lenses protruding a centimeter or so above the plane of the restinga, and would peck rapidly at the surface, all the while spinning in a small circle and sometimes clawing at the mud to expose more food (Fig. 23); feeding rates ranged from 1.0–2.5 pecks per second. Sediments on the restingas were so strongly compacted that I was unable to force a steel trowel more than 2–3 mm below the surface. Thus, the birds obtained their food by gleaning from the surface. They did not forage where traces of former vegetation (apparently *Spartina* sp.) dotted the surface of the restinga, and they avoided beds of tiny mussels at the edge of the restingas, even though Two-banded Plovers fed there extensively.

Near the steep seaward edge of the restingas erosion patterns have created a series of tiny pools in which the birds "dig" when the tide is low. Algae-lined (*Ulva* sp.) pools 30–120 cm. in area and 1–2 cm deep are preferred; deeper pools, which contained a different type of alga, were not utilized. Upon wading into a pool birds begin to kick, spin, and peck at the surface. Their similarity to spinning phalaropes is striking, except that kicking, not spinning of the entire body, creates the eddies that wash prey into view. They do not use a great area but remain near the center of the pool; pecking rates in four sequences averaged 1.4 pecks per second.

After feeding heavily on the restingas for an hour or two on the falling tide, birds retreated to the upper beach and joined resting flocks of Two-banded Plovers; at this time they preen and bathe in small tidal pools and occasionally forage along the beach (Fig. 19). Feeding on the upper beach is usually conducted at high tide, when the restingas are covered.

At low tide at Bahía de los Nodales birds fed on restingas and in small pools, as at Golfo San José. But at high tide they moved to the broad sandy

Figure 24. The sandy beach at Bahía de los Nodales. Partly buried piles of kelp extend along the entire beach; an extensive dig area is present at the left of the photograph.

beach and dug in a hummocky area where sand had covered small piles of kelp (Figures 24, 25). Although only nine birds were seen in this small bay, much of the beach was disturbed, with evidence of digging along 300 m. In one 30 m stretch I counted 26 digs averaging 10 to 15 cm in diameter and 3 to 8 cm deep; the largest measured 56×31 cm.

At Puerto Madryn, where there are no restingas, birds fed turnstone-like, flipping shells and other debris at the base of small sand dunes; I found no evidence of digging. Again, they shunned the shoreline, even after being disturbed repeatedly and even though other shorebirds were feeding on the mudflats.

Food.—On the restingas at Golfo San José and Bahía de los Nodales birds fed exclusively on larval chironomids (Insecta, Diptera, Tendipedidae), which were the only invertebrates found in the upper few millimeters of the almost impenetrable substrate. These larvae were common and widespread, but were particularly abundant on the small sand lenses. I found larvae as small as 3 mm in substrate samples, but most consumed by the birds were longer than 6 mm. Samples in pool habitats revealed large numbers of tanaidaceans (Crustacea, Tanaidacea) 5-7 mm long and tiny annelids 1-2 mm long; lesser numbers of small isopods (Crustacea, Isopoda) 4-5 mm long and larval chironomids were present, and in one pool I collected a single 13 mm amphipod (Crustacea, Amphipoda). Birds consumed these items roughly in proportion to their abundance, except that annelids and amphipods were not found in stomachs. Apparently the former were too small and the latter too rare to constitute an important part of the diet.

No samples or specimens were taken from the beach at Puerto Madryn.

Figure 25. A typical dig, exposing buried kelp, at Bahía de los Nodales.

On the sandy beach at Bahía de los Nodales samples from piles of buried kelp revealed large numbers of fly larvae (Diptera, Muscidae, Phainoiinae) 10-14 mm long, and some small pelecypods 6-12 mm long. The single bird collected there had fed almost exclusively on fly larvae; it also contained the remains of a spider and bits of shell from a tiny mussel *(Mytilus)*.

The stomachs, but not the crops, of all specimens contained bits of sand or tiny pebbles. Two birds also contained fragments of mussel shell and one contained two tiny gastropods. Since the birds avoided mussel beds, these molluscs were probably ingested as grit.

From a sample of five birds in 1971, I estimated that chironomids and tanaidaceans together comprise approximately 80 per cent (by volume) of this species' diet in Golfo San José, with isopods composing the remaining 20 per cent. However, as pool habitats are generally rare along the Argentine coast, I suspect that chironomids are the major winter food resource in intertidal situations and that tanaidaceans and isopods comprise only a small fraction of the diet.

I made no detailed observations on chironomid ecology, except to note that larvae were visible at the surface for a short time after the tide retreated. If, as seems likely, the exposure period of these animals is brief, one would expect *Pluvianellus* to feed heavily on the upper flats as the tide receded and to shift to pool habitats later in the cycle. That seemed to be the case.

Interactions.—Although wintering birds associate in loose flocks, individuals tend to feed singly with no obvious regard for the presence of others, and interindividual distances usually exceed 2 m. Birds gather in more compact groups when pressed or when resting, but these do not approach the degree of tightness one normally associates with shorebirds.

During my observations I saw only one instance of intra-specific aggression. At Bahía de Los Nodales an adult approached a kelp pile where an immature was digging. The immature quickly assumed an erect posture and, retaining this posture, chased the adult to a nearby kelp pile. When the adult began to dig there, the chase was resumed until, finally, the adult flew out of sight.

I saw no interspecific interactions. Two-banded Plovers and White-rumped Sandpipers, and occasionally other species, usually fed nearby, but the association was based on attraction to similar feeding areas. At Bahía de los Nodales, Sanderlings *(Calidris alba)* and Two-banded Plovers investigated active digs but did not interfere with feeding birds.

Pluvianellus is exceptionally quiet on the wintering grounds. The only sound from feeding birds was a low, almost audible, churring note. Unlike typical plovers, which dash off rapidly when disturbed, *Pluvianellus* waddles away at a brisk but not frantic pace. If pressed, they may form a loose flock, or disperse among Two-banded Plovers. When alarmed they assume an "alert" posture and then fly off with the plovers low and fast, for long distances. Alighting, however, they rapidly segregate from the plovers and resume foraging on high ground away from the water's edge.

Pluvianellus responds to alarm calls of Two-banded Plovers but only rarely gives pre-flight alarm calls of its own. Several times I saw birds raise both wings high over the back, exposing the white underwings, in a typical wader alarm posture, but this display did not evoke any obvious response in nearby birds. Even in alarm, flight vocalizations are rare. I never heard more than three single calls from a flock of birds that was flushed repeatedly. The flight note, transcribed as *whee* or *quee,* sometimes *quee-u,* seems identical to the contact note.

MOLTS AND PLUMAGES

Data on molts and plumages, given below, are based largely on the few specimens taken in this study. Material in museum collections is inadequate for a detailed analysis. The natal and juvenal plumages have not been described previously. Notes on the sequence of feather growth and on changes in soft part coloration in the chicks were obtained from observations at Laguna de los Cisnes.

Natal Down.—Head, face, back, and dorsal surface of wings greenish gray tinged with golden, resulting in a ground color unique among the Charadrii. Neck grayish with slight hint of a pale collar. Chin and throat dirty white, shading to golden on upper chest. Lower chest and abdomen pure white. There is no dorsal pattern except for a short dark line on mid crown. Small white-tipped feathers are scattered sparsely over the dorsum: there is a small row over the eye and another down the center of the crown; a tiny row outlines the base of the scapular tract; and a few others are scattered on the back and flanks, but form no obvious pattern.

Newly-hatched chicks have an egg tooth at the tip of the upper mandible only. The iris is gray-brown and the feet and legs are pale orange-pink. (Fig. 26).

Day 14-16. Body covered with down, juvenile feathers erupting on scapulars, remiges, and wing coverts. By Day 16 feathers in capital tract, sides of chest, center of abdomen, and rectrices begin to emerge. Down now more grayish ("salt and pepper") without golden tones. Iris pale blue-gray, legs and feet gray with pinkish tinge. Bill black, beginning to show light spot at base by Day 16 (Fig. 28).

Day 17-18. Juvenal feathers prominent on most of chest, belly, scapulars, and wing coverts and forming a band 10 mm wide in center of capital tract. Most of dorsal surface appears covered with contour feathers; down still present

Figure 26. Chick of *Pluvianellus socialis* in natal down, age (estimated) three days.

Figure 27. *Pluvianellus socialis* in juvenal plumage. This chick (estimated age 28 days) had just completed its first short flight.

on rump, lower abdomen, face, and undertail coverts. Tail stubby. Iris grayish, legs and feet gray with pink tinge.

Day 20. Slightly more advanced, body appearing almost completely covered with contour feathers. Legs and feet orangish.

Day 23. Almost completely in juvenal plumage, except for down on supraorbital area, nape, rump, flanks, upper tail coverts; bits of down persist on all feather tips. Iris gray, legs and feet becoming more pinkish orange, base of bill continuing to lighten.

Day 25. Body fully feathered, pin feathers of capital tract in band trace 13 mm broad. Only traces of down persist. Iris pale lavender, legs and feet fleshy orange.

Day 27. Fully feathered, legs more intensely orangish.

Juvenal Plumage.—The juvenal plumage (Figure 27), like the natal down, is strongly tinged with golden dorsally. Feathers of forehead, crown, nape, and cheeks golden tan with narrow grayish centers. Back somewhat grayer, the dorsal feathers and wing coverts being alternately barred with gray and golden tan. Throat gray-white. Chest buffy gray, lightly streaked longitudinally with darker gray brown. Abdomen white. Undertail coverts white, tipped with golden and gray bars. Central rectrices blackish, narrowly margined gold or whitish; next outer pair marbled black and white on outer vane, blackish on inner vane; remainder largely or entirely white with dusky smudges on outer vane. Primaries gray-brown with white shaft; outer vanes of inner primaries white basally. Iris creamy white with lavender tinge, legs and feet orangish; bill black, yellow spot at base of culmen 3 mm, at base of lower mandible 1.5 mm (at day 35-40).

First Pre-basic Molt.—Timing and extent unknown. Presumably commences by early December for early-hatching chicks and involves head, body, most wing coverts, and tertials, and possibly central rectrices.

First Basic Plumage.—Upper surface pale dove gray, as in adult; venter white, except for mottled gray-brown band on upper chest. Tips of crown, wing coverts, tertials, and chest feathers extensively margined with grayish-white. Iris coral pink, legs and feet orange-yellow (at least until following July—9 months). Yellow patch at base of bill prominent, 6 mm long; patch on lower mandible 3 X 1 mm.

First Pre-alternate Molt.—Timing and extent unknown. Apparently commences in early July; juvenile collected in late August showed scattered molt on chest, head and neck. Some wing coverts (e.g., lesser secondary coverts) may not be replaced.

First Alternate Plumage—Similar to adult, including color of soft parts, but wing coverts of first basic plumage retained and breast band mottled, less well defined.

Second Pre-basic Molt.—A complete molt, beginning with the rectrices. Apparently starts in late October, during incubation. Males may molt slightly earlier than females. The female of a pair whose chicks hatched on 12 November had already replaced all but the outer 3-4 primaries (Figure 14); her mate seemed to have completed wing molt. The female of a post-breeding pair collected on 18 November had molt on the nape and had molted all but the outer two primaries; the male showed no body molt but the molt of the primaries was nearly completed, the outer two being nearly full grown.

Second Basic Plumage.—Head, face, back, wing coverts and tertials dove gray; lores darker dusky gray. Ventral surface white except for broad gray-brown chest band, which becomes more deeply colored at its posterior margin; feathers of breast band tipped with whitish. Lateral undertail coverts margined blackish. Iris, legs, and feet bright coral pink.

Second Pre-alternate Molt.—Timing and extent unknown. Appears to be very

Figure 28. Chick of *Pluvianellus socialis*, age approximately 15 days.

rapid, from early July to late August. The few molting specimens I have seen appear to have replaced only a few feathers on head, upper body, and chest.

Second Alternate (and subsequent) Plumage.—Like preceding, but chest band more pronounced, perhaps as a result of wear of white-tipped feathers.

SYSTEMATIC RELATIONSHIPS

Many aspects of *Pluvianelus'* morphology and behavior differ markedly from the usual plover condition. These include:

- the turnstone-like body form and bill shape
- short, stout legs and blunt claws
- a foraging behavior unlike that of plovers, as well as a new pattern, digging, which is unique among the Charadrii
- a complicated system of territorial defense, conducted by the pair acting together
- complex pre-copulatory and scrape displays, including an apparent attachment to a specific copulatory site
- the presence of courtship feeding
- relatively small eggs, a clutch size of two, and the rearing of a single chick
- the absence of distraction displays
- the semi-precocial nature of the chicks, their slow growth, and prolonged dependence upon the adults
- a unique color pattern of the natal down
- parental feeding of the chicks
- the presence of a crop, which is also used to regurgitate food to the young
- the apparent dove-like drinking behavior.

Because comparative behavioral data from many shorebirds are unavailable, the taxonomic significance of these differences cannot be fully evaluated. The differences do not, however, provide any strong support for *Pluvianellus*' traditional placement among the Charadriidae and other relationships should be considered.

On anatomical grounds, Burton (1974) suggested the *Pluvianellus* was closest to the plovers, but his data did not exclude some other possibilities. Thus, the strong similarities between *Pluvianellus*' territorial display and the "piping" display of oystercatchers (which Heppelston, 1970, has shown to be territorial) could be significant. These include the attack glide posture of flying birds, the upright posture in which the neck is inflated and the bill pointed downward, prolonged bowing, participation (usually) by both members of the pair, and strikingly similar vocalizations. Oystercatchers also feed their young, but, in contrast to *Pluvianellus,* lack pre-coital or scrape displays (Makkink, 1942), and actively defend their nests and chicks. [Pair displays involving bowing, also occur in some lapwings (e.g., *Vanellus novaehollandiae*: Soper, 1972: 132), but their extent in the Vanellinae is unknown.]

The general body form of sheathbills is not unlike that of *Pluvianellus,* and the few available behavioral data reveal other similarities. In *Chionis alba* "the most conspicuous display . . . is the 'bowing ceremony' which is seen during and after pair formation . . . and seems to be important in maintaining the pair-bond" (Jones, 1967:59). Pair formation has not been documented in *Pluvianellus,* but bowing is important in territorial (including a "greeting ceremony?") and, probably, scrape displays. In territorial defense, sheathbills face each other in a forward-oblique pose which is usually accompanied by a 'bill-wiping' action on the ground in front" (Jones, 1967: 59-60). The threat posture and bill-wiping might correspond, respectively, to the Upright and Bowing displays of *Pluvianellus.* In sheathbills there is no evidence of pair territorial display.

According to Jones (1961: 61), in the pre-copulatory display the male sheathbill "strutted stiff-leggedly around the female, which stood still with a slightly lowered head and a raised tail. . . ." "In *Chionis minor* . . . after a similar strutting behaviour the male stands facing in the same direction as the female and after making quick and repeated clutching movements with his feet, mounts." These descriptions seem reminiscent of the Arc Dance and Back Step of *Pluvianellus.* Also, Sheathbills have a relatively small clutch (two or three eggs) and "in a large proportion of cases only one chick is fledged" (in *C. minor*; Downes et al., 1959); they carry food to the young and have a crop (Yudin, 1965), though they are not known to regurgitate food to the young; their chicks grow very slowly and remain in the nest area for prolonged periods; and their general foraging behavior is reminiscent of that of *Pluvianellus.*

Several possible relationships can be ruled out. *Pluvianellus* is not a member of the Scolopacidae (Burton, 1974), and therefore cannot be a "southern hemisphere turnstone." Affinities to the Thinocoridae—an endemic South American family of unknown relationships—can also be discounted. Despite a similar body shape *Pluvianellus* differs so markedly from the seed-snipe in skeletal characters and breeding biology that detailed comparison is not warranted. For similar reasons, possible relationships to the doves (Columbidae), which might be inferred from *Pluvianellus*' general shape, (apparent) drinking behavior, and regurgitation of food to the young, must be rejected.

Color patterns of downy young shorebirds have been valuable in suggesting relationships of problem taxa (Jehl, 1968). Unfortunately, the chick of *Pluvianellus* is essentially unpatterned, and gives no clues to its affinities. Loss of pattern is a common response among shorebirds nesting on gravel substrates (Jehl, 1968; Zusi and Jehl, 1970).

The available biological data indicate *Pluvianellus* represents an offshoot of that branch of the Charadrii that gave rise to the plovers and their relatives (see Jehl, 1968: 42). Its closest affinities are uncertain. They may lie with the Haematopodidae, Chionididae[2], or even the Vanellinae, but *Pluvianellus* differs so markedly that to include it in any of these would imply more about its relationships than is currently justified and would extend the limits of these well-defined taxa beyond practical bounds. Inasmuch as its morphological and behavioral features are at least as distinct as those characterizing other shorebird families, it should be placed in a new monotypic family, Pluvianellidae. This option has the advantage of calling attention to this remarkable bird, which may encourage further study, but the strong disadvantage of making the already top-heavy classification of the Class Aves even more unwieldy. Yet, pending a complete hierarchal revision of the Charadriiformes it seems the best choice at present.

Even though details of *Pluvianellus'* ancestry are unresolved, it seems that we need not seek for its closest relative on now-distant continents. Whatever its ancestry, its evolution in southern South America seems to have been most strongly influenced by two factors—the nature of the Patagonian coast, and the presence of competitors.

The Patagonian coast possesses few lagoons, harbors, river mouths, or natural embayments that provide suitable habitat for many shorebirds. Further, along the exposed outer coast strong currents and extremely high tides combine to erode any sediment that might accumulate; in many areas the beaches are steep and extremely narrow, and are covered with deep gravel deposits. The absence of varied shoreline habitats has certainly been one of the important factors in accounting for the relative paucity of shore-inhabiting Charadrii in temperate South America. Areas suitable for probers (sandpipers) are uncommon, and the few shorebirds that have been able to adapt to the relatively narrow and uniform beach areas are those that make a living either by gleaning food from the surface (plovers and *Pluvianellus*), by harvesting mussel beds or algae (oystercatchers and sheathbills), or by scavenging (sheathbills).

The incidence of shorebird taxa endemic to the Fuegian Region is high, and it follows, therefore, that the fauna has had ample time for extensive differentiation and radiation. Yet, only two species of gleaners utilize the Patagonian coast to any significant degree; evidently it has proved ecologically impractical to subdivide the meagre shoreline habitats more finely. The Two-banded Plover is abundant and feeds primarily in the intertidal zone, concentrating its foraging near the edge of the receding waters. *Pluvianellus* is rare and primarily adapted to feed among debris and in uncompacted sediments at or above the high tide line. When *Pluvianellus* does feed intertidally it utilizes microhabitats (sand lenses, tiny pools) that the plover ignores, and exploits a food source (larval chironomids) that is temporarily superabundant. Indeed, the presence of a well-developed crop in this species may be primarily attributable to its habit of feeding on resources that are unpredictable (e.g., buried fly larvae) or are available for only brief periods (larval chironomids), and must be gathered as the opportunity occurs.

In the northern hemisphere turnstones exploit the kinds of upper beach habitats that *Pluvianellus* uses in Patagonia. However, the similarities of these taxa in general morphology, bill shape, and even foraging behavior are the result of convergence, and represent independent solutions to a similar ecological problem—obtaining food from the upper beach.

---

[2] Since this manuscript was completed, J. G. Strauch, Jr. (pers. comm.) has informed me that on the basis of his morphological studies *Pluvianellus* seems most closely allied to the Chionididae.

SUMMARY

Pluvianellus socialis, the so-called Magellanic Plover, was studied on its wintering grounds in 1971 and 1972, and on its breeding grounds in 1973. Previously, this rare and unusual shorebird was thought to nest only in northern Tierra del Fuego, but it actually nests fairly widely in southern Patagonia as well. It winters locally, in sheltered areas, on the Argentine coast between the Strait of Magellan and the Valdes Peninsula.

In Tierra del Fuego *Pluvianellus* begins nesting in early September, shortly after its return to breeding localities; it is the earliest of the Fuegian shorebirds to breed. Lake shores composed of small rocks and gravel intermixed with mud are requisite for nesting. Breeding territories are linear along the shore; birds also defend feeding territories away from the nesting territory—sometimes even at adjacent lakes. Territorial displays are complicated and involve both members of the pair acting as a unit. Courtship and scrape displays are also unusually complex: in courtship the male feeds the female.

Pluvianellus lays two relatively small eggs but raises only one chick, the later-hatching chick being lost within a few days, apparently through starvation. Adults have a well developed crop, which in addition to its normal function as a storage organ is used to regurgitate food to the young. Chicks are best considered as semi-precocial rather than precocial. Their growth rate is extremely slow and fledging does not occur until they are 28-29 days old. Chicks remain at least loosely associated with the parents, and may still be fed by them, until they are at least 40 days old.

Pluvianellus does not exhibit the "run and peck" foraging behavior of the plovers, but typically feeds by constant pecking as it walks slowly along the beach; it also forages like a turnstone, flipping stones and debris with the bill. Its most characteristic foraging behavior, digging with the feet to expose food, represents a foraging adaptation unique among the Charadrii. Major foods taken in summer are presumably larval dipterans. In winter, birds require specialized feeding areas. They forage mainly on flat terraces as they become exposed by the falling tide. Their major food seems to be larval chironomids, which are available only briefly at that stage of the tidal cycle. At other times they forage on the upper beach. In sharp contrast to their behavior in summer, they avoid the water's edge.

Natal and juvenal plumages are described for the first time, and the sequence of molts and plumages is outlined.

Pluvianellus possesses a large number of characteristics that are not shared by typical plovers, and there is no strong evidence for including it in the Charadriidae where it has traditionally been placed. Closer relationships to the oystercatchers or sheathbills seem more likely but have not been fully demonstrated. Pending further study, *Pluvianellus* should be placed in a monotypic family, Pluvianellidae. General similarities between *Pluvianellus* and the northern hemisphere turnstones are the result of convergence and represent adaptations for exploiting upper beach habitats.

ACKNOWLEDGMENTS

This research was supported by a grant (NSF-GV-32739) from the National Science Foundation. The assistance of Pieter J. Lenie, Master, and the crew of the R/V *Hero* in support of winter field studies is sincerely appreciated. J. P. Winter, M. A. E. Rumboll, W. C. Cummings, J.F. Fish, and P. O. Thompson assisted in field work in 1971 and 1972. Field studies in Tierra del Fuego were enhanced by the assistance of many residents of Isla Grande. I am especially grateful to Sr. and Sra. Adrian Goodall, Sra. Clarita Bridges de Goodall, Sr. Len Bridges, and Sr. Howard Reynolds of Ea. Viamonte, to Sr. and Sra. Juancho Appolonaire of Ea. Maria Behety, and Sr. and Sra. Theodore

Mackay of Ea. San José for their hospitality, friendship, and information. Special thanks are due my good friend Maurice Rumboll, whose contribution to this paper has been immense. His knowledge of Argentine birds and of Argentina, and his unfailing support are major reasons for the success of the research program in the 1973 field season.

T. J. Cohn and A. Ross assisted in identifying the stomach contents. Ken Goldman carefully executed drawings of the courtship, territorial, and digging behavior of *Pluvianellus.* Miss Ruth Bohanon prepared the graphs. Miss Bettie Black persevered through the typing of many drafts of the manuscript.

I am indebted to J. G. Strauch, Jr., J. P. Myers, R. L. Zusi, and R. W. Storer for their constructive comments on the manuscript.

Publication of this paper was made possible, in part, by the National Science Foundation.

LITERATURE CITED

ANON., 1935. Lista sistematica de las aves Argentinas. Hornero 6: 343-364.

BOCK, W. J., 1958. A generic review of the plovers (Charadriidae: Aves). Bulletin of the Museum of Comparative Zoology 118(2): 27-97.

BURTON, P. J. K., 1972. Some anatomical notes on the Wrybill. Notornis 19: 26-32.

————, 1974. Feeding and the feeding apparatus in waders: a study of anatomy and adaptation in the Charadrii. British Museum (Natural History), London. 150p.

CADE, T. J., E. J. WILLOUGHBY, and G. L. MACLEAN, 1966. Drinking behavior of sandgrouse in the Namib and Kalahari deserts, Africa. Auk 83: 124-126.

CRACRAFT, J., 1973. Continental drift, paleoclimatology, and the evolution and biogeography of birds. Journal of Zoology, London 169: 455-545.

CRAWSHAY, R. 1907. The birds of Tierra del Fuego. Bernard Quaritch, London (Original not seen).

DOWNES, M. C., E. H. M. EALEY, A. M. GYNNE, and P. S. YOUNG, 1959. The birds of Heard Island. Australian National Antarctic Research Expedition Reports, ser. B, 1: 1-135.

GRAUL, W. D., 1973. Adaptive aspects of the Mountain Plover social system. Living Bird, Twelfth Annual: 69-94.

HARRIS, M. P., 1967. The biology of oystercatchers *Haematopus ostralegus* on Skokholm Island, S. Wales. Ibis 109: 180-193.

HEPPELSTON, P., 1970. The function of Oystercatcher piping behavior. British Birds 63: 133-135.

HOHN, E. O., 1967. Observations on the breeding biology of Wilson's Phalarope *(Steganopus tricolor)* in Central Alberta. Auk 84: 220-244.

HUMPHREY, P. S., D. BRIDGE, P. W. REYNOLDS, and R. T. PETERSON, 1970. Birds of Isla Grande (Tierra del Fuego). Preliminary Smithsonian Manual. University of Kansas Museum of Natural History. viii + 411p.

JEHL, J. R., JR., 1968. Relationships in the Charadrii (Shorebirds): A taxonomic study based on color patterns of the downy young. San Diego Society of Natural History, Memoir 3.

————, 1973. Breeding biology and systematic relationships of the Stilt Sandpiper. Wilson Bulletin 85: 115-147.

————, M. A. E. RUMBOLL, and J. P. WINTER, 1973. Winter bird populations of Golfo San José, Argentina. Bulletin British Ornithologists' Club 93: 56-63.

JOHNSON, A. W. and J. D. GOODALL, 1965. The birds of Chile and adjacent regions of Argentina, Bolivia, and Peru. Vol. 1. Buenos Aires, Platt Establecimientos Graficos, S. A.

JONES, N. V., 1963. The Sheathbill, *Chionis alba* (Gmelin), at Signy Island, South Orkney Islands. British Antarctic Survey Bulletin 2: 53-71.

LOWE, P. R., 1931. An anatomical review of the "Waders" (Telmatomorphae), with special references to the families, subfamilies, and genera within the Suborders *Limicolae, Grui-Limicolae,* and *Lari-Limicolae.* Ibis 1931: 712-771.

MACLEAN, G. L., 1966. Studies on the behavior of a young Cape Dikkop *Burhinus capensis* (Lichtenstein) reared in captivity. Ostrich, Sup. 6: 155-170.

————, 1967a. Die systematische Stellung der Flughühner (Pteroclidae). Journal für Ornithologie 108: 203-217.

————, 1967b. The breeding biology and behaviour of the Double-banded Coursor *Rhinoptilus africanus* (Temminck). Ibis 109: 556-569.

————, 1969. A study of sneedsnipe in southern South America. Living Bird, Eighth Annual: 33-80.

MACLEAN, G. L., 1972. Clutch size and evolution in the Charadrii. Auk 84: 299-324.

MAKKINK, G. F., 1942. Contribution to the knowledge of the behaviour of the Oyster-Catcher (*Haematopus ostralegus* L.). Ardea 31: 23-74.

MURPHY, R. C., 1936. Oceanic birds of South America, 2 vols. New York, American Museum of Natural History

OLROG, C. C., 1948. Observaciones sobre la avifauna de Tierra de Fuego y Chile. Acta Zoologica Lilloana 5: 435-531.

PARMELEE, D. F., H. A. STEPHENS, and R. H. SCHMIDT, 1967. The birds of southeastern Victoria Island and adjacent small islands.

National Museum of Canada Bulletin 222.

PETERS, J. L., Check-list of birds of the world. Vol. 2. Cambridge, Harvard University Press., 410p.

PETTINGILL, O. S., 1939. The American Woodcock. Memoirs at the Boston Society of Natural History 9(2): 167-391.

REYNOLDS, R. T., 1953. Sobre nidificacion del chorlo de Magallanes. Hornero 10: 90-92

RICKLEFS, R., 1968. Patterns of growth in birds. Ibis 110: 419-451.

————, 1973. Patterns of growth in birds. II. Growth rate and mode of development. Ibis 115: 177-201.

RICH, P. V., 1975. Antarctic dispersal routes, wandering continents, and the origin of Australia's Non-Passeriform avifauna. Memoirs of the National Museum of Victoria 36: 63-125

SEEBOHM, H., 1887. The geographical distribution of the family Charadriidae, or the plovers, sandpipers, snipes and their allies. London, Henry Southeran & Co. 524p.

SHARPE, R. B., 1896. Catalogue of the Limicolae in the collection of the British Museum. London, British Museum (Natural History). 794p.

SIMMONS, K. E. L., 1957. The taxonomic significance of the head-scratching methods of birds. Ibis 99: 178-181.

SOPER, M. F., 1972. New Zealand birds. Whitcombe and Tombs, Christchurch. 216p.

TUCK, L. M., 1972. The Snipes: a study of the genus *Capella*. Canadian Wildlife Service Monograph Series, No. 5, 429p.

YUDIN, K. A., 1965. Fauna S. S. S. R., Zool. Inst. Nauk, S. S. S. R. nov. ser., no. 91; Ptitsy, 2, no. 1, pt. 1 (Phylogeny and classification of the Charadriiformes) Moscow-Leningrad, Akademia Nauk S. S. S. R.

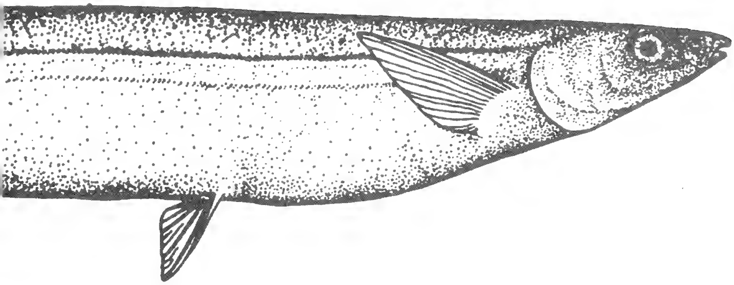
ZISWILER, V., and D. S. FARNER, 1972. Digestion and the Digestive System, p. 343-430. *In*, D. S. FARNER and J. R. KING (eds.), Avian Biology, vol. 2. Academic Press, New York and London.

ZUSI, R. L., AND J. R. JEHL, JR., 1970. The systematic relationships of *Aechmorphynchus*, *Prosobonia*, and *Phegornis* (Charadriiformes: Charadrii). Auk 87: 760-780.

Department of Birds and Mammals, Natural History Museum, San Diego, California 92112

TAXONOMIC STATUS OF THE GULF GRUNION *(LEURESTHES SARDINA)* AND ITS RELATIONSHIP TO THE CALIFORNIA GRUNION *(L. TENUIS)*

Nancy M. Moffatt and Donald A. Thomson



TRANSACTIONS

OF THE SAN DIEGO
SOCIETY OF
NATURAL HISTORY

VOL. 18, NO. 4 18 DECEMBER 1975

Taxonomic status of the Gulf Grunion *(Leuresthes sardina)* and its relationship to the California Grunion *(L. tenuis)*

Nancy M. Moffatt and Donald A. Thomson

ABSTRACT.—Statistical comparisons of morphometric and meristic characteristics of the grunions *Leuresthes sardina* and *L. tenuis* support their present status as distinct species. Similarities in fin-ray formulae, gill-raker counts, body proportions and especially reproductive habits justify their placement in *Leuresthes.* The only significant meristic difference between the two is the larger and fewer scales of *L. sardina* (typically 55 lateral scale rows as compared to 75 for *L. tenuis*). Morphologically, *L. sardina* is a longer, more slender fish with shorter pectoral fins and longer pelvic fins than *L. tenuis.* The two species are allopatric: *L. sardina* ranges in the northern Gulf of California from Bahía Concepción, Baja California Sur, and Guaymas, Sonora to the mouth of the Río Colorado; *L. tenuis* ranges from Monterey Bay, California to Bahía Magdalena, Baja California Sur. Their distributions seem to be restricted more by availability of adequate spawning beaches than by sea temperatures.

The Gulf of California grunion, *Leuresthes sardina* (Jenkins and Evermann 1888), and the well-known California grunion, *L. tenuis* (Ayres 1860), are the only two species of fishes known to leave the water and deposit their eggs in beach sand (Figs. 1, 2; Thompson 1919; Walker 1952). Both spawn on a descending series of high spring tides following new and full moons. Their fortnightly spawning runs can be predicted with reasonable accuracy by noting the times of the full and new moon in relation to the height of the high tide (Walker 1952; Thomson 1972). The species are allopatric. *Leuresthes sardina* is endemic to the upper Gulf of California, from Bahía Concepción, Baja California Sur and Guaymas, Sonora to the Río Colorado Delta (Fig. 3). *Leuresthes tenuis* ranges from Monterey Bay, California to Bahía Magdelena on the outer coast of Baja California Sur.

No critical taxonomic comparisons have validated the congeneric status of *L. sardina* and *L. tenuis,* nor fully documented their specific distinction. The forms differ in scale row numbers, body shape and in spawning behavior, as recently noted by Thomson and Muench (1974). The purpose of this study is to statistically compare the morphometric and meristic characteristics of each species, to clarify their taxonomic status, and to elucidate their phyletic relationships.

Taxonomy.—The California grunion was described as *Atherinopsis tenuis* from a specimen taken from a San Francisco fish market by Ayres (1860), and was made the type of a separate genus, *Leuresthes,* by Jordan and Gilbert (1880). In 1896, Jordan and Evermann described a second species in the genus, *L. crameri,* from "Ballenas Bay, Lower California, near Cape Abreojos," and distinguished it from *L. tenuis* on the basis of having fewer lateral scale rows (67 versus 75) and a narrower silvery lateral band. Schultz (1948), however, concluded that *Leuresthes tenuis* and *L. crameri* are conspecific, presumably discounting the lower scale count reported for *L. crameri.*

Taxonomy of the Gulf of California grunion, *Leuresthes sardina,* has been more confused than that of *L. tenuis.* This species was described as *Atherina sardina* by Jenkins and Evermann (1888). *Menidia clara* (Evermann and Jenkins 1891) was synonymized with *A. sardina* by Schultz (1948). Jordan and Evermann (1896) referred *Atherina sardina* to the genus *Menidia* and were the first to suggest

Figure 1. Male Gulf grunion *(L. sardina)* aggregating on the beach at the start of a run at El Golfo de Santa Clara, Sonora, Mexico. (Photo by D. A. Thomson)

a close relationship between *M. clara (=sardina)* and *Leuresthes*, an opinion subsequently supported by Jordan and Hubbs (1919), Breder (1936), Schultz (1948), and Walker (1952, 1960).

Breder (1936) erected a new genus, *Hubbsiella*, for *Menidia clara* on the basis of several characteristics, including that of more lateral scale rows (54-56 as compared with 36-46 in *Menidia*). However, Schultz (1948) stated that the count of 45 lateral scale rows reported by Jenkins and Evermann (1888) for the type of *Atherina sardina* was in error, the actual number being 54. On the basis of similar scale sizes, along with similar structure of gas bladders and vertebral hypophyses, he synonymized *Menidia clara* with *M. sardina*. Schultz accepted the genus, *Hubbsiella*, but noted that *L. tenuis* and *H. sardina* are undoubtedly in the same phyletic line.

Hubbsiella is now generally recognized (e.g. Walker 1960) as being congeneric with *Leuresthes* but the synonymy has not been formally documented.

An otolith from an Eocene deposit at the mouth of the Thames River has been described as *Leuresthes distans* by Stinton (1966), but John E. Fitch and Carl L. Hubbs (pers. comm.) believe this otolith can not be assigned to any living genus, though it is probably from an atherinid. Its reference to a strictly New World genus and subfamily (Atherinopsinae) is highly improbable.

MATERIALS AND METHODS

The specimens of *L. sardina* studied in detail were collected near the head of the Gulf of California at San Felipe in Baja California Norte and at El Golfo

Figure 2. Two Gulf grunion females attended by several males on the beach at El Golfo de Santa Clara. Female in the center of the photo is depositing eggs and males are ejecting milt; female below the center is leaving after spawning. (Photo by D. A. Thomson)

de Santa Clara and Puerto Peñasco in Sonora (Fig. 3). Those of *L. tenuis* were secured in California at Morro Beach, San Luis Obispo, and at Santa Monica, El Segundo, Santa Catalina Island, Cabrillo Beach, Torrey Pines, and La Jolla Shores, in southern California; and from Bahía de Todos Santos, Bahía de Santa Rosalia, and Bahía Magdalena, in Baja California.

Study specimens are housed in fish collections at the University of Arizona (UA), Scripps Institution of Oceanography (SIO), University of California, Los Angeles (UCLA), Los Angeles County Museum of Natural History (LACM), and the California Academy of Sciences (CAS).

Museum catalog numbers, followed by numbers of specimens examined in parentheses, for *L. sardina* are: UA 70-39 (44); UA 70-64-1 (56); UA 72-44-10 (7); UA 73-45 (68); UA 74-9-2 (29); and SIO 65-86 (3). Those for *L. tenuis* are: UA 73-107-1 (42); UA 74-18 (6); UA 74-19-1 (2); SIO H44-40 (19); SIO 74-57 (20); UCLA W51-210 (1); UCLA W49-113 (5); UCLA W49-117 (14); UCLA W55-143 (1); LACM W55-115 (2); LACM 33139-1 (1); LACM 4382 (3); LACM 31306-3 (2); LACM 32597-1 (12); LACM 22307 (2); LACM 31864-12 (2); CAS 25483 (6); CAS 30548 (5); CAS 47320 (1).

Measurements and counts on specimens follow the specifications by Hubbs and Lagler (1947). Body depth was measured vertically above the anus; body width as the distance across the body between the bases of the pectoral fins; and the anal-caudal distance as the length from the anus to the lower midline base of the caudal fin. Anal-fin height was measured from the front base of the fin to the tip of its longest front ray.

Figure 3. Geographical distributions of the Gulf of California grunion, *Leuresthes sardina*, and the California grunion, *L. tenuis*.

Results were analyzed using the student *t*-test and differences are considered to be significant at the 95% probability level. Coefficients of variation were also compared.

RESULTS

Comparison of coefficients of variation show that all meristic counts (V = 0.99 — 9.18) and morphometric measurements (V = 3.56 — 10.75) show average variability (Simpson, *et al.* 1960) except the width of *L. sardina* (V = 14.46). This is probably an artifact of the unavoidable mixing of age classes sampled during

TABLE 1. Means, 95% confidence intervals (CI), samples sizes (N), ranges, and *p*'s of *L. sardina* and *L. tenuis* body measurements expressed as ratios of standard length i.e. SL/measurement. Eye diameter and gill-raker length is reported in proportion to head length.

	L. sardina	*L. tenuis*	
Body measurement	$\bar{x}$ ± 95% CI N(Range)	$\bar{x}$ ± 95% CI N(Range)	*p*
Standard length (mm)	163.5 ± 1.60 207(136-191)	143.8 ± 2.20 145(104-179)	< 0.001
Head length	5.39 ± 0.06 200(6.49-4.68)	5.40 ± 0.45 140(6.67-4.44)	> 0.8
Snout length	17.0 ± 0.21 199(22.3-13.8)	16.6 ± 0.24 144(20.7-13.1)	< 0.01
Eye diameter	4.87 ± 0.16 197(6.70-4.25)	4.10 ± 0.06 150(5.00-3.13)	< 0.001
Bony interorbital width	18.5 ± 0.21 198(23.8-15.1)	18.7 ± 0.23 146(22.8-14.6)	> 0.4
Depth	6.54 ± 0.07 200(8.05-5.08)	6.30 ± 0.07 145(7.14-4.98)	< 0.001
Width	10.8 ± 0.22 145(14.5-8.55)	9.95 ± 0.11 133(11.7-8.41)	< 0.001
Anal-caudal length	2.52 ± 0.04 146(3.11-2.00)	2.36 ± 0.02 108(2.52-2.17)	< 0.001
Gill-raker length	4.59 ± 0.31 30(7.38-4.17)	4.27 ± 0.73 14(5.44-4.00)	> 0.3
Pectoral-fin length	5.99 ± 0.04 200(6.93-5.34)	5.67 ± 0.04 141(6.44-5.14)	< 0.001
Pelvic-fin length	9.65 ± 0.13 198(12.3-8.42)	10.3 ± 0.10 146(11.8-9.21)	< 0.001
Anal-fin height	10.0 ± 0.17 92(12.6-8.06)	11.0 ± 0.23 52(12.5-9.23)	< 0.001

spawning runs. The pelvic and anal spines are always single and the pelvic soft rays always number 5, as in the Atherinidae in general.

All body measurements made, expressed as a ratio of standard length or of head length, are significantly different at the 0.05 probability level except for head length and the bony interorbital width (Table 1). In each species the head length averages 18.5% of standard length, and interorbital widths average 5.4% of the standard length.

Standard length averages about 10 mm longer in *Leuresthes sardina* than *L. tenuis*. Adult females of each species are significantly longer than males, averaging 10 mm longer in *L. sardina* and 13 mm longer in *L. tenuis*. In body depth and body width *L. tenuis* is 4% and 8% the greater, respectively. These differences are significant at $p < 0.001$. *Leuresthes tenuis* is significantly shorter but its anal-caudal length is 4.7% longer ($p < 0.001$). Therefore, the distinctive elongation of the body in *L. sardina* lies between head and anus.

The eye of *L. sardina* is significantly smaller, averaging about 19.6% of head length, as compared to 24.4% in *L. tenuis* ($p < 0.001$). *Leuresthes sardina* has a 2.4% shorter snout than *L. tenuis* thus placing the eye of the Gulf grunion in a slightly more anterior position than that of the California grunion.

Also, there are significant differences in fin lengths. In *L. sardina* the pectoral fins are shorter, and the pelvic fins are longer than those of *L. tenuis* but with overlap in the ratios. Anal-fin height is 9% greater in *L. sardina.*

TABLE 2. Means, 95% confidence intervals (CI), samples sizes (N), ranges, and *p*'s of all counts for *L. sardina* and *L. tenuis*.

Count	*L. sardina* $\bar{x}$ ± 95% CI N(Range)	*L. tenuis* $\bar{x}$ ± 95% CI N(Range)	*p*
Dorsal$_1$ spines	5.15 ± 0.14 48(4-6)	5.03 ± 0.14 33(4-6)	>0.2
Dorsal$_2$ soft-rays	9.40 ± 1.39 48(8-10)	9.48 ± 0.31 33(8-10)	>0.9
Anal soft-rays	20.9 ± 0.39 48(19-23)	21.7 ± 0.10 33(19-23)	>0.7
Caudal rays	17.1 ± 0.07 48(17-18)	17.0 ± 0.06 33(17-18)	>0.1
Pectoral rays	13.8 ± 0.17 66(12-15)	13.5 ± 0.27 33(12-15)	>0.05
Gill-rakers	33.4 ± 0.51 48(30-36)	33.7 ± 1.36 33(30-36)	>0.5
Lateral scale rows above lateral band	4.02 ± 0.002 48(4-5)	4.03 ± 0.36 33(4-5)	>0.9
Lateral scale rows below lateral band	5.50 ± 0.12 52(4-7)	7.12 ± 0.19 33(6-8)	<0.001
Lateral scale rows	55.3 ± 0.25 177(51-60)	74.5 ± 0.43 143(69-80)	<0.001

Fin-ray formulae (Table 2) for these species show no statistical difference: D V-I, 9; A I, 20-21; P_1 13-15; as in other atherinids the pelvic-fin rays number I,5 and the principal caudal rays 17 (8 + 9). The first dorsal originates slightly in advance of the anal. The second dorsal is inserted above the middle of the anal fin and the insertion of the last dorsal ray precedes the insertion of the last anal ray. In *L. tenuis* there are 10 to 13 scales between the end of the first dorsal fin and the origin of the second dorsal fin and 8 to 11 interdorsal scales in *L. sardina.* Pelvic fins in each species are inserted far in advance of the first dorsal fin, nearer the tip of the snout than the base of the caudal fin.

Each species has 30 to 36 slender gill rakers on the lower limb of the first gill arch. The longest rakers are about 35% of the head length.

The most diagnostic differences between these two species is in the non-overlapping number of body lateral scale rows. These number 51 to 60 (averaging 55) in *L. sardina,* and 69 to 80 (averaging 75) in *L. tenuis* ($p < 0.001$). Each species has 4 longitudinal scale rows above the lateral band, whereas the number below differs significantly; on the average the Gulf grunion has 6 and the California grunion has 7.

There appears to be no evidence of latitudinal clines within either species in the characteristics discussed above.

Scales also differ conspicuously in shape and size. Although each species has cycloid scales as is usual in the family, those of *L. tenuis* are approximately one-half the anteroposterior dimension and two-thirds the dorsoventral dimension of those of *L. sardina.* Scales on the mid-lateral band of *L. sardina* are entire, with 2 or 3 scallops in the center of the posterior margin, whereas those from the mid-lateral band of *L. tenuis,* are highly and irregularly crenulate. Scales from the last two to three longitudinal rows below the lateral band and above the anal fin in *L. tenuis* are more entire, and similar to those found over the whole body of *L. sardina.* Scales just dorsal to the anal fin in both species are stiffer and tend

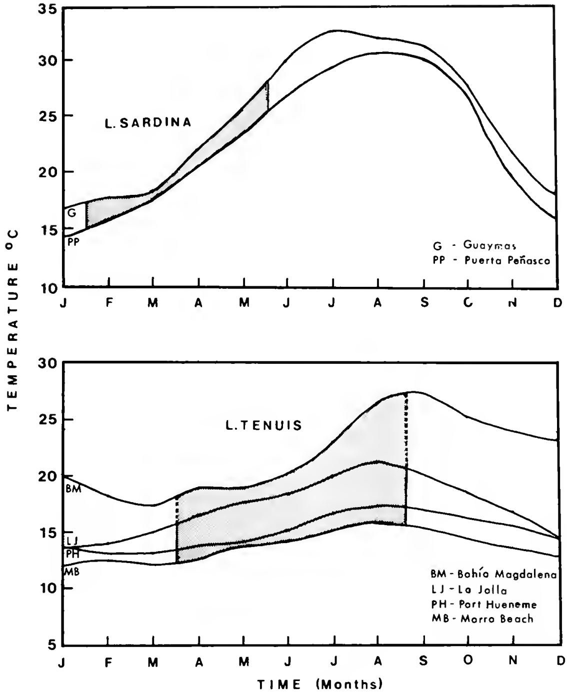


Figure 4. Monthly mean sea-surface temperatures (Robinson 1973; USCGS 1967; and Hendrickson 1974) at several locations in the geographical ranges and the respective spawning seasons (shaded) of *L. sardina* and *L. tenuis*. Sea-surface temperatures at San Felipe and El Golfo de Santa Clara are similar to those at Puerto Peñasco but are not given because long-term temperature records are not available. Dotted lines between temperature curves BM and LJ indicate that frequency of spawning runs have not been established south of Bahía de Todos Santos.

to stand away from the body rather than to lie smoothly as do other body scales. This scale pattern (the "sheath" of Breder 1936, Schultz 1948, and others) is observable in living as well as preserved material, but is less obvious in specimens of *L. tenuis* than those of *L. sardina.* In each species scales extend onto the caudal fin as far posteriad as the first branching of the rays.

Both species have minute and weak recurved teeth, usually in a single row on a strongly downwardly protrusible premaxillary, as described by Jenkins and Evermann (1888) and others. Usually the upper jaw must be dried to see the minute teeth. Teeth of *L. tenuis* are generally weaker and uniserial, and the premaxillary is fleshy. Teeth in *L. sardina* are stronger and sometimes biserial. Occasionally teeth are absent in either species, in which case the jaws are fleshier.

DISCUSSION

Since Jordan and Evermann (1896) first suggested a close phyletic relationship between "*Menidia*" *sardina* of the Gulf of California and *Leuresthes tenuis* of the Californias, some studies have provided supportive evidence, but none have substantiated this relationship by detailed taxonomic analysis. Breder (1936) noted likenesses between the two species in protractile premaxillaries, weak mandibles, general body shapes, short pectoral fins, location of insertion of the first dorsal fins, coloration, and scale sculpturing. Results of the present study show that both species have premaxillaries that can be protruded strongly downward; overall fin insertion is similar; fin-ray formulae do not differ; gill rakers are alike in size and number; and head length and interorbital widths are similar, as is gas bladder and posterior hemal arch morphology (Schultz 1948).

Walker (1960) suggested that the two species are congeneric and he was first to note their "almost identical" beach spawning habit and similar dates of spawning runs (Walker 1952). In view of morphological and behavioral similarities, one might suggest that these fishes represent two allopatic populations of a single species recently isolated, and that any morphological differences between them are clinal ones correlated with past or present environmental gradients; or in light of the description of *L. crameri* (Jordan and Evermann 1896) from Lower California as having a scale count intermediate between *L. sardina* and *L. tenuis* that hybridization has occurred.

None of the differences between *L. sardina* and *L. tenuis* show evidence for latitudinal clines. Nor is there any indication of an intraspecific cline despite the fact that *L. tenuis* specimens were collected from over a 720 mile latitudinal range (Fig. 3). Examination of 26 "*L. tenuis*" specimens from Baja California, 19 of these from Punta Abreojos and Bahía Magdalena, show no significant variation, in any of the characteristics discussed, from *L. tenuis* specimens collected at more northern sites. This supports Schultz's (1948) conclusion (from 2 specimens) that *L. crameri* and *L. tenuis* are conspecific. Gulf grunion populations samples cover too narrow a range to test for clinal variations.

A behavioral difference is also indicated between the two species. *Leuresthes tenuis* is a strictly nocturnal spawner (Walker 1949), whereas *L. sardina* spawns during the day as well as at night. It may be significant that *L. tenuis*, the exclusively nocturnal spawner, has a 20% larger relative eye diameter than *L. sardina.*

Both species spawn over a rather wide range of sea-surface temperatures. *Leuresthes sardina* spawns beginning in late January when monthly mean sea-surface temperatures range from 14° to 17° C throughout its range (Fig. 4). Spawning ceases in May in the northern Gulf when mean sea-surface temperatures range between 23° and 26° C. Throughout the remainder of its geographic range, *L. sardina* is less abundant, and spawning runs are sporadic and not presently predictable.

California and Baja California sea-surface temperatures range from 12° to 16° C when spawning by *L. tenuis* begins in mid-March, from Bahía de Todos Santos to its northern limits. Spawning ceases in this region by mid-August (14° — 19° C). It is not known when spawning begins and ends in the more southern portions of the range of *L. tenuis,* where sea-surface temperatures range from 4° — 11° C higher.

Though little is known of the life history of these two species apart from the spawning behavior, it is believed (Walker 1949) that the California grunion remains in shallow waters not far from spawning beaches. This seems to be the case with *L. sardina* as well. If so, then these fishes are subject to temperatures ranging from 10° to 26° C along the California coasts and from 8° to 31° C in the northern Gulf of California. *Leuresthes sardina* and *L. tenuis* larvae have been shown to have wide temperature tolerance ranges of 7.5° — 32° C (Reynolds, *et* *al.* MS) and with acclimation from 30° to 35° C *L. sardina* tolerates up to 35° C (Reynolds and Thomson 1974).

It seems unlikely that temperature presently limits the distribution of these species in Baja California from Bahía Magdalena southward to Cabo San Lucas and in the Gulf of California as Walker (1960) and Hubbs (1960) suggest, since larvae of these species easily tolerate temperatures occurring in the southern Gulf at Cabo San Lucas. It may be, because of the predilection of young grunion to remain near spawning grounds, that the absence of appropriate spawning beaches in the lower Gulf of California limit the distribution of the grunion in this area.

Hubbs (*in* Breder 1936) suggested that the Gulf grunion ancestral type was probably a form resembling *Hubbesia gilberti.* Schultz (1948) disagreed with this, saying the gas bladders in *Hubbesia* and the other genera retained by him in the subfamily Atherinopsinae, are too dissimilar to postulate *Hubbesia* to be the ancestral type leading to *Leuresthes.* Both Hubbs and Schultz (1948) agree that "*L. sardina* is possibly near the ancestor of *L. tenuis.*" We suggest that *L. sardina* is more primitive than *L. tenuis* because of its stronger dentition and larger scales. Walker (1959) suggested that the grunion's nearest relative is either the California jack smelt *(Atherinopsis californiensis)* or the top smelt *(Atherinops affinis)* both of which, like many members of the Atherinidae, spawn close inshore. Schultz (1948) classified *Atherinops* and *Atherinopsis* in the subfamily Atherinopsinae on the basis of tapering gas bladders somewhat like those in *Leuresthes.* Although none of the Atherinidae possess well-developed lateral-line systems, Freihofer (1972) noted that *L. tenuis* and *Atherinops affinis* have similar distributions of tubed scales.

Hubbs (pers. comm.) supports his earlier suggestion that *L. sardina,* or its ancestor, was ancestral to *L. tenuis,* by pointing out that *L. sardina* more closely resembles the Atherinids as a group than does *L. tenuis,* particularly in view of larger scales and stronger dentition. Hubbs maintains that the finer scales of *L. tenuis,* are typical of the anti-tropical atherinids at terminal evolutionary lines.

The Gulf of California and California grunions have long been recognized to belong to the same phyletic line, the similarities herein described, and particularly their unique spawning behavior justify their congeneric placement. We suggest that major differences here discussed substantiate the specific distinction of *Leuresthes sardina* and *L. tenuis.*

ACKNOWLEDGMENTS

We express our gratitude to C. L. Hubbs and R. H. Rosenblatt, Scripps Institution of Oceanography, J. E. Fitch, California Department of Fish and Game, and B. W. Walker, University of California, Los Angeles for their assistance during this investigation. We also thank C. L. Hubbs, L. T. Findley, University of Arizona, and Manuel Molles, University of New Mexico, for their valuable comments and suggestions in review of the manuscript.

We acknowledge the museum staffs for their cooperation in loaning specimens: J. E. Copp and R. H. Rosenblatt at Scripps Insitution of Oceanography; C. C. Swift and J. W. Newman at the Los Angeles County Museum of Natural History; W. L. Eschmeyer at the California Academy of Sciences; and particularly L. T. Findley at the University of Arizona.

We also thank V. J. and O. M. Moffatt, the R. H. Dutcher family, J. E. Copp and others for help in obtaining fresh specimens.

REFERENCES CITED

AYRES, W. O., 1860. On new fishes of the California coast. Proceedings of the California Academy of Sciences 2: 75.

BREDER, C. M. 1936. Scientific results of the second oceanographic expedition of the "Pawnee" 1926. Bulletin of the Bingham Oceanograhic Collection 2: 6-10.

EVERMANN, B. W. and O. P. JENKINS, 1891. Report upon a collection of fishes made at Guaymas, Sonora, Mexico, with descriptions of new species. Proceedings U.S. National Museum 14: 121-165.

FREIHOFER, W. C., 1972. Trunk lateral line nerves, hyoid arch gill rakers, and olfactory bulb location in atheriniform, mugilid, and percoid fishes. California Academy of Sciences Occasional Papers 95: 31p.

HENDRICKSON, J. R., 1974. Study of marine environment of the northern Gulf of California. National Technical Information Service Publication No. 74-16008: 95p.

HUBBS, C. L., 1960. The marine vertebrates of the outer coast. Systematic Zoology 9: 134-147.

HUBBS, C. L. and K. F. LAGLER, 1947. Fishes of the Great Lakes region. Bulletin of the Cranbrook Institute of Science 26: 1-186.

JENKINS, O. P. and B. W. EVERMANN, 1888. Descriptions of eighteen new species of fishes from the Gulf of California. Proceedings of the U.S. National Museum 11: 137-158.

JORDAN, D. S. and B. W. EVERMANN, 1896. The fishes of North and Middle America: A descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, North of the Isthmus of Panama. Bulletin of the U.S. National Museum 47: 796-808.

JORDAN, D. S. and C. H. GILBERT, 1880. Synopsis of the fishes of North America. Proceedings of the U.S. National Museum 3: 29.

JORDAN, D. S. and C. L. HUBBS, 1919. Studies in Ichthyology: A monographic review of the family Atherinidae or silversides. Leland Stanford Jr. University Publication, University Series 40: 87p.

REYNOLDS, W. W. and D. A. THOMSON, 1974. Temperature and salinity tolerances of young Gulf of California grunion, *Leuresthes sardina*. Journal of Marine Research. 32: 37-45.

REYNOLDS, W. W., D. A. THOMSON and M. E. CASTERLIN, MS Temperature and salinity tolerances of larval California grunion, *Leuresthes tenuis*: a comparison with the Gulf of California grunion, *L. sardina*.

ROBINSON, M. K., 1973. Atlas of monthly mean sea-surface and subsurface temperatures in the Gulf of California, Mexico. San Diego Society of Natural History Memoir 5: 97p.

SCHULTZ, L. P., 1948. A revision of six subfamilies of atherine fishes, with descriptions of new genera and species. Proceedings of the U.S. National Museum 98: 1-50.

SIMPSON, G. G., A. ROE and R. C. LEWONTIN, 1960. Quantitative zoology. Harcourt, Brace and World, Inc. New York.

STINTON, F. G., 1966. Appendice-otolithes des poissons du London Clay, pp. 404-464. *In*, Faune ichthyologique de London Clay. Edgard Casier. British Museum (Natural History).

THOMPSON, W. F., 1919. The spawning of the grunion *(Leuresthes tenuis)*. California Fish and Game Bulletin 3: 1-29.

THOMSON, D. A., 1972. Tide calendar for the northern Gulf of California with predictions of Gulf grunion spawning runs. Bur. Mimeo., and Multilith., University of Arizona, Tucson.

THOMSON, D. A. and K. A. MUENCH, 1974. Spawning rhythmicity of the Gulf of California grunion, *Leuresthes sardina* (Jenkins and Evermann). Resumenes. Quinto Congreso Nacional de Oceanografia, Guaymas, Sonora, Mexico. 22-25 October 1974.

USCGS, 1967. Surface water temperature and density, Pacific coast, North and South America and Pacific Ocean islands. Department of Commerce, Environmental Service Administration p. 79.

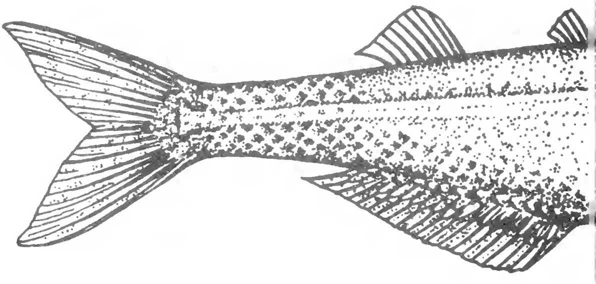
WALKER, B. W., 1949. The periodicity of spawning by the grunion, *Leuresthes tenuis*, an atherine fish. Ph.D. Thesis, Scripps Institution of Oceanography.

1952. A guide to the grunion. California Fish and Game 38: 409-420.

1959. The timely grunion. Natural History 68: 302-306.

1960. Distribution and affinity of the marine fish fauna of the Gulf of California. Systematic Zoology: 123-133.

Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona



DIDELPHIDS (MARSUPIALIA) AND *UINTASOREX* (?PRIMATES) FROM LATER EOCENE SEDIMENTS OF SAN DIEGO COUNTY, CALIFORNIA

Jason A. Lillegraven

TRANSACTIONS

OF THE SAN DIEGO
SOCIETY OF
NATURAL HISTORY

VOL. 18, NO. 5 26 JANUARY 1976

Didelphids (Marsupialia) and *Uintasorex* (?Primates) from later Eocene Sediments of San Diego County, California

Jason A. Lillegraven

ABSTRACT.—Fossil teeth of three species of small mammals from early Uintan (roughly mid Eocene) terrestrial deposits of western San Diego Co., California are compared with approximately contemporaneous similar species from the North American Rocky Mountain and High Plains states. Two species of opossums (didelphid marsupials) were discovered: *Peratherium* sp. cf. *P. knighti* and *Nanodelphys californicus*. The former cannot be distinguished from *P. knighti* McGrew, 1959 common in Bridgerian (roughly late early Eocene) sediments of Wyoming. *Peratherium* sp. cf. *P. knighti* is also present in the lower Sespe Formation of Ventura Co., California and was first recognized as "*Peratherium* species" by Stock (1936). *Peratherium californicum* Stock, 1936 in actuality represents a species of *Nanodelphys* McGrew, 1937. The suffix of the trivial name is here emended. *Nanodelphys californicus* is morphologically indistinguishable from *N. minutus* McGrew, 1937 from Oligocene sediments of Nebraska but a separate species designation is maintained for strictly stratigraphic reasons. The San Diego *Nanodelphys* specimens are the oldest yet known, but show fully developed all the characters diagnostic of the genus. Thus Bridgerian or even Wasatchian (early Eocene) species might someday be expected to be found. The new species of tiny uintasoricine ?primate, *Uintasorex montezumicus*, shows several dental specializations beyond those seen in *U. parvulus* (common in Bridgerian sediments of Wyoming). *Nanodelphys* and *Uintasorex* were previously recognized only from the Rocky Mountain and High Plains states.

All three species were represented by rat- to tiny mouse-sized animals, were probably at least semi-arboreal in habits, and are extremely similar to or conspecific with species from the Rockies and High Plains. Overland dispersal routes must have been readily available between the two areas during at least part of the early Eocene and they probably involved rather continuous tropical forest or at least savannah-like settings.

Among the large and diverse land vertebrate fauna recently collected from the later Eocene sediments of San Diego Co., California are the teeth of three species of small mammals that are of considerable interest because of their biogeographical implications. They represent two genera previously unrecorded from the North American West Coast as well as a new species. The study is one part of a larger revision of the West Coast later Eocene terrestrial vertebrate fauna. Completed parts include papers by Lillegraven and Wilson (1975), Novacek (in prep.), Schatzinger (1975), and Schiebout (Ms).

All measurements are in millimeters and were taken on an Ehrenreich Photo-Optical Industries (EPOI) "Shopscope." Criteria used for orientation of axes of measurement are described below for each taxon.

ABBREVIATIONS USED

AMNH, Department of Vertebrate Paleontology, American Museum of Natural History. LACM (CIT), Section of Vertebrate Paleontology, Natural History Museum of Los Angeles County (specimen numbers and locality numbers from an older California Institute of Technology collection purchased by the LACM). UCMP, Museum of Paleontology, University of California, Berkeley. V-72157, UCMP vertebrate locality number (detailed locality descriptions on file at UCMP). YPM, Peabody Museum of Natural History, Yale University.

A-P, Anteroposterior length. ANT-W, Anterior width of upper cheek teeth. POST-W, Posterior width of upper cheek teeth. W, Width of premolars. W-TRI, Width of trigonid. W-TAL, Width of talonid. O. R., Observed range of variation. $\bar{X}$, mean of sample. $SE_{\bar{X}}$, Standard error of mean. S. D., Standard deviation. V, Coefficient of variation.

SAN DIEGO SOC. NAT. HIST., TRANS. 18(5:) 85-112, 26 JANUARY 1976

SYSTEMATIC PALEONTOLOGY

Subclass THERIA Parker & Haswell, 1897
Infraclass METATHERIA Huxley, 1880
Order MARSUPIALIA Illiger, 1811
Family DIDELPHIDAE Gray, 1821
Genus *Peratherium* Aymard, 1850

Peratherium sp. cf. *P. knighti* McGrew, 1959

Pl. 1, fig. 1; Pl. 2, figs. 1-3; Pl. 3, figs. 1-3; Pl. 4, figs. 1-4; Pl. 5, figs. 1-2

Type.—AMNH 55684, right maxilla with M$^{1-3}$.

Type locality.—University of Wyoming loc. 5, Bridger Fm., Tabernacle Butte, Sublette Co., Wyoming.

West Coast referred specimens.—7 “DP^3's,” 5 P^2's, 2 P^3's, 23 M^1's, UCMP 106376 (maxillary fragment with M$^{2-3}$), 11 M^2's, 13 M^3's, 11 M^4's, 2 “DP$_3$'s,” 3 P$_2$'s, 6 P$_3$'s, UCMP 110224 (dentary fragment with M$_{1-2}$), 16 M$_1$'s, 12 M$_2$'s, 10 M$_3$'s, 13 M$_4$'s (all UCMP specimens).

West Coast localities.—Friars Fm.: V-6882, V-68116, V-71175, V-71183; Mission Valley Fm.: V-71180, V-71211, V-72157, V-72158, V-72176, V-72179, V-73138, V-73139; ?Santiago Fm.: V-72088.

Distribution of species.—Bridger (Bridgerian) and Tepee Trail (Hendry Ranch Member, Uintan) formations, Wyoming; Friars and Mission Valley formations (Uintan), California.

Remarks.—Publications on North American early Tertiary didelphids are numerous, scattered, and probably far to many species have been named to account for the actual diversity. Setoguchi (1973) recently provided an extremely useful summary of species-level systematic problems within the group, and the present paper should be considered supplementary to his.

The San Diego specimens of *Peratherium* are indistinguishable from *P. knighti* McGrew, 1959 from the Bridgerian of Wyoming and are identical in most respects to specimens identified as *P.* sp. cf. *P. knighti* by Setoguchi (1973) from the Uintan Tepee Trail Fm. of Wyoming. All measurements (Tables 1 and 2) agree well with those of *P.* sp. cf. *P. knighti* as described by Setoguchi (1973, Table 2, p. 20) and are significantly smaller than those referred by him (Table 1, p. 15) to *P. marsupium* (Troxell, 1923).

Measurements on marsupial molars in this paper were taken as illustrated by me in 1969 (p. 16, Fig. 5). Premolar measurements were simply taken with the A-P axis being designated parallel to the longest axis of the tooth with W measurements taken at right angles to it at the widest part of the tooth. Although teeth from 13 localities and 3 formations are included within the San Diego sample, the vast majority of specimens were recovered from but 2 spatially close localities (V-72157 and V-72158) in the Mission Valley Fm. Only three specimens (UCMP 106613, 106731, and 110368) were collected from the more distant ?Santiago Fm. locality (V-72088). No significant differences could be detected between specimens from the various localities and almost surely only a single species is involved. Thus I felt justified in lumping all data into a single statistical sample. Minor differences between the San Diego specimens (Pl. 1, fig. 1; Pl. 2, figs. 1-3; Pl. 3, figs. 1-3) and those identified as *Peratherium* sp. cf. *P. knighti* by Setoguchi (1973) from the Tepee Trail Fm. include the following. A paraconule is commonly seen in M^1 of the San Diego sample, although the cuspule is quite weak; there is no trace of a paraconule on M^1 in the Wyoming sample. The San Diego M^3's usually have a small stylar cusp C (very conspicuous in Tepee Trail specimens) and usually possess a small stylar cusp D (absent in Tepee Trail M^3's). Finally, the vertical part of the buccal border of the stylar shelf of M^3's from San Diego is variably crenulated rather than smooth as in the Wyoming specimens. If one assumes that Tertiary didelphids were ultimately derived from Late Cretaceous ancestral stocks similar to *Alphadon marshi* (see Clemens, 1966, p. 5) or *A. wil-*

TABLE 1. Standard statistics for lower teeth of *Peratherium* sp. cf. *P. knighti* from San Diego County, California.

		N	O. R.	$\bar{x}$	S. D.	$SE_{\bar{x}}$	V
"DP_3"	A-P	1	1.563				
	W-TRI	1	0.802				
	W-TAL	1	0.883				
P_2	A-P	3	1.123-1.340	1.258			
	W	3	0.535-0.621	0.577			
	A-P/W	3	2.099-2.280	2.179			
P_3	A-P	6	1.568-1.778	1.691	0.085	0.035	5.0
	W	6	0.661-0.826	0.746	0.060	0.025	8.0
	A-P/W	6	2.153-2.629	2.274	0.177	0.072	7.8
M_1	A-P	16	1.703-2.136	1.923	0.113	0.027	5.9
	W-TRI	16	0.832-0.990	0.894	0.045	0.011	5.0
	W-TAL	16	0.818-1.052	0.973	0.059	0.014	6.1
	W-TRI/W-TAL	16	0.852-1.039	0.920	0.048	0.012	5.2
	A-P/W-TRI	16	1.999-2.320	2.153	0.097	0.023	4.5
	A-P/W-TAL	16	1.814-2.082	1.977	0.075	0.018	3.8
M_2	A-P	12	1.823-2.165	1.999	0.118	0.033	5.9
	W-TRI	12	0.970-1.232	1.128	0.070	0.019	6.2
	W-TAL	12	0.973-1.228	1.130	0.066	0.018	5.8
	W-TRI/W-TAL	12	0.952-1.132	0.999	0.051	0.014	5.1
	A-P/W-TRI	12	1.513-1.969	1.779	0.152	0.042	8.5
	A-P/W-TAL	12	1.518-1.945	1.775	0.130	0.036	7.3
M_3	A-P	10	1.848-2.274	2.044	0.130	0.041	6.4
	W-TRI	10	1.102-1.305	1.199	0.065	0.021	5.4
	W-TAL	9	1.010-1.193	1.113	0.056	0.019	5.0
	W-TRI/W-TAL	9	1.037-1.107	1.075	0.023	0.008	2.1
	A-P/W-TRI	10	1.661-1.777	1.705	0.039	0.012	2.3
	A-P/W-TAL	9	1.730-1.924	1.837	0.071	0.024	3.9
M_4	A-P	11	1.718-2.205	1.955	0.150	0.045	7.7
	W-TRI	10	0.966-1.171	1.065	0.071	0.022	6.7
	W-TAL	12	0.613-0.935	0.758	0.100	0.029	13.2
	W-TRI/W-TAL	10	1.188-1.732	1.413	0.168	0.053	11.9
	A-P/W-TRI	10	1.691-1.985	1.823	0.101	0.032	5.5
	A-P/W-TAL	10	2.280-3.160	2.571	0.290	0.092	11.3

TABLE 2. Standard statistics for upper teeth of *Peratherium* sp. cf. *P. knighti* from San Diego County, California.

		N	O. R.	$\bar{x}$	S.D.	SE$_{\bar{x}}$	V
"DP^3"	A-P	7	1.387-1.623	1.500	0.078	0.030	5.2
	ANT-W	7	0.868-0.992	0.929	0.043	0.016	4.6
	POST-W	7	1.162-1.500	1.326	0.100	0.038	7.5
	$\frac{\text{ANT-W}}{\text{POST-W}}$	7	0.610-0.769	0.703	0.052	0.020	7.4
	$\frac{\text{A-P}}{\text{ANT-W}}$	7	1.526-1.691	1.615	0.069	0.026	4.3
	$\frac{\text{A-P}}{\text{POST-W}}$	7	0.975-1.301	1.137	0.107	0.040	9.4
P^2	A-P	5	1.278-1.565	1.435	0.111	0.050	7.7
	W	5	0.590-0.707	0.661	0.047	0.021	7.1
	$\frac{\text{A-P}}{\text{W}}$	5	1.888-2.334	2.176	0.174	0.078	8.0
P^3	A-P	2	1.746-1.819	1.783			
	W	2	0.900-1.048	0.974			
	$\frac{\text{A-P}}{\text{W}}$	2	1.666-2.021	1.844			
M^1	A-P	16	1.334-2.137	1.902	0.198	0.050	10.4
	ANT-W	18	1.189-1.820	1.594	0.163	0.038	10.2
	POST-W	17	1.578-2.458	2.046	0.218	0.053	10.7
	$\frac{\text{ANT-W}}{\text{POST-W}}$	14	0.718-0.874	0.817	0.041	0.011	5.0
	$\frac{\text{A-P}}{\text{ANT-W}}$	14	1.002-1.319	1.154	0.089	0.024	7.7
	$\frac{\text{A-P}}{\text{POST-W}}$	14	0.742-1.073	0.943	0.089	0.024	9.4
M^2	A-P	7	1.681-2.227	2.008	0.200	0.076	10.0
	ANT-W	7	1.665-2.258	2.074	0.216	0.082	10.4
	POST-W	8	2.143-2.488	2.360	0.099	0.035	4.2
	$\frac{\text{ANT-W}}{\text{POST-W}}$	5	0.883-0.921	0.908	0.015	0.006	1.6
	$\frac{\text{A-P}}{\text{ANT-W}}$	5	0.913-0.990	0.957	0.032	0.014	3.3
	$\frac{\text{A-P}}{\text{POST-W}}$	5	0.835-0.899	0.868	0.030	0.013	3.5
M^3	A-P	13	1.664-2.107	1.937	0.150	0.041	7.7
	ANT-W	12	1.872-2.538	2.293	0.170	0.049	7.4
	POST-W	11	1.993-2.918	2.508	0.222	0.067	8.9
	$\frac{\text{ANT-W}}{\text{POST-W}}$	11	0.848-0.961	0.914	0.036	0.011	3.9
	$\frac{\text{A-P}}{\text{ANT-W}}$	11	0.752-0.927	0.849	0.054	0.016	6.4
	$\frac{\text{A-P}}{\text{POST-W}}$	11	0.714-0.835	0.775	0.041	0.012	5.3
M^4	A-P	8	1.250-1.529	1.387	0.118	0.042	8.5
	ANT-W	5	1.935-2.408	2.133	0.173	0.077	8.1
	POST-W	7	1.218-1.590	1.381	0.128	0.048	9.3
	$\frac{\text{ANT-W}}{\text{POST-W}}$	5	1.381-1.727	1.581	0.150	0.067	9.5
	$\frac{\text{A-P}}{\text{ANT-W}}$	5	0.605-0.738	0.649	0.053	0.024	8.2
	$\frac{\text{A-P}}{\text{POST-W}}$	5	0.908-1.083	1.022	0.068	0.031	6.7

soni (see Lillegraven, 1969, p. 39), all the comparisons discussed above show the more primitive conditions in the San Diego specimens and have similarity with the holotype of *P. knighti* (see McGrew, 1959, p. 147, Fig. 3).

Description of permanent premolars.—No upper or lower premolars have yet been found in association with molars of *Peratherium* from the San Diego samples. Identification of permanent premolars was thus made with good confidence on the basis of similarities with Late Cretaceous species of *Alphadon* (see Lillegraven, 1969:32-42) and Oligocene species of *Peratherium* (*e.g.*, Stock and Furlong, 1922: 313-316). Because there are no adequate descriptions of the premolars of *Peratherium*, I briefly describe them here.

The P^3 (Pl. 5, fig. 2) has a single main cusp with a rounded anterior face and a sharp posterior crest. Only a hint of an anterior accessory cusp occurs and short cingula extend from it posterodorsad on either side of the tooth. The posterior crest of the main cusp has a distinct elevation at about the midpoint of its length in the unworn condition. The posterolabial surface of the tooth is slightly convex while the posterolingual surface is distinctly concave. The widest part of the tooth is approximately two-thirds the distance posterior from the front margin. A distinct cingulum extends anterodorsad to the widest part of the tooth on both sides from the posterior termination of the crest of the main cusp. The anterior root is markedly convex anteriorly and the anterior-most part of the convexity projects well ahead of the forward-most part of the crown. The posterior root is vertically straight and centers above the midpoint of the posterior ridge of the main cusp.

The P^2 (Pl. 5, fig. 1) is basically similar to P^3 except for its smaller size, generally more transversely compressed proportions, and vertically straighter anterior root. More anterior parts of the upper dentition have not as yet been recognized from the available samples.

The P_3 (Pl. 4, fig. 3) has the apex of the main cusp directly above the center of the anterior root. The anterior border of the main cusp is markedly convex and bluntly keeled. Only the slightest bump on some specimens suggests the incipient development of an anterior accessory cusp. A sharper crest curves gracefully from the main cusp posteroventrad to a small but sharp posterior accessory cusp. A cingulum curves linguad then anteriad from the apex of the posterior accessory cusp to terminate on the posterolingual base of the main cusp. The area between the cingulum and the posterior ridge of the main cusp is strikingly concave and usually is heavily worn. The entire labial surface of the tooth is distinctly convex and quite smooth.

The P_2 (Pl. 4, fig. 2) is virtually identical to the P_3 except for its smaller size and slightly greater tendency toward the development of an anterior accessory cusp. No parts of the more anterior lower dentitions of *Peratherium* have yet been recognized from the San Diego samples.

Description of "deciduous premolars."—A series of seven upper and two lower teeth has been recovered from the San Diego samples that show features characteristic of teeth usually designated as "DP^3_3" in modern didelphids. Archer (1974) documented the fact that, at least in some generalized Australian polyprotodont marsupials, the tooth usually referred to as "DP^3" in American kinds (or "dP^4" in traditional Australian terminology) is in reality the first tooth developed in a molariform series of sequentially related teeth including "$DP^3M^{1\text{-}4}$." He showed that it is not a member of the premolar series at all and especially should not be considered a "deciduous" precurser for another later-developing premolar. Nevertheless, the terminology of "DP^3_3" and "deciduous" as used for those teeth is deeply entrenched in the literature and is widely used. Until the phenomenon characteristic of Australian polyprotodonts is found to be general for the American kinds, it is probably best to retain the older terminology; I have done so in the present paper but have consistently placed "DP^3_3" and "deciduous" within quotation marks.

To my knowledge, "deciduous premolars" have not previously been described for either *Peratherium* or *Nanodelphys*. Even the smallest of these peculiar teeth is as large or larger than the M^1_1 of *Nanodelphys*. In all modern didelphids seen by me the "DP^3_3" is roughly one-third smaller than M^1_1. This size relation holds between the "DP^3_3's" in question and the M^1_1's of *Peratherium* within the San Diego samples. Thus I have identified all the "deciduous" teeth as representing *Peratherium*. That being the case, no "deciduous premolars" are yet recognized for *Nanodelphys* from the San Diego localities. The washing-screen size used in collecting the sample had spaces between the wires measuring roughly 0.72 mm. Unfortunately, therefore, one might expect common loss during the collecting process of teeth in the size range expected for "DP^3_3's" of *Nanodelphys*.

The "DP^3" (Pl. 4, fig. 4) is a highly distinctive tooth in its usual lack of a stylar shelf anterior to a transverse line drawn through the postparacrista. On two of seven specimens the stylar shelf lateral to the paracone is represented by a mere cingulum. The posterior part of the stylar shelf, however, is dramatically produced as a great wing projecting well posterior to the metacone. The result is that the apex of the metacone is only a slight distance posterior and labial to the geometrical center of the tooth as seen in occlusal view. Cuspules in the comparable position of "C" and "D" in molars are conspicuously developed and elongated parallel to the labial margin of the tooth. The two cuspules tend to merge to varying degrees and a raised crest proceeds posteriad along the labial margin of the tooth from cuspule "D" to the extreme posterolabial corner of the tooth. There is no stylar cusp "E" as such. A small "parastyle" is present directly anterior to the paracone such that a straight line can usually be drawn through the apices of the "parastyle," paracone, and metacone.

The metacone of "DP^3" is a significantly taller and more voluminous cusp than the paracone. The latter is a conical spire that usually lacks a preparacrista and has a weak postparacrista that heads directly toward the apex of the metacone. The premetacrista is generally weak, but the postmetacrista is a strong crest that projects all the way to the posterolabial corner of the tooth. A tendency exists for the development of a weak crest from the apex of the metacone to stylar cusp "D." Conular development is highly irregular, but para- and metaconules usually are present but miniscule and are essentially without wings. The protocone is low, transversely narrow, and anteroposteriorly broad. It lacks lingual cingula and has a broadly rounded lingual face. The preprotocrista usually continues as a cingulum to the apex of the "parastyle." The postprotocrista terminates on the lingual base of the metacone. The protoconal basin is deep. Although usually completely broken away, UCMP 109671 shows that the "DP^3" was three-rooted as in living didelphids with the metaconal root being the broadest and strongest.

The paraconid of "DP_3" (Pl. 4, fig. 1) is very low, being little more than an anterolingual inflection of the strong, sharp anterior crest of the protoconid. The posterior face of the trigonid has a shallow posterior slope down from apices of the proto- and metaconids. The talonid is complete with the cuspules arranged in the fashion characteristic of molars of *Peratherium* in that the low and flattened hypoconulid is nearly directly posterior to the entoconid. The cristid obliqua terminates at the base of the transverse center of the trigonid wall. A short posterior cingulum courses sharply labioventrad from near the apex of the hypoconulid. There seems to have been no anterolingual cingulum in contrast to molar structure.

Genus *Nanodelphys* McGrew, 1937

Nanodelphys californicus (Stock, 1936)

Pl. 5, fig. 3; Pl. 6, fig. 1; Pl. 7, figs. 1-2; Pl. 8, fig. 1; Pl. 9, figs. 1-3

Peratherium californicum Stock, 1936.

Type—LACM (CIT) 1943, right dentary fragment with $P_3M_{1\text{-}2}$.

Type locality.—LACM (CIT) locality 202, Sespe Fm., Ventura Co., California.

Referred specimens from San Diego County—3 P^2's, 1 P^3, UCMP 101933 (maxillary fragment with incomplete P^3 and $M^{1\text{-}2}$), 14 M^1's, 13 M^2's, UCMP 104414 (maxillary fragment with $M^{2\text{-}3}$), 14 M^3's, 4 M^4's, 16 miscellaneous upper molar fragments, 3 P_3's, UCMP 104153 (dentary fragment with talonid of M_1 and $M_{2\text{-}3}$), 17 M_1's, 12 M_2's, 12 M_3's, 6 M_4's, 3 miscellaneous lower molar fragments (all UCMP specimens).

Localities.—Friars Fm.: V-6871, below V-68101, V-68116, V-68118, V-71175, V-71183, V-72175; Mission Valley Fm.: V-71180, V-71187, V-71211, V-72157, V-72158, V-73138; ?Santiago Fm.: V-72088; Sespe Fm.: LACM (CIT) loc. 202.

Distribution of species.—Friars, Mission Valley, ?Santiago, and Sespe formations (Uintan), California.

Remarks.—Specimens of the genus *Nanodelphys* have previously been recovered from Orellan (roughly middle Oligocene) deposits in Nebraska, Colorado, South Dakota, and possibly in Chadronian (early Oligocene) deposits of Saskatchewan. Numerous upper molars (Pl. 5, fig. 3; Pl. 6, fig. 1; Pl. 7, fig. 1) have been found in the San Diego area having features characteristic of the genus. These are primarily: (1) that the para- and metacones are roughly equal in height (paracone markedly reduced in $M^{1\text{-}3}$ in *Peratherium*); (2) that the conules are greatly reduced or absent (usually clearly present in *Peratherium*); and (3) that stylar cusp "C" is greatly reduced or absent (usually well-developed in *Peratherium*). The specimens are the same size as those of *N. minutus* McGrew, 1937 and are indistinguishable morphologically. The lower molars (Pl. 8, fig. 1; Pl. 9, figs. 1-3) in the San Diego sample referred to *Nanodelphys,* using the criteria for recognition discussed by Setoguchi (1973, p. 29-31), are indistinguishable from those in the holotype of *Peratherium californicum* Stock, 1936. There is little doubt that *P. californicum* in actuality should be considered a species of *Nanodelphys*. It seems very likely, indeed, that "*P. californicum*" and *N. minutus* could be considered conspecific using the paleontological morphospecies concept; they are morphologically indistinguishable. Nevertheless, the referred specimens are from quite different time intervals and geographic areas. I believe that different specific names should be maintained. Thus I here refer "*P. californicum*" to *Nanodelphys* but emend the suffix of the specific name to "*californicus.*"

The fact that "*Peratherium californicum*" has been found to represent a species of *Nanodelphys* does not eliminate *Peratherium* from the faunal list of the lower Sespe Fm. In the same paper in which *P. californicum* was named, Stock (1936:124) documented the presence of a second didelphid and referred to it as "*Peratherium* species" as represented by specimens LACM (CIT) 1942 and 1944. These specimens are indistinguishable from the San Diego material referred to above as *Peratherium* sp. cf. *P. knighti* and probably should be considered conspecific.

Dental measurements were taken as described above for *Peratherium.* Basic statistics on teeth are presented in Tables 3 and 4. As for *Peratherium,* all localities have been lumped as one statistical sample as no significant interlocality differences could be detected.

Premolars.—Specimens here identified as $P^{2\text{-}3}$ of *Nanodelphys* are done so with less certainty than was the case for *Peratherium.* The morphology of these specimens is virtually indtinguishable from those described for *Perathium* except for decidedly smaller size. The posterior one-third of P^3 (Pl. 6, fig. 1) is preserved in association with molars of *Nanodelphys* in UCMP 101933 and what remains in that specimen supports the identifications made.

TABLE 3. Standard statistics for upper teeth of *Nanodelphys californicus* from San Diego County, California.

		N	O. R.	$\bar{x}$	S. D.	SE$_{\bar{x}}$	V
P^3	A-P	3	1.124-1.280	1.205			
	W	3	0.580-0.645	0.616			
	A-P/W	3	1.743-2.207	1.966			
P^3	A-P	1	1.496				
	W	2	0.565-0.783	0.674			
M^1	A-P	11	1.327-1.593	1.455	0.086	0.026	5.9
	ANT-W	15	0.999-1.267	1.151	0.090	0.023	7.8
	POST-W	11	1.311-1.593	1.436	0.077	0.023	5.4
	ANT-W/POST-W	11	0.736-0.882	0.810	0.051	0.015	6.3
	A-P/ANT-W	11	1.078-1.536	1.259	0.126	0.038	10.0
	A-P/POST-W	11	0.858-1.180	1.016	0.079	0.024	7.8
M^2	A-P	9	1.215-1.496	1.337	0.091	0.030	6.8
	ANT-W	11	1.228-1.566	1.373	0.120	0.036	8.7
	POST-W	11	1.338-1.793	1.562	0.145	0.044	9.3
	ANT-W/POST-W	9	0.792-0.990	0.879	0.069	0.023	7.9
	A-P/ANT-W	8	0.901-1.060	0.988	0.055	0.019	5.6
	A-P/POSTW	8	0.829-1.008	0.877	0.060	0.021	6.8
M^3	A-P	12	1.213-1.618	1.462	0.107	0.031	7.3
	ANT-W	13	1.532-1.818	1.665	0.081	0.023	4.9
	POST-W	10	1.590-1.979	1.794	0.143	0.046	8.0
	ANT-W/POST-W	10	0.880-1.004	0.939	0.038	0.012	4.0
	A-P/ANT-W	10	0.757-0.935	0.868	0.052	0.016	6.0
	A-P/POST-W	10	0.714-0.907	0.815	0.060	0.019	7.4
M^4	A-P	4	0.980-1.082	1.043	0.045	0.022	4.3
	ANT-W	4	1.631-1.957	1.765	0.137	0.069	7.8
	POST-W	4	1.110-1.337	1.241	0.112	0.056	9.0
	ANT-W/POST-W	4	1.300-1.469	1.426	0.084	0.042	5.9
	A-P/ANT-W	4	0.553-0.617	0.592	0.028	0.014	4.7
	A-P/POST-W	4	0.802-0.883	0.843	0.044	0.022	5.2

TABLE 4. Standard statistics for lower teeth of *Nanodelphys californicus* from San Diego County, California.

		N	O. R.	$\bar{x}$	S. D.	SE $\bar{x}$	V
P_3	A-P	3	1.039-1.158	1.091			
	W	3	0.487-0.531	0.509			
	A-P/W	3	1.957-2.378	2.149			
M_1	A-P	16	1.178-1.691	1.453	0.152	0.038	10.5
	W-TRI	16	0.570-0.859	0.713	0.086	0.022	12.0
	W-TAL	17	0.572-0.877	0.715	0.074	0.018	10.4
	W-TRI/W-TAL	16	0.892-1.121	1.001	0.067	0.017	6.7
	A-P/W-TRI	16	1.837-2.388	2.045	0.157	0.039	7.7
	A-P/W-TAL	16	1.911-2.229	2.040	0.102	0.026	5.0
M_2	A-P	13	1.365-1.625	1.514	0.100	0.028	6.6
	W-TRI	13	0.737-0.917	0.817	0.057	0.016	7.0
	W-TAL	13	0.699-0.889	0.775	0.056	0.015	7.2
	W-TRI/W-TAL	13	1.014-1.166	1.056	0.041	0.011	3.9
	A-P/W-TRI	13	1.675-2.091	1.856	0.113	0.031	6.1
	A-P/W-TAL	13	1.776-2.173	1.957	0.104	0.029	5.3
M_3	A-P	12	1.298-1.636	1.498	0.095	0.027	6.3
	W-TRI	13	0.726-0.894	0.824	0.047	0.013	5.7
	W-TAL	11	0.608-0.784	0.730	0.057	0.017	7.8
	W-TRI/W-TAL	11	1.076-1.212	1.137	0.041	0.012	3.6
	A-P/W-TRI	12	1.601-1.904	1.806	0.076	0.022	4.2
	A-P/W-TAL	11	1.846-2.282	2.050	0.135	0.041	6.6
M_4	A-P	6	1.368-1.538	1.460	0.071	0.029	4.9
	W-TRI	5	0.693-0.842	0.753	0.060	0.027	8.0
	W-TAL	6	0.503-0.639	0.588	0.051	0.020	8.7
	W-TRI/W-TAL	5	1.124-1.497	1.311	0.146	0.065	11.1
	A-P/W-TRI	5	1.817-2.027	1.926	0.101	0.045	5.2
	A-P/W-TAL	5	2.279-2.720	2.515	0.160	0.072	6.4

P_3 (Pl. 7, fig. 2) is preserved in the holotype of *Peratherium californicum*, here transferred to a species of *Nanodelphys*. Three isolated teeth from the San Diego samples closely match this tooth in size and morphology. The description closely follows that for the P_3 of *Peratherium* except that the labial convexity of the *Nanodelphys* tooth is less marked, the posterior accessory cusp is much lower or absent, the size is smaller, and there is less concavity on the posterolingual part of the tooth. More anterior parts of the lower dentition for *Nanodelphys* from the San Diego samples have not yet been recognized.

Antiquity of the genus.—*Nanodelphys* was originally recognized from rocks of Oligocene age in Nebraska. It has been recognized subsequently in the Hendry Ranch Member of the Tepee Trail Fm. of Wyoming. Potassium-argon dating techniques on different levels within the Hendry Ranch Member give dates of 41 and 39 million years before present (Riedel, 1969), well up within what is generally considered to be Uintan of the late Eocene (see Evernden, *et al.*, 1964). Numerous elements of the mammalian fauna from the San Diego Eocene also suggest a Uintan age, but of a considerably older part of it. Faunal similarities are greater with Bridgerian (roughly late early Eocene) than with Chadronian (early Oligocene) assemblages in contrast to the Hendry Ranch Member in which the opposite is largely true. The San Diego terrestrial Eocene deposits interdigitate with marine sediments considered to be of Narizian and Ulatisian age (Kennedy and Moore, 1971) in West Coast stratigraphic terminology, which probably correlate with Lutetian strata in Europe (see Bukry and Kennedy, 1969 and Bukry, 1971). These units are generally considered to be mid or early late Eocene in age. Thus the San Diego specimens seemingly represent the oldest known record of *Nanodelphys*. Nevertheless, the specimens somewhat unexpectedly show fully the characters used to diagnose the genus and one might expect to find more primitive species of *Nanodelphys* in Bridgerian or even Wasatchian deposits.

Infraclass EUTHERIA Gill, 1872
Order ?PRIMATES Linnaeus, 1758
Superfamily MICROSYOPOIDEA (Osborn and Wortman, 1892)
Family MICROSYOPIDAE Osborn and Wortman, 1892
Subfamily UINTASORICINAE Szalay, 1969b
Genus *Uintasorex* Matthew, 1909

Uintasorex montezumicus n. sp.

Pl. 10, figs. 1-4; Pl. 11, figs. 1-4

Type.—UCMP 104179, isolated right M^2 (Pl. 11, fig. 3).

Type locality.—V-71211, "Solstice Slope," Mission Valley Fm., San Diego, San Diego Co., California.

Referred specimens.—2 P^4's, 13 M^1's, 18 M^2's, 5 M^3's, 4 P_4's, 18 M_1's, 13 M_2's, 8 M_3's (all UCMP specimens).

Localities.—Friars Fm.: V-6871, V-6882, V-6888, V-68116, V-71175, V-71176, V-71183; Mission Valley Fm.: V-71180, V-71211, V-72157, V-72158, V-72176, V-72177, V-72179, V-73138, V-73139.

Distribution of genus.—Green River Fm. (Bridgerian), Utah; Wasatch (Wasatchian), Bridger (Bridgerian), and Tepee Trail (Hendry Ranch Member, Uintan) formations, Wyoming; Friars and Mission Valley formations (Uintan), California.

Diagnosis.—Basically similar dentally to *Uintasorex parvulus* except *U. montezumicus* has longer talonid on P_4 relative to trigonid, completely basined talonid on P_4, no cingulum on labial base of P_4 trigonid, paracnid of M_1 closely appressed to metaconid, reduced labial cingulum on M_{1-3}, protocone of M^{1-3} shifted anteriorly to position nearly directly lingual to paracone, anterolingual cingulum lacking or greatly reduced on M^{1-3}, posterolingual cingulum hypertrophied on M^{1-2}, paraconule lacking or reduced to bump on preprotocrista.

The entire *Uintasorex* sample from San Diego is represented by isolated teeth including only $P^4_4M^{1-3}_{1-3}$; not a single jaw fragment of significance has yet been recovered. Nevertheless, the San Diego collection represents the largest yet available for the genus. The material was recovered from two geological formations and 16 separate localities. However, no significant differences could be detected between the specimens from the Friars and Mission Valley formations nor between the various localities. Thus all statistical data were lumped in the preparation of Tables 5 and 6 and the descriptions were written as though but a single species were involved.

A-P measurements on M^{1-2} were taken along an axis that parallels an imaginary line connecting the apices of the paracone and metacone. On M^3 the A-P measurement was taken at right angles to the anterior border of the tooth. A-P measurements on the P_4 and lower molars were taken along an axis that parallels an imaginary line that roughly divides the tooth in occlusal view into equal right and left halves. All width measurements were taken from labial to lingual edges of teeth at right angles to the A-P axis. Details are as follow.

P^4 measurements

A-P From edge of anterior-most projection of anterior paracrista to edge of posterior-most projection of posterior paracrista perpendicular to axis that divides the tooth into roughly equal anterior and posterior halves.

W Along transverse line measuring greatest width between edges of paracone (posterior paracrista) and protocone.

Upper molar measurements

A-P M^{1-2} from edge of anterior-most projection of anterior paracrista to edge of posterior-most projection of posterior metacrista.

M^3 from edge of anterior-most projection of anterior paracrista to edge of posterior-most bulge of metacone.

ANT-W M^{1-3} along transverse line measuring greatest width between edges of paracone and protocone.

POST-W M^{1-2} along transverse line measuring greatest width between edges of metacone and protocone. M^3 not taken.

P_4 measurements

A-P From edge of anterior-most projection of trigonid to posterior-most edge of talonid.

W Greatest width of trigonid area.

Lower molar measurements

A-P From edge of anterior-most projection of paraconid to edge of posterior-most projection of hypoconulid.

W-TRI Greatest width between edges of protoconid and metaconid.

W-TAL Greatest width between edges of hypoconid and entoconid.

Description of lower dentition.—The P_4 (Pl. 10, fig. 1) is apparently highly variable in construction. A small paraconid is present, for example, on only two of the four available specimens. When present, the paraconid is little more than a sharp lingual turn in the anterior crest of the protoconid. When absent, the anterior face of the protoconid is fully rounded with no anterior crest. A small metaconid is consistently present as a shoulder on the much taller protoconid. The metaconid is either placed directly lingual to the apex of the protoconid or posterolingual to it. The trigonid lacks any trace of a labial cingulum. A talonid is consistently well developed and is usually completely rimmed as a basin by a more or less continuous ridge that runs down the posterolabial corner of the protoconid, turns linguad along the posterior border of the talonid then runs anteriad and eventually up to the apex of the metaconid. The result is a concave posterior face of the trigonid. Two or three variably

TABLE 5. Standard statistics for lower teeth of *Uintasorex montezumicus* n. sp. from San Diego County, California.

		N	O. R.	$\bar{x}$	S. D.	SE $\bar{x}$	V
P_4	A-P	3	0.739-0.817	0.778			
	W	3	0.449-0.612	0.553			
	A-P/W	3	1.301-1.646	1.427			
M_1	A-P	18	0.901-1.063	0.985	0.042	0.010	4.3
	W-TRI	18	0.596-0.774	0.681	0.047	0.011	6.9
	W-TAL	18	0.694-0.835	0.784	0.038	0.009	4.9
	W-TRI/W-TAL	18	0.792-0.946	0.869	0.047	0.011	5.4
	A-P/W-TRI	18	1.261-1.621	1.452	0.095	0.022	6.5
	A-P/W-TAL	18	1.166-1.418	1.259	0.067	0.016	5.3
M_2	A-P	11	0.941-1.085	0.999	0.046	0.014	4.6
	W-TRI	11	0.617-0.784	0.691	0.052	0.016	7.5
	W-TAL	12	0.693-0.894	0.796	0.063	0.018	7.9
	W-TRI/W-TAL	11	0.820-0.920	0.858	0.029	0.009	3.4
	A-P/W-TRI	11	1.287-1.614	1.451	0.099	0.030	6.8
	A-P/W-TAL	11	1.085-1.359	1.244	0.076	0.023	6.1
M_3	A-P	8	0.928-1.243	1.131	0.103	0.037	9.1
	W-TRI	8	0.519-0.710	0.612	0.059	0.021	9.6
	W-TAL	8	0.601-0.800	0.701	0.074	0.025	10.6
	W-TRI/W-TAL	8	0.812-0.968	0.891	0.051	0.018	5.7
	A-P/W-TRI	8	1.516-2.304	1.861	0.255	0.090	13.7
A-P	A-P/W-TAL	8	1.434-1.990	1.654	0.205	0.073	12.4

developed cuspules are found on the posterior rim of the talonid. The talonid comprises at least half of the total length of the P_4.

The paraconid of the lower molars (Pl. 10, figs. 2-4) is either miniscule or completely absent as a discrete cusp. On 12 of 16 molars identified as M_1 a minute gap is present between the closely-appressed apices of the paraconid and metaconid. Most commonly on M_1 a ridge runs straight anteriad from the apex of the protoconid then turns sharply linguad and continues to curve posteriad in the general direction of the metaconid apex, increasing in elevation as it goes. The highest point on the ridge, usually immediately adjacent to the gap from the metaconid, is here referred to as the paraconid; it is generally not expanded as a distinct cusp. The remaining 4 of the abovementioned 16 molars show no gap whatever between the paraconid region and the apex of the metaconid; the anterior ridge is complete between the apices of the protoconid and metaconid. Such is also the case in all molars here identified as M_2 and M_3. A second transverse ridge is usually present on the

TABLE 6. Standard statistics for upper teeth of *Uintasorex montezumicus* n. sp. from San Diego County, California.

		N	O.R.	$\bar{x}$	S. D.	SE $_{\bar{x}}$	V
P^4	A-P	2	0.728–0.795	0.762			
	W	2	0.814–0.898	0.856			
	A-P/W	2	0.885–0.894	0.890			
M^1	A-P	13	0.876–1.085	1.014	0.060	0.017	5.9
	ANT-W	12	0.957–1.150	1.055	0.071	0.021	6.7
	POST-W	13	1.022–1.238	1.124	0.075	0.021	6.7
	ANT-W/POST-W	12	0.898–0.983	0.944	0.025	0.007	2.7
	A-P/ANT-W	12	0.898–1.035	0.962	0.041	0.012	4.3
	A-P/POST-W	12	0.817–0.996	0.908	0.046	0.013	5.1
M^2	A-P	18	0.881–1.092	0.980	0.056	0.013	5.7
	ANT-W	18	1.046–1.275	1.152	0.060	0.014	5.2
	POST-W	18	1.035–1.272	1.165	0.068	0.016	5.8
	ANT-W/POST-W	18	0.953–1.040	0.990	0.026	0.006	2.6
	A-P/ANT-W	18	0.780–0.927	0.851	0.031	0.008	3.6
	A-P/POST-W	18	0.796–0.901	0.842	0.029	0.007	3.4
M^3	A-P	5	0.906–1.001	0.957	0.039	0.017	4.1
	ANT-W	5	1.020–1.113	1.085	0.039	0.017	3.6
	A-P/ANT-W	5	0.825–0.962	0.883	0.055	0.025	6.2

posterior end of the trigonid of the molars that connects the apices of the protoconid and metaconid. The general presence of these two ridges results in an isolated enamel lake in the center of the trigonid. A rather weakly developed labial cingulum is found on about half of the molars in the area of the junction of the trigonid and talonid.

The talonid is shorter relative to the trigonid in teeth here identified as M_1 than in those identified as M_2. The talonid is deeply basined in all molars, being completely rimmed. The hypoconulid on $M_{1\text{-}2}$ is by far the weakest of the talonid cuspules, being little more than an elevation that is sometimes crenulated in the ridge connecting the apices of the entoconid and hypoconid. The hypoconulid on M_3, however, is grotesquely enlarged and rivals or exceeds in height the entoconid, which is generally the tallest of the talonid cusps. The hypoconulid on all molars is set significantly more closely to the entoconid than to the hypoconid and is invariably well separated from the other cusps by sharply-formed gaps. The cristid obliqua strikes the trigonid near the transverse center of the posterior wall of the protoconid and almost always stops well short of contact with its apex.

Comparisons of lower dentitions with those from Rocky Mountain localities.—The San Diego specimens of lower teeth are generally remarkably similar in detail to those from Utah and Wyoming (see Szalay, 1969b:7-15). However, a few significant differences do exist. For example, the talonids of P_4's from San Diego are longer relative to the total length of the tooth (50% or more *vs.* about 30-40%). Also, the talonid of P_4 is completely basined in the San Diego specimens in contrast to the anteroposteriorly-aligned central ridge seen in the holotype of *Uintasorex parvulus* and YPM 13519 (see Szalay, 1969b, fig. 1), another specimen referred to that species. The construction of the talonid in the San Diego specimens thus seems to be more advanced than in those from Bridgerian localities. A weak cingulum is present on the labial base of the trigonid of YPM 13519; no hint of such a cingulum is seen in any of the four San Diego specimens of P_4's.

The paraconid region of M_1's in the San Diego specimens is also more specialized than in the homologous teeth from the Bridgerian and apparently from Uintan (see Robinson, 1968, fig. 11) localities as well as in the Rocky Mountains in that the trigonids of the San Diego specimens are not wide open lingually. That is, the gap between the apices of the paraconid and metaconid is extremely constricted in the San Diego specimens and, as described above, is sometimes nonexistent. Such a condition makes separation of isolated M_1's from isolated M_2's quite difficult and assignment errors likely have been made in the present study. In any case, the condition seen in the San Diego M_1 paraconids is considerably specialized from the primitive therian condition. Also, the degree of development of the labial cingulum in $M_{1\text{-}3}$ is much less in the San Diego specimens than in those from the Western Interior. The cingulum in the latter is usually stronger and more extensive anteroposteriorly, commonly running nearly the entire length of the tooth (*e.g.*, YPM 13519 and AMNH 55664).

Finally, assuming that the system used here in taking dental measurements is approximately that used by Szalay (1969b, Tables 1 and 2), the San Diego specimens are generally smaller (Tables 5 and 6) than those from the Rocky Mountain localities. Indeed, *Uintasorex montezumicus* from San Diego must have ranked among the tiniest primates to have ever lived.

Description of upper dentition.—Two isolated teeth have been found that I identify as likely candidates for P^4's (Pl. 11, fig. 1) of *Uintasorex*, teeth that have never before been described. The teeth are three-rooted with a strong protocone, paracone, and no metacone. The protocone is much lower than the paracone and has a well-developed preprotocrista and postprotocrista that run respectively to the anterolabial and posterolabial corners of the tooth. There is no separate anterior cingulum. Conules are lacking. The protocone is separated by a broad valley from the laterally compressed paracone. A strong preparacrista and postparacrista run to the anterolabial and posterolabial corners of the tooth to join with their respective protocristae. There is no separate parastyle.

The upper molars (Pl. 11, figs. 2-4) have a broadly flattened protocone that is displaced anteriorly such that its apex is nearly directly lingual to the apex of the paracone. A posterolingual cingulum is consistently present and strong in $M^{1\text{-}2}$ but usually rather weak in M^3. The cingulum usually begins labially at the base of the metaconule and runs linguad to terminate at the posterolingual edge of the protocone. Commonly the edge of the cingulum projects slightly lingual to the edge of the protocone, especially in M^1. Usually there is no ridge connecting the apices of the cingular cusp and protocone, but occasionally one is present (*e.g.*, UCMP 106884). The lingual root is usually quite round in cross-section and supports only the anterior-most part of the posterolingual cingulum; the bulk of the cingulum projects posteriad from the base of the root. An anterolingual cingulum is not present on any available M^1 or M^3, but is present as a weak structure on 4 of 18 M^2's and as a strong cingulum on 1 M^2 (UCMP 106810). When present, the cingulum begins in the paraconular region and projects to a point well short of the lingual edge of the protocone.

The paracone and metacone of the upper molars are generally conically shaped, but show tendencies toward lateral compression in M^1. The paracone is almost always the largest of the molar cusps, even in M^1. Pre- and post-paracristae are well developed and anteroposteriorly aligned. A stylar shelf is lacking. The metaconule is a very conspicuous cusp. Its posterior crista runs labiad to join at the posterolabial corner of the tooth with the posterior metacrista. The anterior crista of the metaconule invariably terminates at the anterolingual base of the metacone. The paraconule, on the other hand, is frequently lacking entirely. Most commonly, it is represented only by a rather weak bump on the extension of the anterior protocrista. The latter continues labiad to the anterolabial corner of the tooth where it joins with the anterior paracrista. The posterior protocrista terminates at the base of the metaconule immediately anterolingual to its apex.

Comparisons of upper dentitions with those from Rocky Mountain localities.—Differences between the upper molars of the San Diego species and those of *Uintasorex parvulus* (see Gazin, 1958, Pl. 14, fig. 2) and *Uintsorex* sp. (see Szalay, 1969b, figs. 7, 9, and 10) from Bridgerian Green River beds of Utah are rather obvious. The most important revolve around the construction of the protocone and its attached cingula. The protocone in the Utah specimens is transversely more centrally placed between the apices of the paracone and metacone; the protocone from the San Diego specimens is shifted more anteriorly to rest more directly lingual to the apex of the paracone. As a result, the anterolingual cingulum is greatly reduced or lost in the San Diego specimens in contrast to its strong development in those from Utah. Concommitantly, the posterolingual cingulum in the San Diego teeth is hypertrophied in comparison to those from the Rockies. The paraconule seems to be better developed in the Utah specimens than in those from San Diego in which it is either absent or little more than a lump on the preprotocrista. The conditions seen in the San Diego specimens are clearly more specialized from the primitive therian condition than those seen in the Bridgerian specimens from the Western Interior.

Affinities.—The new species from San Diego sheds no new light on the affinities of the genus beyond the discussions by Szalay (1969a and b). He emphasized (1969b:17) the similarities of *Uintasorex parvulus* with *Niptomomys doreenae* from the Wasatchian of Colorado (see McKenna, 1960 and Bown and Gingerich, 1972). As would perhaps be expected, *U. montezumicus* shows less similarity with *Niptomomys.* For example, the P^4 of *Niptomomys* (*e.g.*, YPM 23600) has a ridge that runs labiad from the apex of the protocone more or less continuously to the apex of the paracone; such a ridge is lacking in *U. montezumicus* and the condition has not been described in *U. parvulus.* Additionally, a distinct anterior cingulum exists on the P^4 of *Niptomomys* that runs labiad from the anterolingual base of the protocone to a distinct parastyle. Both these structures are absent on the P^4 of *U. montezumicus* in which the function of an anterior cingulum is accomplished by the preprotocrista. The upper molars of *Niptomomys* also show numerous differences from those of *U. montezumicus* in that the former has a well developed anterolingual cingulum, somewhat weaker posterolingual cingulum, a stronger paraconule, and a hint of a mesostyle (*e.g.*, YPM 23600). Differences between the two species in the lower molars are less obvious and agree with those already spelled out by Szalay (1969b:18). In short, I fully agree with Szalay's argument (1969b:17) that the generic separation between *Uintasorex* and *Niptomomys* is justified and desirable.

Importance of U. montezumicus.—The new species of *Uintasorex* described here is primarily of significance because of its aid in helping to recognize the much greater geographic range of the genus than was realized before. Although clearly distinct at the species level from *U. parvulus,* the two species are certainly similar morphologically and probably were very closely related. In fact, no features are present in the known antomy of *U. parvulus* that would eliminate the possibility of its phylogenetic ancestry to *U. montezumicus.* Although *U. montezumicus* shows numerous dental characters advanced beyond those seen in *U. parvulus,* genetic continuity between *Uintasorex* populations in the Rocky Mountain states and southern California during the earlier Eocene is strongly suggested.

BIOGEOGRAPHICAL IMPLICATIONS

All three California species discussed in this paper are either conspecific with or very closely similar to taxa originally described from localities in the Rocky Mountain or High Plains states. Other species of mammals and lower vertebrates (see Schatzinger, 1975) have also been found in common within approximately contemporaneous strata in the two areas. The extent of faunal similarities will be more thoroughly reviewed elsewhere, but it now seems clear that overland dispersal routes were readily available between the West Coast and midcontinent of North America during at least some of the earlier part of the Eocene. The three species discussed here (two small opossums and a tiny ?primate) were probably semi-arboreal forest-associated kinds, dependent upon vegetative cover. Detailed information on their ecological requirements, of course, will never be known. It seems likely, however, that the more tropical Eocene climate allowed the development of a continuous forest cover or at least savannah-like environment that provided broad areas of suitable habitat for long-distance intracontinental dispersal of these kinds of small animals. Paleobotanical evidence is also consistent with the presence of geographicaly widespread warm-environment floras in the Northern Hemisphere during the Eocene (see Wolfe, 1975: 269-271).

ACKNOWLEDGMENTS

Collection of the fossils and their curation was supported jointly by a grant to me from the National Science Foundation (GB-30519) and financial assistance for curation by the Museum of Paleontology, University of California, Berkeley. For the latter I particularly thank Drs. Joseph T. Gregory and Donald E. Savage. Individuals who aided above and beyond the call of duty in collecting efforts include Dr. Savage and Messrs. Michael J. Novacek, Richard A. Schatzinger, and John J. Chiment. Prime localities could not have been exploited without generous assistance from Mr. Paul L. V. Campo, Base Geologist and from The Commanding General, Camp Pendleton Marine Corps Base. Rev. Wernor E. Wagner, Pastor, Shepherd of the Hills Evangelical Lutheran Church, La Mesa also allowed collecting on property under his supervision. Valuable discussions on the taxonomy of early Tertiary didelphids were had with Mr. Takeshi Setoguchi and Ms. Sylvia Graham. Drs. William A. Clemens and Joseph R. Jehl, Jr. provided numerous suggestions for improvement of the manuscript. Drs. David P. Whistler and David J. Golz provided access to the Sespe collections at the Natural History Museum of Los Angeles County. Finally, kindest thanks go to my wife, Bernice A. Lillegraven, who helped in all stages of the preparation of the manuscript.

LITERATURE CITED

Archer, M., 1974. The development of the cheek-teeth in *Antechinus flavipes* (Marsupialia, Dasyuridae). Journal of the Royal Society of Western Australia 57:54-63.

Aymard, A., 1850. Mammifères fossiles des calcaires du Puy. Annales de la Société d'agriculture, sciences, arts et commerce du Puy 14: 80-86.

Bown, T. M. and P. D. Gingerich, 1972. Dentition of the early Eocene primates *Niptomomys* and *Absarokius*. Postilla No. 158: 10p.

Bukry, D., 1971. Cenozoic calcareous nannofossils from the Pacific Ocean. Transactions of the San Diego Society of Natural History 16: 303-327.

Bukry, D. and M. P. Kennedy, 1969. Cretaceous and Eocene coccoliths at San Diego, California. California Division of Mines and Geology, Special Report 100: 33-43.

Clemens, W. A., 1966. Fossil mammals of the type Lance Formation, Wyoming. Part II. Marsupialia. University of California Publications in Geological Sciences 62: 1-122.

Evernden, J. F., D. E. Savage, G. H. Curtis and G. T. James, 1964. Potassium-argon dates and the Cenozoic mammalian chronology of North America. American Journal of Science 262: 145-198.

Gazin, C. L., 1958. A review of the Middle and Upper Eocene primates of North America. Smithsonian Miscellaneous Collections 136: *iii* + 112p.

Kennedy, M. P. and G. W. Moore, 1971. Stratigraphic relations of Upper Cretaceous and Eocene formations, San Diego coastal area, California. Bulletin of the American Association of Petroleum Geologists 55: 709-722.

Lillegraven, J. A., 1969. Latest Cretaceous mammals of upper part of Edmonton Formation of Alberta, Canada, and review of marsupial-placental dichotomy in mammalian evolution. The University of Kansas Paleontological Contributions, Article 50 (Vertebrata 12): 1-122.

Lillegraven, J. A. and R. W. Wilson, 1975. Analysis of *Simimys simplex*, an Eocene rodent (?Zapodidae). Journal of Paleontology 49: 856-874.

McGrew, P.O., 1937. New marsupials from the Tertiary of Nebraska. Journal of Geology 45: 448-455.

McGrew, P. O., 1959. The geology and paleontology of the Elk Mountain and Tabernacle Butte area, Wyoming. Bulletin of the American Museum of Natural History 117: 117-176.

McKenna, M. C., 1960. Fossil Mammalia from the early Wasatchian Four Mile fauna, Eocene of northwest Colorado. University of California Publications in Geological Sciences 37: 1-130.

Matthew, W. D., 1909. The Carnivora and Insectivora of the Bridger basin, middle Eocene. Memoirs of the American Museum of Natural History 9: 289-567.

Novacek, M. J., in prep. Insectivora and Proteutheria (Mammalia) of the later Eocene (Uintan) of San Diego County, California. Contributions of the Natural History Museum of Los Angeles County.

Novacek, M. J., in prep. *Proterixoides* and *Sespedectes* (Adapisoricidae, Insectivora) from the later Eocene of southern California.

Riedel, D. W., 1969. Geology of the Tepee Trail Formation, Badwater area, Fremont and Natrona counties, Wyoming. *In*, Twenty-first Annual Field Conference 1969, Wyoming Geological Association Guidebook: 39-41.

Robinson, P., 1968. The paleontology and geology of the Badwater Creek area, central Wyoming. Part. 4. Late Eocene Primates from Badwater, Wyoming, with a discussion of material from Utah. Annals of Carnegie Museum 39: 307-326.

Schatzinger, R. A., 1975. Later Eocene (Uintan) lizards from the greater San Diego area, California. M.A. Thesis, San Diego State University (San Diego).

Schiebout, J., in prep. Eocene Perissodactyla from the La Jolla and Poway groups, San Diego County, California.

Setoguchi, T., 1973. The late Eocene marsupials and insectivores from the Tepee Trail Formation, Badwater, Wyoming. M.A. Thesis, Texas Tech University (Lubbock).

Stock, C., 1936. Sespe Eocene didelphids. Proceedings of the National Academy of Sciences 22: 122-124.

Stock, C. and E. L. Furlong, 1922. A marsupial from the John Day Oligocene of Logan Butte, eastern Oregon. University of California Publications, Bulletin of the Department of Geological Sciences 13: 311-317.

Szalay, F. S., 1969a. Mixodectidae, Microsyopidae, and the insectivore-primate transition. Bulletin of the American Museum of Natural History 140: 193-330.

Szalay, F. S., 1969b. Uintasoricinae, a new subfamily of early Tertiary mammals (?Primates). American Museum Novitates 2363: 1-36.

Troxell, E. L., 1923. A new marsupial. American Journal of Science, Fifth Series, 5: 507-510.

Wolfe, J. A., 1975. Some aspects of plant geography of the Northern Hemisphere during the Late Cretaceous and Tertiary. Annals of the Missouri Botanical Garden 62: 264-279.

Department of Zoology, San Diego State University, San Diego, California 92182. Present address: Department of Geology, The University of Wyoming, Laramie, Wyoming 82071.

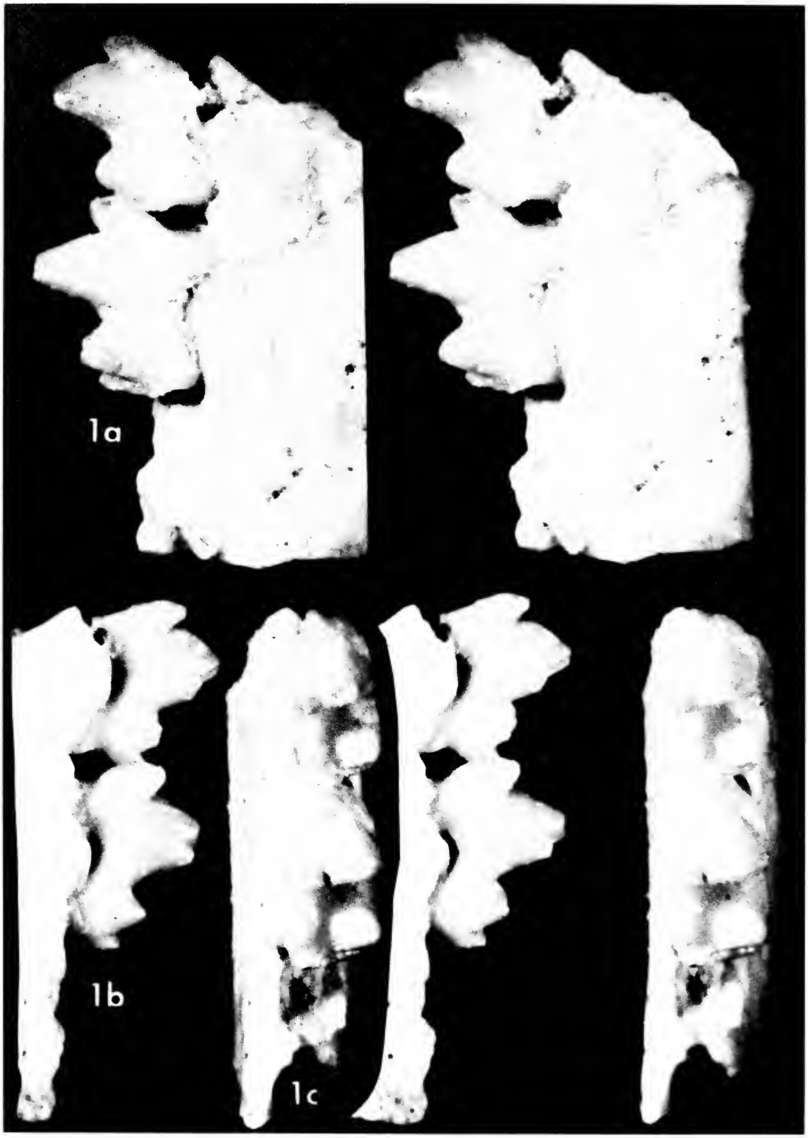


Plate 1. Stereophotographs (15×) of right mandibular fragment (UCMP 110224) with $M_{1\text{-}2}$ of *Peratherium* sp. cf. *P. knighti* from San Diego Co., California. a, b, and c represent labial, lingual, and occlusal views, respectively.

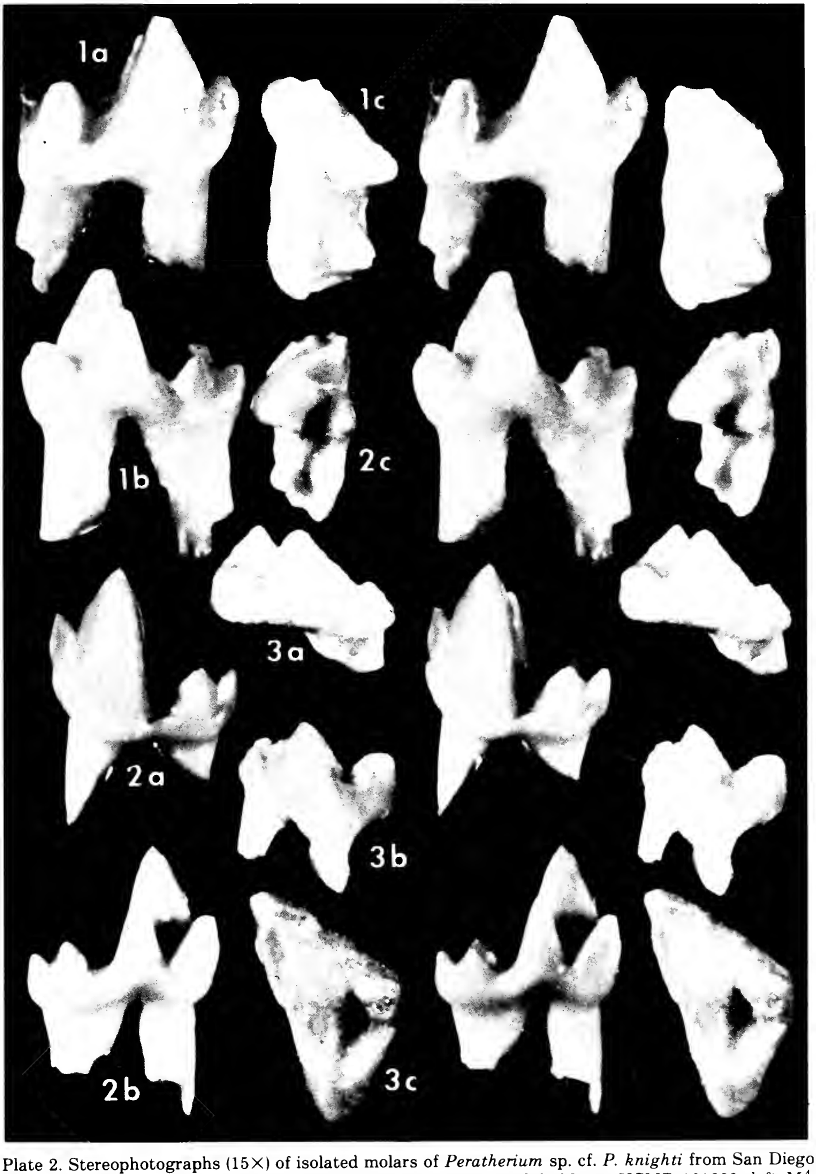


Plate 2. Stereophotographs (15×) of isolated molars of *Peratherium* sp. cf. *P. knighti* from San Diego Co., California. 1. UCMP 109910, right M_3; 2. UCMP 106384, left M_4; 3. UCMP 101220, left M^4. a, b, and c represent labial, lingual, and occlusal views, respectively.

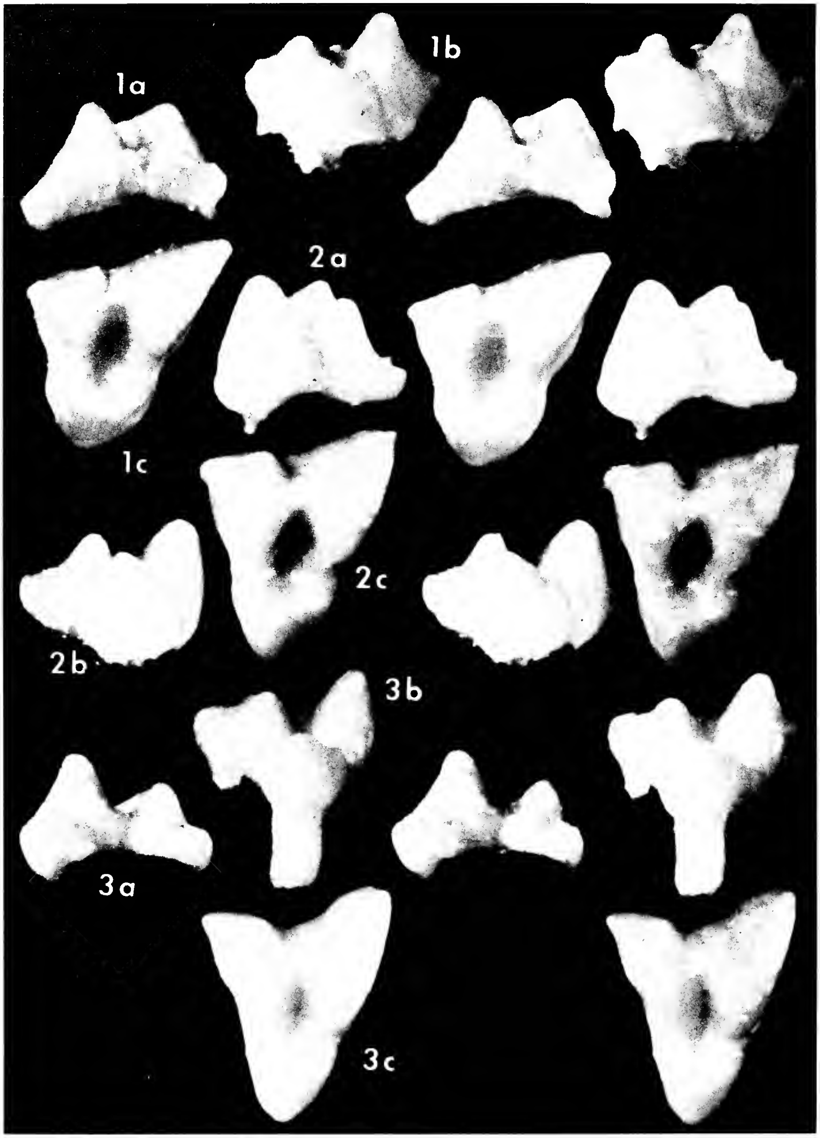


Plate 3. Stereophotographs (15×) of isolated upper molars of *Peratherium* sp. cf. *P. knighti* from San Diego Co., California. 1. UCMP 101549, left M^1; 2. UCMP 101132, left M^2; 3. UCMP 109647, left M^3. a, b, and c represent labial, lingual, and occlusal views, respectively.

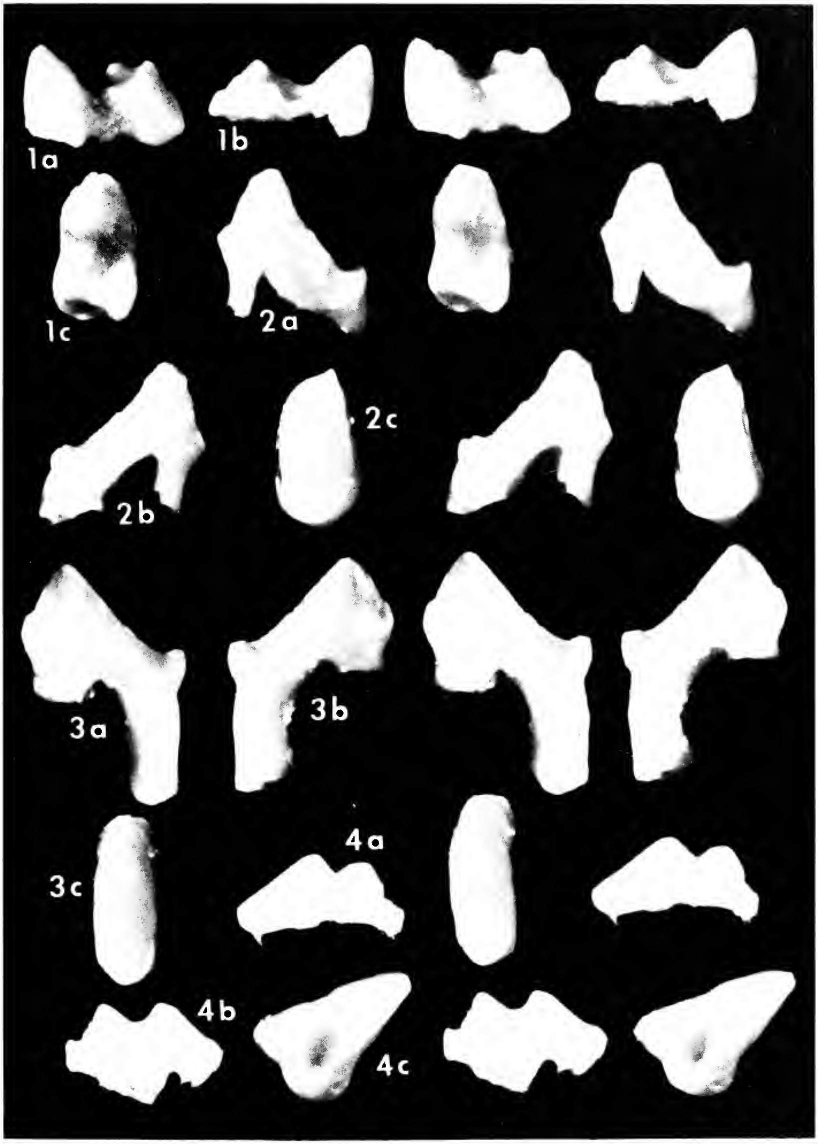


Plate 4. Stereophotographs of isolated premolars of *Peratherium* sp. cf. *P. knighti* from San Diego Co., California. 1. UCMP 106523, left "DP$_3$" (15×); 2. UCMP 106051, left P$_2$ (20×); 3. UCMP 101188, left P$_3$ (15×); 4. UCMP 101548, left "DP^3" (15×). a, b, and c represent labial, lingual, and occlusal views, respectively.

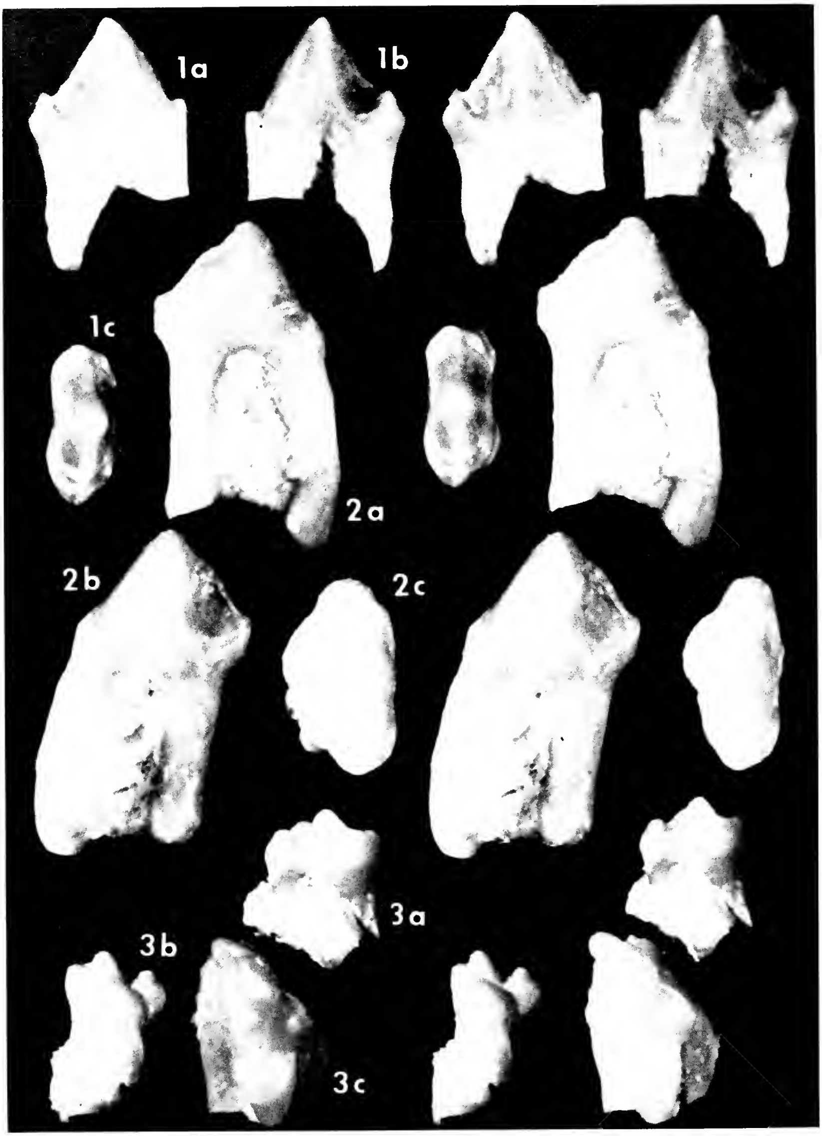


Plate 5. Stereophotographs of isolated teeth of didelphids from San Diego Co., California. 1. UCMP 106273, left P^2 (20×) of *Peratherium* cf. *P. knighti*; 2. UCMP 106371, left P^3 (15×) of *P.* cf. *P. knighti*; 3. UCMP 109578, left M^4 (15×) of *Nanodelphys californicus*. a, b, and c represent labial, lingual, and occlusal views, respectively.

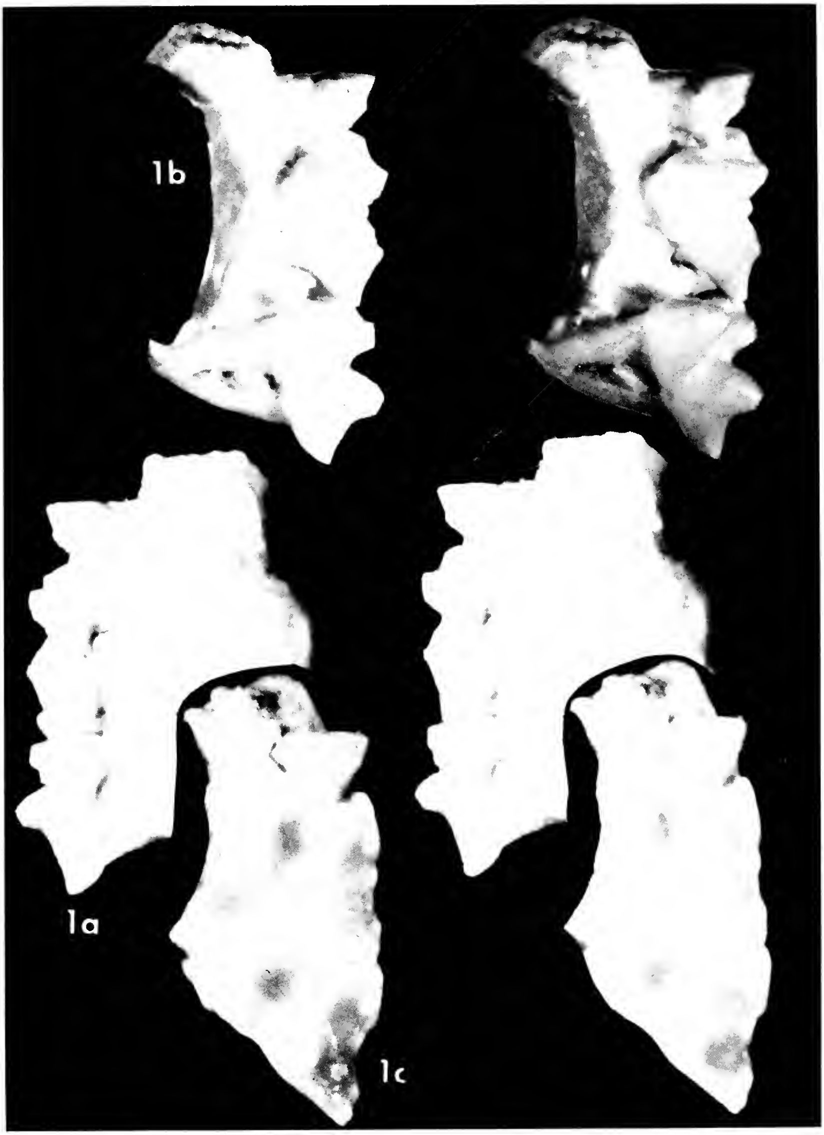


Plate 6. Stereophotographs (20×) of left maxillary fragment (UCMP 101933) with part of P^3 and complete $M^{1\text{-}2}$ of *Nanodelphys californicus* from San Diego Co., California. a, b, and c represent labial, lingual, and occlusal views, respectively.

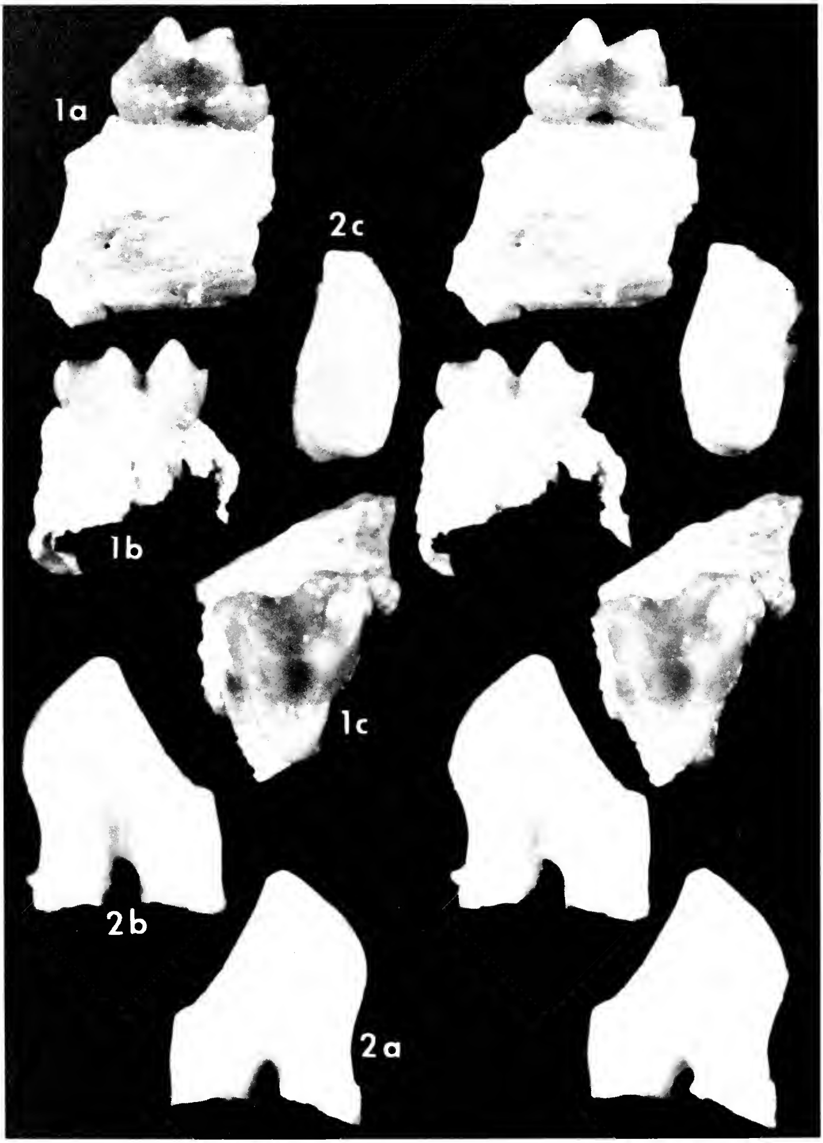


Plate 7. Stereophotographs of teeth of *Nanodelphys californicus* from San Diego Co., California. 1. UCMP 96474, left M^3 (15×); 2. UCMP 101521, right P$_3$ (30×). a, b, and c represent labial, lingual, and occlusal views, respectively.

Plate 8. Stereophotographs (20×) of left mandibular fragment (UCMP 104153) with talonid of M_1, complete M_2, and trigonid of M_3 of *Nanodelphys californicus* from San Diego Co., California. a, b, and c represent labial, lingual, and occlusal views, respectively.

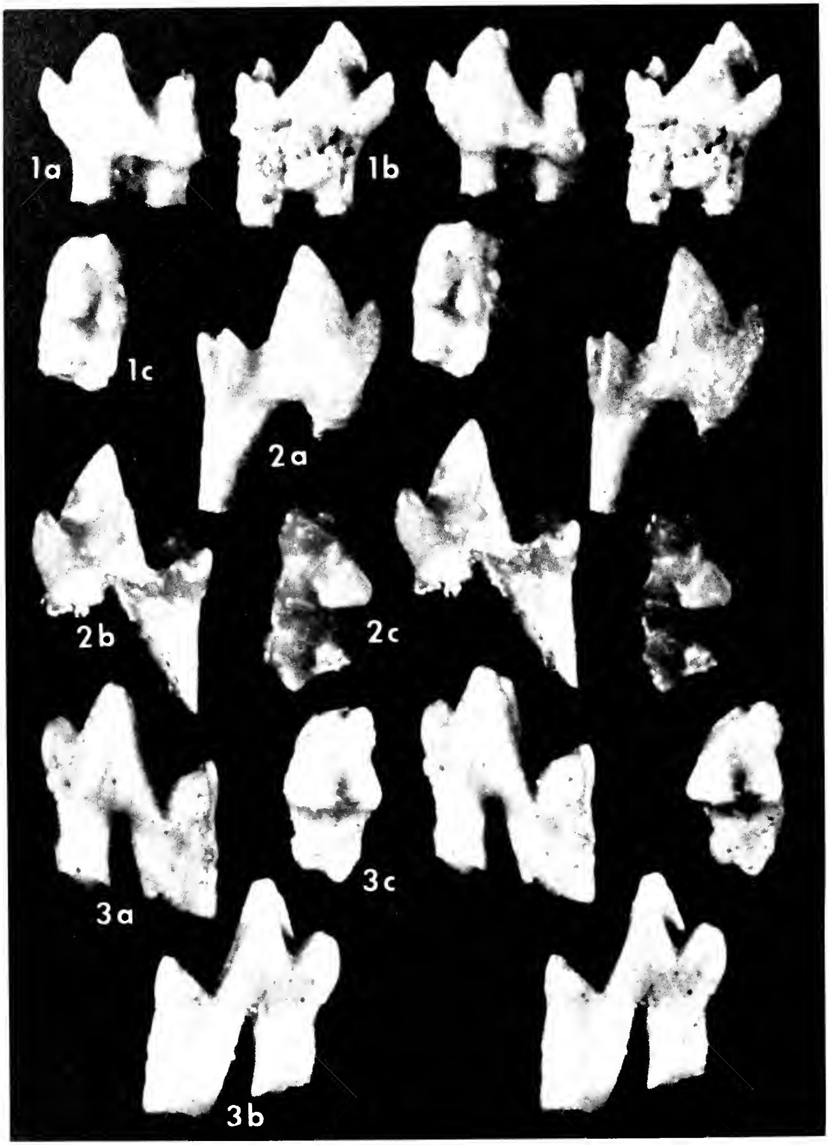


Plate 9. Stereophotographs (20×) of isolated lower molars of *Nanodelphys californicus* from San Diego Co., California. 1. UCMP 106372, left M_1; 2. UCMP 109783, right M_3; 3. UCMP 96165, left M_4. a, b, and c represent labial, lingual, and occlusal views, respectively.

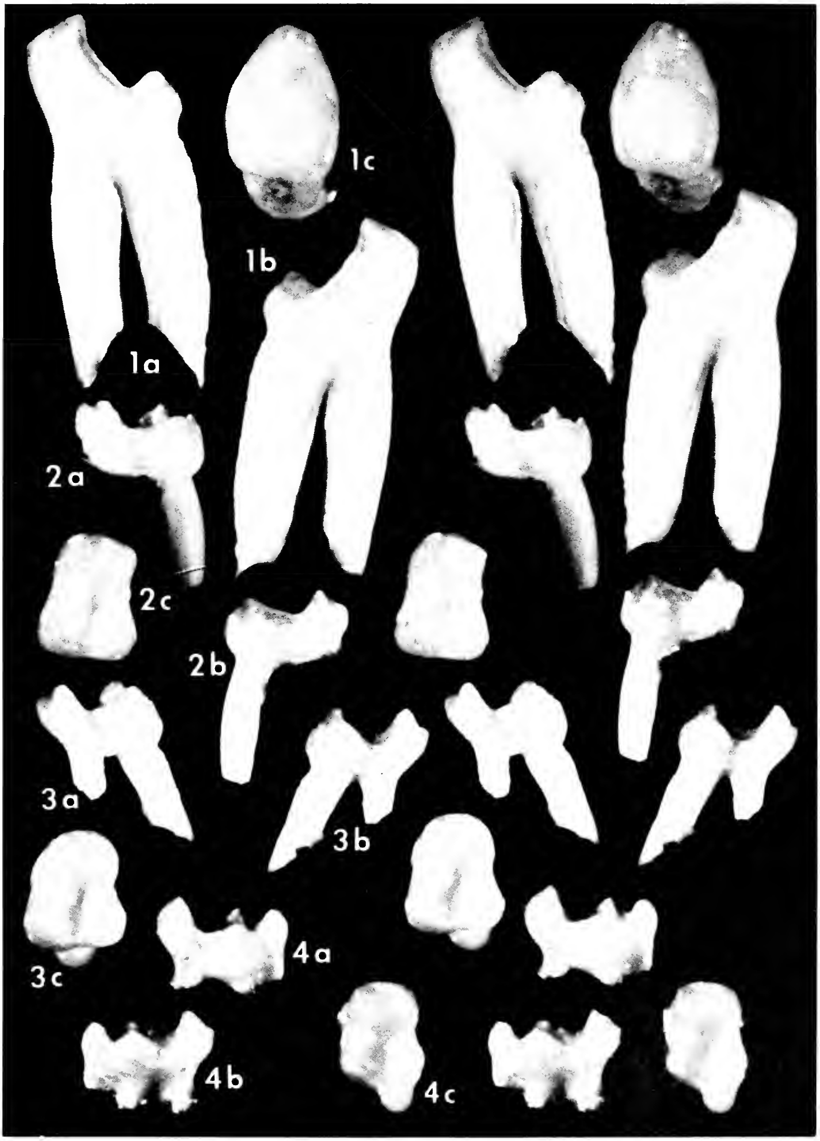


Plate 10. Stereophotographs of left isolated lower teeth of *Uintasorex montezumicus* n. sp. from San Diego Co., California. 1. UCMP 109808, P_4 (30×); 2. UCMP 101504, M_1 (20×); 3. UCMP 109997, M_2 (20×); 4. UCMP 109569, M_3 (20×). a, b, and c represent labial, lingual, and occlusal views, respectively.

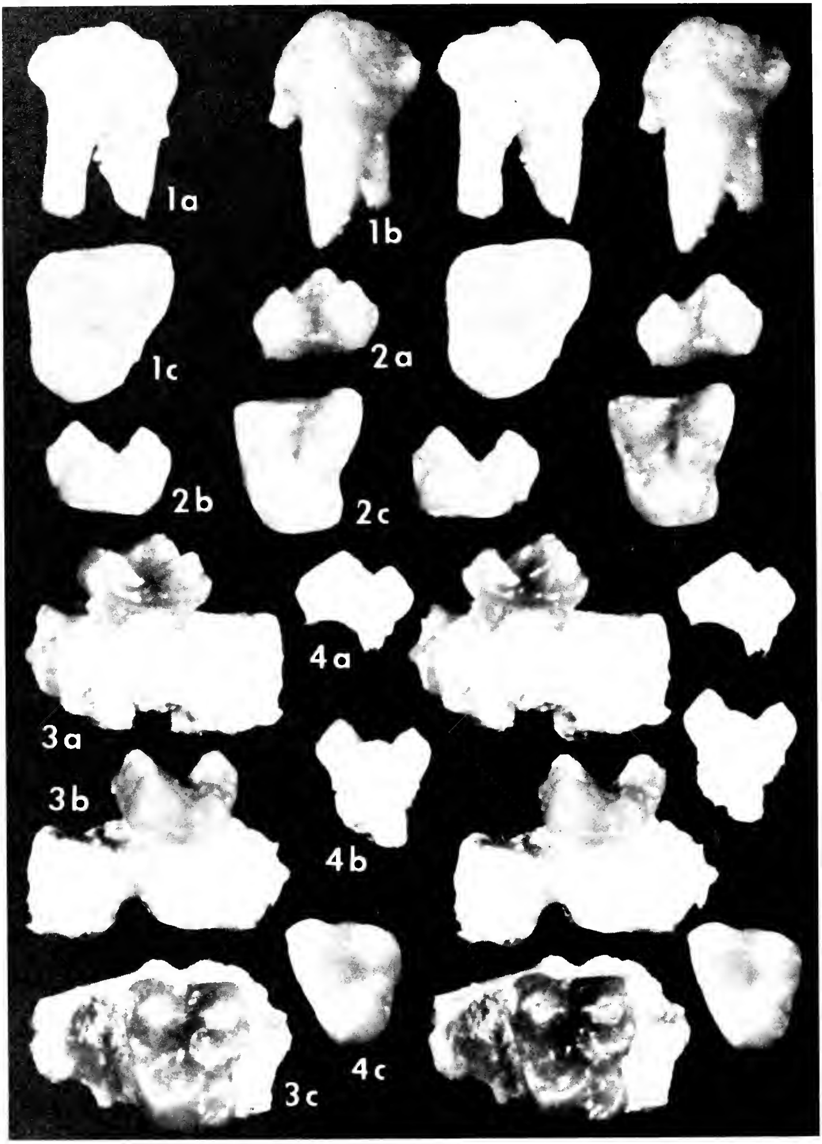
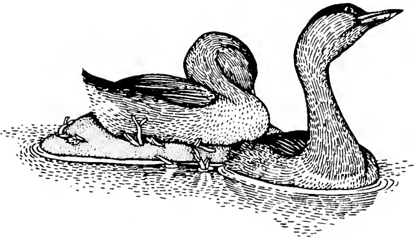
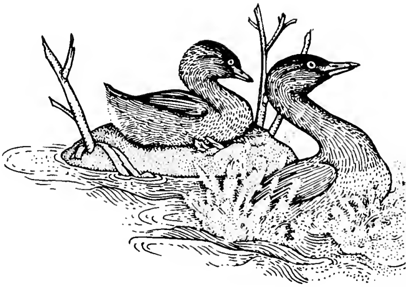


Plate 11. Stereophotographs of upper teeth of *Uintasorex montezumicus* n. sp. from San Diego Co., California. 1. UCMP 106886, isolated left P^4 (30×); 2. UCMP 106784, isolated right (photographically reversed) M^1 (20×); 3. UCMP 104179 (holotype), right (photographically reversed) maxillary fragment with M^2 (20×); 4. UCMP 103914, isolated left M^3 (20×). a, b, and c represent labial, lingual, and occlusal views, respectively.

THE BEHAVIOR AND RELATIONSHIPS OF THE LEAST GREBE

Robert W. Storer





TRANSACTIONS

OF THE SAN DIEGO
SOCIETY OF
NATURAL HISTORY

VOL. 18, NO. 6 10 MARCH 1976

The behavior and relationships of the Least Grebe

Robert W. Storer

ABSTRACT.—The Least Grebe, *Tachybaptus dominicus*, is widely distributed in the warm parts of the New World. It feeds on a wide variety of animals, including dragonflies and ants, the latter taken from emergent vegetation. Reverse mounting and copulation were filmed and analyzed. The former differed from the latter in that there was no cloacal contact and the series of post-mounting displays was less regular in timing and in alternation between members of the pair. The posture of the head in inviting differed from that of other grebes. No rearing or wing-quivering was observed. Four calls are described and the contexts in which they were used are discussed. The Least Grebe resembles the Old World little grebes, *Tachybaptus ruficollis* and *T. novaehollandiae*, in its cryptic resting posture, duet trills, and general habits; and it is probably more closely related to them than to any other grebes.

RESUMEN.—El zambullidor chico, *Tachybaptus dominicus*, tiene una distribución difusa sobre las partes calurosas del Nuevo Mundo. La comida de este zambullidor consiste de una variedad extensiva de animales, incluyendo libélulas y hormigas, éstas siendo cogidas de la vegetacion emergente. El montaje reverso y la copulación fueron filmados y analizados. Aquél fue distinguido del éste en que no hubo contacto cloacal y los despliegos después del montar fueron menos regulares en duración y en alternación entre los miembros de la pareja. La postura de la cabeza en invitando no es como lo que se observa en los otros zambullidores. Ni la levantadura ni el estremecimiento de las alas fueron observados. Cuatro llamadas son descritas, y el contexto en que fueron usadas es discutido. El zambullidor chico es parecido a los zambullidores pequeños del Mundo Antiguo *(Tachybaptus ruficollis* y *T. novaehollandiae)* en su postura secreto de descanso, trino duo, y en hábitos generales; y es probable que es más estrechamente emparentado con ellos que con los otros zambullidores.

The Least Grebe *(Tachybaptus dominicus)* has a wide range, from the Greater Antilles and southern Texas south to northern Argentina. (Early records from central and southern Argentina are probably erroneous, Storer, 1975.) Birds of this species take wing more readily than most grebes and have a high reproductive potential (Gross, 1949); they are thus thought to be adapted for utilizing temporary ponds (Smithe and Paynter, 1963). On the other hand, the northern population is not migratory; in southern Texas many of these birds are killed in cold winters when the ponds on which they live are frozen (James, 1963). Least Grebes are found on still waters in the tropical and subtropical zones. In some areas, for example Costa Rica, they are said to be more numerous in the latter zone (Carriker, 1910; Slud, 1964). Not infrequently specimens have been taken as high as 6000 feet elevation; the highest elevation from which I have seen specimens is "about 9000 feet" at La Lejia, north of Chachapoyas, Peru (American Museum of Natural History Nos. 234,318; 234;319). The species has also been taken at 2500m elevation in Bolivia (Carnegie Museum No. 120,163, from Comarapa, Dept. Santa Cruz).

In spite of the species' wide range, little is known about its biology. Much of the meagre literature is summarized in Palmer (1962), but even there one finds little on courtship, nothing on mating behavior or thermoregulation; and food habits are based on the examination of but ten stomachs. In order to learn more about this species, I made two trips to southern Texas, from 21 March to 4 April and from 24 April to 4 May, 1971. Most observations were made with the aid of 9 X binoculars, behavior was filmed with a 16 mm Bolex motion picture camera, and vocalizations were recorded with a Uher tape recorder. The field work was done primarily at the Santa Ana National Wildlife Refuge and at Anzalduas State Park, both in Hidalgo Co. This was supplemented by observations made at the Rob and Bessie Welder Wildlife Foundation near Sinton, San Patricio Co., and at a pond near Hargill, Hidalgo Co. Additional information was gained from examining and measuring over 700 specimens of the species from 24 collections in the United States and

San Diego Soc. Nat. Hist., Trans. 18(6):113-126, 10 March 1976

Canada. Analysis of geographic variation will be presented in a later paper. I am especially indebted to Robert W. Dickerman for specimens, Joseph G. Strauch, Jr., and Thomas E. Moore for stomach analyses, Daniel H. Janzen for identifying ants and for information on their habits, L. K. Gloyd for help identifying dragonflies, Gene Blacklock, the late Clarence Cottam, Pauline James, Albert McGrew, and Wayne A. Schifflett for their assistance with the field work, Patricia J. Wynne for preparing the illustrations, Rafael Alvarez for translating the abstract, to the National Science Foundation (through Grant GB-8269) for financing the study, and to the curators of the collections studied for making their material available. The kindness and hospitality of these people have made the work a great pleasure.

The Least Grebe is appropriately named. The mean weights of 18 males and 18 females from North and Central America are 140 g and 123 g, respectively. Birds of the Greater Antillean population are somewhat heavier (mean weight of four males, 167 g) and those of the South American population somewhat lighter (mean weight of three males, 114 g). The Least Grebe's ecological counterpart in much of the Old World, the Little Grebe *(T. ruficollis)*, is somewhat larger: mean weights of six males and six females from East Africa are 180 and 152 and for 187 winter-taken birds from Germany, not segregated by sex, 192 g (Hölzinger and Schilhansl, 1968). Philippine birds are still larger.

The Least Grebe is one of the drabbest members of the family with less difference between winter and nuptial plumages than most grebes. In nuptial plumage, the chin and throat are black and those parts of the plumage which are below the waterline when the bird is swimming are heavily marked with sooty. In winter, the chin, throat, and underparts are white. In contrast with the widespread Old World little grebes *(T. ruficollis* and *T. novaehollandiae)* there is no bright patch at the gape during the breeding season. Instead, the eye is bright yellow or orange in breeding Least Grebes. As is usual in grebes, the remiges are shed simultaneously, but the timing of this molt appears to be irregular. I have examined seven specimens from Texas with new remiges which had not completed growth. These birds were taken in August (1), September (2), January (2), March (1), and May (1). It is clear that the timing of the molt in this species merits further study.

These birds often gather in small flocks outside the breeding season, when they also associate with other species of water birds. When breeding, they are territorial but may nest in loose aggregations. Predation by Bat Falcons *(Falco rufigularis)* has been reported by Dickey and van Rossem (1938). A possible means of accidental death is indicated by data on a specimen of Least Grebe in the University of Michigan Museum of Zoology, collected on the Laguna de Sotz, Petén, Guatemala, by C. L. Hubbs. This bird had climbed onto a waterlily leaf, the center of which sank with the bird's weight and formed a funnel which trapped it.

Least Grebes move very quickly compared with larger species. This is quite noticeable in their comfort movements, which are in general similar to those of other grebes. I observed bathing, preening, oiling, head-shakes, head-scratches, jaw-stretches, foot-shakes, wing-and-leg-stretches, two-wing-stretches, swimming-shakes, and wing-flaps (the last two especially rapid). Bathing was particularly vigorous, the birds sending up a spray two to three feet high. I could detect no lateral motion of the tail as in swimming-shakes of Anatidae (McKinney, 1965). In both-wings-stretches, Least Grebes raise and partially stretch out their wings to a position intermediate between that of the Horned Grebe *(Podiceps auritus)* and that of most other species (Storer, 1969).

Miller (1932) and Wetmore (1965) comment on the flying ability of Least Grebes, and I agree that they probably take wing more readily than other North American grebes. They frequently flutter across the surface in the course of aggressive encounters or when frightened. I also saw what I believed was an upwind flight, when a bird flew low over the water against the wind, apparently to keep away from the lee side of a pond. (The habit of resting in clumps of emergent vegetation may also be a means of keeping from being blown to shore.) I saw several flights in which the birds went higher (to 5 or 6 ft. above the water) but could not see other birds which might have been involved in triggering this behavior. I saw no flights which I could attribute to courtship behavior (cf. Palmer, 1962).

The resting or "pork-pie" posture of the Least Grebe is like that of other grebes in that the head is held forward beside the neck, but it differs from the comparable posture of larger species in that the scapulars, and probably also the inner secondaries, are raised like a tent, hiding the nape and sides of the head (Fig. 1D). Birds in this posture show little or no white and appear more like a small stump than a bird. This unbirdlike form probably has survival value in permitting the birds to escape notice of visual predators. The resting posture of the Little Grebe (Bandorf, 1970: 19, fig. 5) resembles that of the Least Grebe very closely.

Food and foraging.—The feeding habits of the Least Grebe are poorly known. Stomach contents and feeding habits have been reported by Bond (1934), Cottam and Knappen (1939), Friedmann and Smith (1950), Gross (1949), and Wetmore (1965). According to these reports, the food taken includes aquatic beetles and true bugs, dragonfly and damselfly nymphs and adults, shrimp-like crustaceans, crayfish, small fishes, and tadpoles. (The decayed vegetable matter, algae, and mud reported as food of this species by Gross, 1949, and filamentous green alga *(Chara)* found in the Least Grebe stomach by Bond, 1934, may have been ingested accidently with their usual animal food.) To the analyses of the nine stomachs mentioned in the above references, I have been able to add data from eight birds collected by Robert W. Dickerman in Mexico and Guatemala and examined by J. G. Strauch, Jr. The results of these analyses are presented in the appendix.

As suggested by the variety of foods taken, Least Grebes use a variety of foraging techniques. I saw them forage not only by the usual grebe method of diving, but also by immersing only the head and neck, by picking objects off the surface of the water and off emergent vegetation, and by snapping at passing insects. I have observed all these methods but the last in at least one other species of grebe, and the last has been reported for the Great Crested Grebe *(Podiceps cristatus)* by Chance (1970) and Crow (1951). Once I saw a female Least Grebe stop preening to dash after a mating pair of dragonflies, apparently catching them as they came to the surface of the water. She ate first one and then the other, which meanwhile had lain immobilized on the water. Each was larger in body size than the bird's bill. Another time, I saw a Least Grebe, which had been sunning, start swimming rapidly with its head forward and wings down after a fairly large, red-bodied dragonfly with red on the wings (probably *Libellula [Belonia]) saturata*, fide L. K. Gloyd). The grebe snapped at the dragonfly as it flew over, but missed. Shortly the bird dived and emerged, snapping at the insect as the latter came near the surface. This trout-like foraging method is one which I have never seen performed by any other bird. The largest dragonfly which I saw a Least Grebe eat was perhaps 4 inches long (possibly an *Anax*). After catching it, the bird swam rapidly away from the nearby grebes and eventually swallowed the insect headfirst, wings and all. As is the case with other grebes, large prey are shaken and pinched with the bill before being swallowed.

On March 23, at Welder, I watched six Pied-billed Grebes *(Podilymbus podiceps)* and two Least Grebes diving and feeding together among the roots of a patch of *Scirpus*. At times they were almost touching. They were getting small, whitish objects (shrimp or small fishes) about ¾ inch long. The lack of antagonism was strikingly different from the situation later in the spring at Santa Ana Refuge when the Pied-billed Grebes were nesting. Commensal feeding of Least Grebes with domestic Mallards and Horned Grebes with a Surf Scoter have been reported by Paulson (1969). Feeding associations between Little Grebes *(Tachybaptus ruficollis)* and ducks and coots have been reported by several observers and summarized by

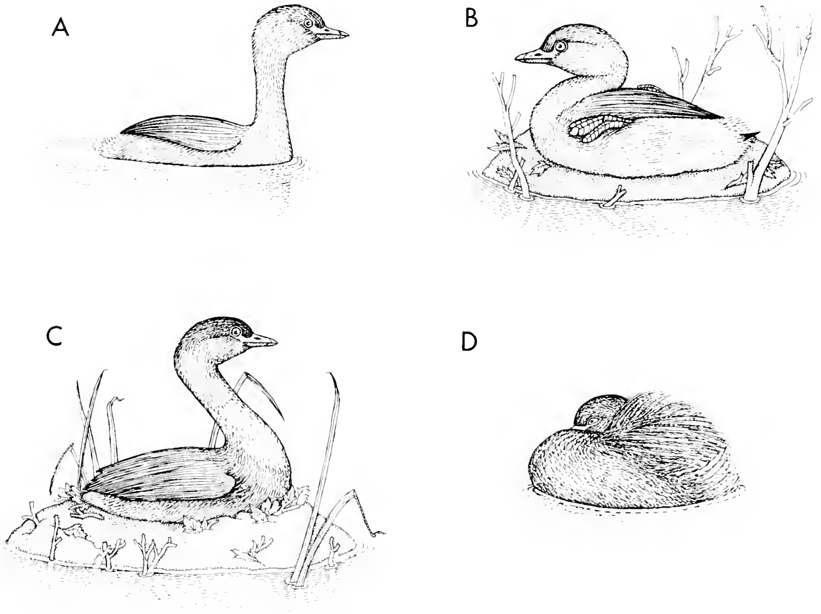


Figure 1. Postures of the Least Grebe. A. Alert posture. B. Resting on nest with feet held out. C. Z-neck posture on nest. D. Pork-pie resting posture.

Siegfried (1971). The association between the two species of grebes differed from those between Little Grebes and unrelated species in that the two grebes apparently used the same foraging techniques and ate the same food.

Other food items which I saw brought to the surface were a fish less than an inch long, and a somewhat smaller tadpole. My observations are probably biased in favor of large prey items, for, like Horned Grebes (Storer, 1969), Least Grebes probably swallow small prey items before surfacing. This is further indicated by the stomach analyses. However, it is evident that dragonflies are a much sought-after prey.

The occurrence of ants in seven of the eight stomachs and their presence in large numbers in two deserves special comment. Daniel H. Janzen looked at samples of these ants and identified most as belonging to the genus *Crematogaster* and others to the genera *Pseudomyrmex* and *Camponotus*. According to him, members of these three genera nest in hollow twigs, dead branches, or stumps and but rarely in the ground. Thus they may be found in numbers in dead bushes or trees standing in bodies of water, which are either temporary or have wide seasonal fluctuations in size. Many of the head capsules were crushed, so it is likely that most of the ants were taken one by one from emergent vegetation.

Least Grebes are thus opportunistic feeders, taking a variety of small animals both in and on the water, in the air, and on emergent vegetation. This flexibility in foraging and in particular taking many terrestrial insects which either land on the surface or are found on emergent vegetation probably enables them to use temporary bodies of water, where invertebrate populations may be unstable or transitory.

Cottam and Knappen (1939) commented on the small volume of feathers in the stomachs of Least Grebes which they examined. Of the eight stomachs which we analyzed, four had few feathers, two had many, and two moderate numbers. In at least three, there was a plug in the pyloric lobe similar to that which I reported for the Horned Grebe (1969). Such a plug was present in each of six stomachs of the Pied-billed Grebes examined recently and may prove to be the rule in all species of the family. The paucity of feathers in so many of these stomachs can, I believe, be explained by the high proportion of insects in the diet and the consequent need for frequent pellet casting to get rid of indigestible chitin.

Agonistic behavior.—Like most or all others of their family, Least Grebes meet in breast-to-breast combat, kicking out at each other like coots. Because of the great strength of the shank muscles, which power the swimming strokes of the feet, the comparable downstroke in fighting is presumably the one used to the greatest effect. At least seven such fights were observed, the earliest on March 27 and the latest on May 3. The birds involved were, as far as I could tell, all males, some with white throats and some with black or pied throats.

Chases were frequent, one bird skittering across the water after another, both moving their wings and feet rapidly. On one occasion an apparently mated male dived and chased an odd male, who made three zig-zag skitters, each six to eight feet in length, while the aggressor underwater evidently followed its path. The aggressor emerged in a posture like that used in bathing (but here apparently of aggressive significance) before returning to his mate. This bathing posture was not unlike the bouncy posture used by species of *Podiceps* in the discovery ceremony (Storer, 1969) and might be an evolutionary source of this courtship display.

The most frequently noted threat posture was one in which the head was held high and somewhat back, the head, neck, and body forming a Z, and the head and neck feathers rasied (Fig. 1C). This posture closely resembled the "bridling dog display" of the Atitlán Grebe *(Podilymbus gigas)* figured by LaBastille (1974: fig. 11) and the similar display of the Pied-billed Grebe which I have seen on several occasions. That these displays are probably homologous is suggested by an observation of two male Least Grebes using the Z posture with the feathers raised in an aggressive encounter, presumably near the boundary of their territories. I saw a Least Grebe, which had just fled from another, assume a similar posture, but with the head and neck feathers flattened. This posture resembled closely the appeasing z-neck posture of the Horned Grebe (Storer, 1969) and probably had a similar appeasing motivation. An alert posture (Fig. 1A) was used when the birds were disturbed or appeared curious.

A stronger threat than the z-neck posture with the features raised is holding the head low as in the forward threat of other grebes. In still more aggressive situations, a Least Grebe may lunge, skitter, or dive toward a second bird. These actions are listed in what I believe to be their increasing intensity of threat. The similarity of the two z-neck postures in everything except the raising or lowering of the head and neck feathers suggests that both may have somewhat similar motivation. The head is held high in alarm and in advertising, both situations in which fear or anxiety is expressed; in strongly aggressive situations, the head is held low or forward. Thus there is probably a strong element of appeasement in both z-neck postures. Raising the feathers of the head and neck adds a balancing aggressive element, which may permit one bird to use this display against another bird using the same display on neutral ground.

Pied-billed Grebes were found on all waters where I observed Least Grebes. Early in the season, when the birds were in winter groups, individuals of both species foraged in close association. But at Santa Ana Refuge, after Pied-bills had mated and had started to nest, they were intolerant of Least Grebes. In late March and early April, two pairs of Pied-bills and up to eleven Least Grebes lived on the long, narrow, diked West Lake. The pair of Pied-bills established near the north end of the lake kept the Leasts in the south end by repeated aggression. Frequently a

Pied-bill would dive and move underwater toward one or a group of Least Grebes on the open water. This resulted in the Leasts skittering over the water, often into the cattails around the edge. After encounters with Pied-bills, Least Grebes often looked underwater and then raised their heads in an alarm posture. At times a Pied-bill would rout Least Grebes by swimming toward them in the flat-headed threat posture, whereas Least Grebes did not flee from Pied-bills in neutral postures. It was clear that the Least Grebes recognized the threat displays of the Pied-bills. In early May on the resaca at Anzalduas State Park where I photographed the mating behavior of Least Grebes, a male of this species near its nest twice threatened a Pied-bill, once with the z-neck aggressive posture, once by diving toward it. In both cases the Pied-bill moved away. Antagonism between these two species in Cuba has been described by Gross (1949) and LaBastille (1974) mentions a male Atitlán Grebe seizing a Least Grebe by the neck and thrashing it vigorously.

Thermoregulation.—Least Grebes sunbathe regularly, facing away from the sun and erecting the white feathers of the back. Solar energy is absorbed by the heavily pigmented bases of these feathers and by the black skin beneath them (Storer, Siegfried, and Kinahan, 1975). While on the nest platform, Least Grebes occasionally rested with the back feathers down and the spread toes held out from the body (Fig. 1B). The function of this behavior is unknown, but it may serve as a cooling mechanism.

Courtship.—It is not clear which courtship displays function in pair formation. I have observed neither the rushing display reported and figured by Zimmerman (1957) nor display flights like those described by Palmer (1962), which I could attribute to courtship. As in most other grebes, advertising is probably involved, but the other display or displays remain to be determined. Once pairs are formed, duetting trills upon meeting and after aggressive encounters with other grebes are probably important in strengthening the pair bond.

Platform behavior.—Between April 29 and May 3, I observed mating behavior of a pair of Least Grebes on a small resaca, 300 to 400 feet long and 75 to 100 feet wide on the east side of Anzalduas State Park. There were two pairs of Least Grebes and a pair of Pied-billed Grebes on this resaca, which contained considerable emergent vegetation, most of it dead shrubs. The pair which I spent most time watching had a platform in a dead shrub in full view from the slope leading down to the water. The members of this pair were readily distinguishable, the female by her shorter bill, more rounded, dove-like head, and completely black throat, and the male by his longer bill, flatter head, and white chin. When I first saw the platform, it was well built and easily supported the birds, who nevertheless added material, mostly algae, to it from time to time throughout the period of observation. When I left at 7 p.m. May 3, no eggs were as yet in it.

The pair bond appeared strong from the time of my first visit, and inviting was performed frequently by both birds. On April 30 and May 1, observation periods of approximately five and five and one half hours, respectively, inviting by the female was observed 8 and 10 times, and by the male, 7 and 7 times; mounting by the female 2 and 4 times, and by the male, 2 and 2 times. The female more frequently got onto the platform but tended to remain there for shorter periods than the male. In 13½ hours of observations on three days, the female was on the nest 31 times to the male's 21; but she remained there longer than 8 minutes only twice in 22 times (maximum 17 minutes), whereas the male remained longer than 8 minutes in 5 out of 15 observations (maximum, 25 minutes). This may well have been correlated with the female's spending more time away from the nest foraging during this period of development of the eggs, but foraging times could not be taken owing to the density of vegetation in the resaca.

On the basis of the single pair which I watched at their platform, Least Grebes differ from other species so far studied in their soliciting postures. I observed no rearing or wing-quivering, and in the inviting posture the head was not extended but drawn back and the bill pointed downward at an angle of approximately 45° (Fig. 2D). This angle varied considerably, at times a bird would point the bill more downward at its mate's approach. The inviting bird also tended to turn its head away from its mate. Frequently when the mate was on the water beside or in front of the inviting bird, the latter would get up, turn, and settle down again in the inviting posture with the tail toward the mate. It has been suggested that rearing might be a ritualized intention movement of sitting down on the nest (McAllister, 1958), that it also resembles the posture of the active bird during copulation and that of a bird turning its eggs, and that it may be a "ritualized version of the waddling on the nest rim, shaking the wings to remove water from the plumage, and showing intentions to uncover the eggs, before settling to incubate (Schmidt, 1970, fide Fjeldså, 1973). A fourth possibility is that rearing arose as a ritualization of a getting up and turning away from the mate like that performed by the Least Grebe.

An elaboration of the inviting posture was seen once, the female turning the head from facing forward to facing left to forward to right, etc., stopping briefly each time the head faced forward and at the extreme of each turn. During copulation, the female also turned her head in this way, gradually raising it until her nape stroked the breast of the male (Fig. 1A). A similar type of head turning was observed in the New Zealand Dabchick *(Poliocephalus rufopectus)* (Storer, 1971) both in inviting and during copulation. Elaborations of this type of head turning are found in courtship displays of the latter species (Storer, 1971) and of the Great Grebe *(Podiceps major)* (Storer, 1963a).

Inviting in the Least Grebe is often accompanied by *gup* notes.

As in other grebes, mounting is preceded by a fairly long period during which the male remains on the water, moving about "nervously," as though getting up courage to mount. At this time, the male does not appear to perform any stereotyped movements. Mounting is not accompanied by loud calls, as is the case in most other grebes. After the male has mounted, he moves the tail from side to side (28 or 29 times in about six seconds in one film), then presses it against that of the female as cloacal contact is made. He then rises up a little and finally dismounts over the female's head. Upon hitting the water, he treads water rapidly as his body subsides onto it and his head is raised and held back in the z-neck posture. Water treading is done in front of and with one side toward the female, who remains on the nest.

While the male is treading water (Fig. 2C), the female initiates a series of postcopulatory displays. These include presumed calls (Fig. 2F), head flicks or shakes (Fig. 2D), and head turns. The first consists of opening the bill as though calling and lasts from four to seven frames with a mean of roughly one-fifth of a second. I noticed no sound, but one could easily have been unnoticed while the camera was running. Head flicks consist of two or three rapid sideways movements of the head and include a turning of the head approximately 45° on its long axis so that one side is turned partway up (cf. McKinney, 1965). Head shakes lack this turning on the long axis but are otherwise similar. Both are accomplished in approximately one-tenth of a second (2 or 3 frames of ciné film taken at 24 frames per second). Because of the speed of the actions it is likely that the turning may have been missed in some instances. For this reason and because I could see no significant difference in the use of the two displays, I have combined them under head flicks. Head turns are quick turns of the head in one direction, either toward or away from the mate. Turns also take approximately one tenth of a second, and their amplitude was estimated at 15° (once), 30° (19), 60° (29), and 90° (9 times). When the male turns his head, very often he subsequently turns his body slowly until its axis is parallel with that of his head. The female remains on the nest and turns only the head and neck. Between display movements, the birds hold their heads motionless as though posturing (Fig. 2E).

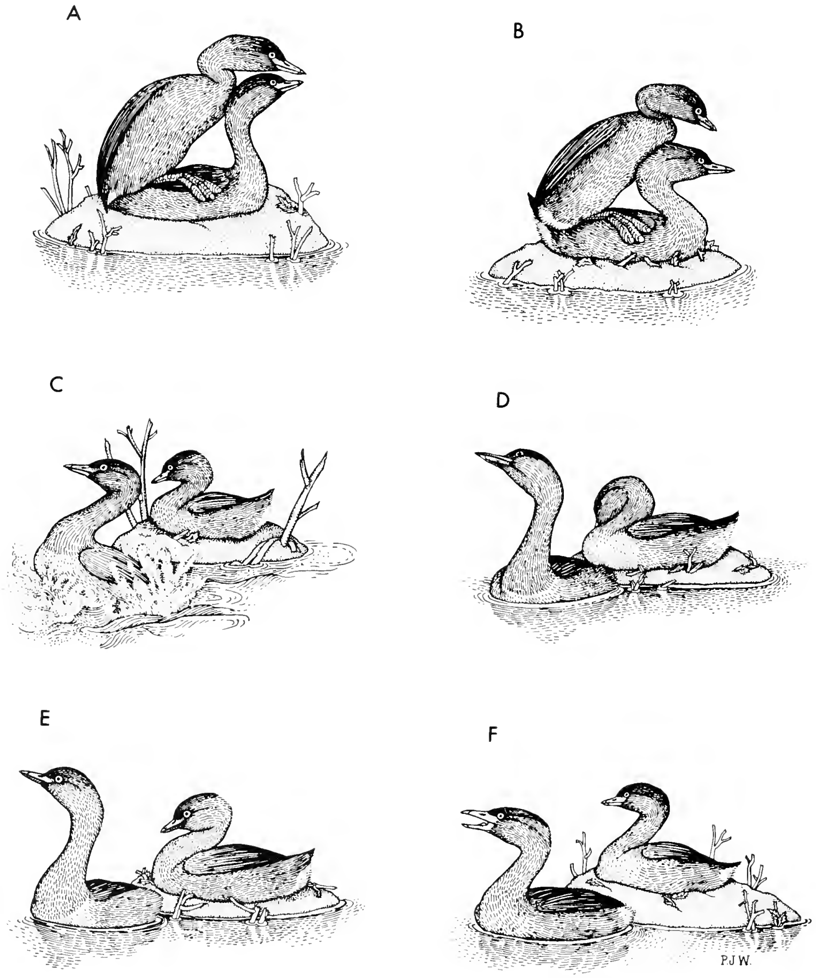


Figure 2. Platform behavior of the Least Grebe. A. Copulation. B. Reverse mounting. C. Water-treading. D. Head flicking by male, inviting by female. E. Posturing between head turns. F. Male calling.

The postcopulatory displays are performed alternately by the members of the pair. The female uses only head turns, except once when she gave a flick about one second (26 frames) after she gave a turn given while the male was water treading. This was also the only exception to the regular alternation between the sexes following copulation. The displays given by the male follow a general pattern—first a call, then one or more flicks (or shakes), and finally one or more turns. As the sequence of displays progresses, the intensity appears to wane until one or both birds move off. Thus by the position of the displays within the series one can postulate the relative intensities of the displays. Calls are presumed more intense than flicks, which are more intense than turns. The mean reaction time, that is, the interval between

TABLE 1. Reaction Times[1] between Postmounting Displays of the Least Grebe

	N	Mean	S.D.	S.E.
Male after copulation	11	15.6	8.15	2.45
Female after copulation	11	15.5	6.39	1.92
Male after reverse mounting	10	24.8	11.31	3.57
Female after reverse mounting	11	7.4	5.26	1.58

[1] The number of frames of cine film between the start of a display by one bird and the succeeding display of its mate.

successive displays, was 15.6 frames and was the same for both sexes (Table 1). With a progressive decline in intensity of displays, one might expect a progressive increase in the intervals between displays. No such change was shown in the data; long and short intervals were found both early and late in the series. Nor was there evidence that the length of the interval was affected by whether the preceding motion of the head was toward or away from the responding bird.

Reverse mounting.—As mentioned earlier, reverse mounting (Fig. 2B) was observed more frequently than copulation. Although the two acts are superficially similar, studies of three copulation sequences and five sequences of reverse mounting with a film analyzer showed several significant differences. It was evident from the film that reverse mounting did not result in cloacal contact although the female did make side-to-side movements with the tail. The alternation of displays after copulation was more regular (in 23 of 24 displays) than after reverse mounting (in 23 of 33 displays, including one instance in which the female displayed three times in succession). After reverse mounting, there was a considerable difference between the sexes in the reaction time between displays, that of the male averaging more than three times that of the female (Table 1).

Reverse mounting has usually been dismissed without comment as aberrant or incidental behavior. In grebes it occurs frequently and probably regularly in most species. Hence, I believe that it must have a positive selective value to outweigh the rather obvious disadvantages of using energy which otherwise would be conserved or put to more direct reproductive effort and of drawing attention of potential predators to both the nest platform and the birds themselves. What the advantages are is unclear but worthy of speculation in the hope that further evidence or proof can be obtained. The lack of cloacal contact rules out fertilization. Some possibilities which remain include strengthening the pair bond, a change in dominance relationships, and providing a stimulus for the growth of the ovarian follicles or for ovulation.

Advertising call.—A loud, rather high-pitched note (Fig. 3), which I transcribed as *gamp*, apparently serves as an advertising call. In intense advertising, the note is given with the head held high and slightly puffed out, the neck thin, the white of the underparts showing above the water anteriorly, and the body feathers slicked down. This posture corresponds to that in advertising Horned Grebes (Storer, 1969: Fig. 3A), but it is not used in low-intensity advertising. The two pairs of Least Grebes at Anzalduas State Park, April 29 to May 3 gave this call or series of this call at least 40 times in approximately 11½ hours of observations. The call varied in intensity and was given under a variety of circumstances, but almost always when the members of a pair were separated and often when the calling bird was somewhat alarmed. (Only twice was I certain that a bird advertised when its mate was near; in each case it was the female which called and the calls were of low intensity.) Advertising calls were given by the male (14 times) and the female (4 times) when alone and undisturbed on or near the nest, in all but two of these instances the call was of low or moderate intensity. Twice when the male was at the nest calling, the female

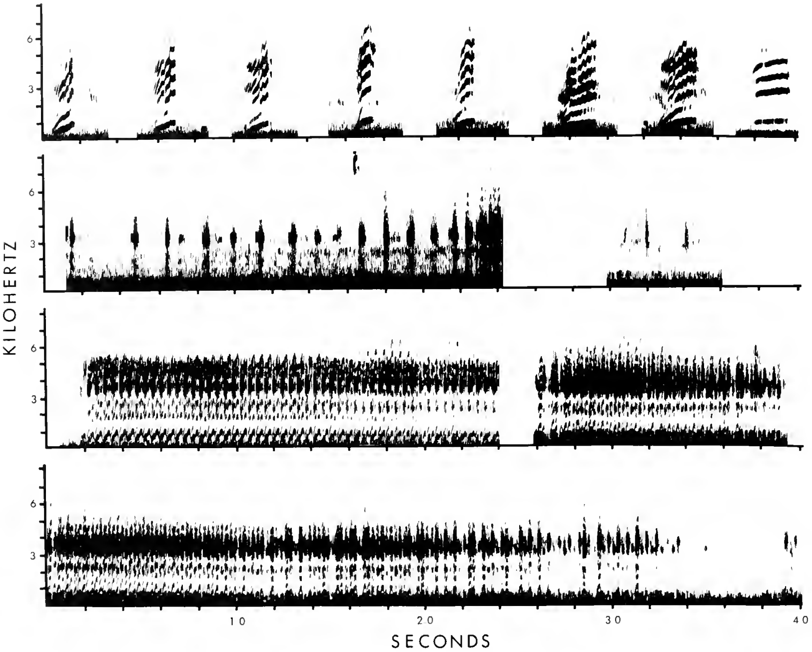


Figure 3. Vocalizations of the Least Grebe. *Top row,* advertising notes. *Second row, left,* start of trill, *right,* contact notes. *Third and fourth rows,* trills.

answered with similar advertising notes. Four times I disturbed lone birds (the male three times and the female once) on the nest, and they gave loud, high-intensity *gamps.* Other disturbances eliciting advertising calls included a splash, possibly made by a frog jumping into the water, and the presence of a Pied-billed Grebe or another pair of Least Grebes nearby.

Earlier at Santa Ana advertising notes were also heard.

While it is difficult to match verbal descriptions in the literature with calls heard in the field, I believe that the "reedy, somewhat nasal . . . *queek*" of Palmer (1962) and the "call which varies from a loud, goose-like honk to the reedy little honk of a toy horn" of Slud (1964) and the "nasal *yank* surprisingly similar to that of a red-breasted nuthatch" of Friedmann and Smith (1955) all refer to advertising calls.

Trills.—The most familiar and conspicuous call of this species is a loud, rapid trill, which is frequently heard when the members of a pair are together. Audiospectrograms (Fig. 3) indicate that at least part of the time both members of the pair call simultaneously, but with alternate notes. Trills may end abruptly or the tempo of the notes may slow down and then accelerate.

The two pairs at Anzalduas State Park gave at least 73 trills or series of trills in 11½ hours. Often it appeared to be in greeting, as when one bird joined its mate at the nest (11 times) or elsewhere (8 times). It was used when the pair approached the nest (11 times) or swam away from it (11 times). It seemed to function also as a triumph note, as after an aggressive encounter with a Pied-billed Grebe (4 times) or with another pair of Least Grebes (3 times). In this context it was very similar to the triumph duets of the Horned Grebe (Storer, 1969) and also to that triggering the more complex patter ceremonies of the New Zealand Dabchick (Storer, 1971). In three instances, trills by the Least Grebes followed my disturbing the birds. Four times when I could not see the birds, one pair responded in kind when the other pair trilled, and in four others, trills followed aggressive notes. When trills were used as a greeting, more frequently (19 out of 23 times) the male swam up to the female. These observations suggest that the call is important in reinforcing the pair bond and in announcing or maintaining territory, somewhat as song serves this purpose in many passerines.

This call has apparently been reported by several authors. Gross (1949) refers to a "prolonged rapidly-uttered, rattle-like call" and a "trill," both given by the male. Palmer (1962) lists a "trill," and Slud (1964) calls it "a kind of watery churr or shushing whinney." Zimmerman (1957) in describing a rushing display reported that "one bird uttered a high-pitched, nasal *nye, nye, nye, nye.*" This might have been the trill or an otherwise undescribed note.

Contact notes.—A soft note, which I have transcribed as "gup," is frequently given by both members of the pair in the vicinity of the nest. I heard it given by birds coming to, at, or on the nest (24 times), during inviting (4 times) and building (once), and as the mates approached each other (3 times) away from the nest. As the mate approaches, a bird may switch from advertising to contact notes; and, conversely, when a distant mate does not respond to contact notes a bird may switch to advertising. One or both birds may use contact notes as they swim together before trilling. The use of contact notes in these situations and the softness of these notes suggest that their use is associated with low-intensity situations. This note is evidently the "low short note used during copulation and sometimes between pair at nest" (Palmer, 1962) and also the "series of faint notes" which the male gave as he approached the nest containing newly hatched young (Gross, 1949).

Aggressive call.—A high-pitched nasal note, which I transcribed as "anh," is often given singly or in series in the course of aggressive encounters. I heard it on at least six occasions. Once I was able to determine that it was the male which gave the call. At other times the birds were too far away or out of sight behind vegetation. The call was given while birds flew toward (unseen) antagonists and during actual territorial fights and was followed by trilling as fighting birds returned to their mates. I have not been able to equate this with other notes described in the literature.

RELATIONSHIPS

The Least Grebe belongs to a group of species which can be characterized by having downy young with one or more patches of rufous down on the crown (Storer, 1967). This includes the species listed by Peters (1931) in the genera *Poliocephalus* and *Podilymbus.* For purposes of discussion here, these species can best be combined into four subgroups, each consisting of forms which comprise a superspecies or group of closely related species. These subgroups center around the species *podiceps* (with *gigas*), *ruficollis* (with *novaehollandiae, rufolavatus,* and *pelzelnii*), *dominicus,* and *poliocephalus* (with *rufopectus*). The relationships of *dominicus* have been unclear (Storer, 1963b), but sufficient new evidence has accumulated to merit a reassessment of its systematic position. This will be done by first presenting an arrangement based on morphological characters, and then by testing this arrangement with information based on behavior.

The birds in the *podiceps, ruficollis,* and *dominicus* subgroups share many similarities. In winter plumage, all have white underparts and throats, dark caps, and light brownish cheeks. In the breeding season, the underparts become heavily mottled with blackish, the throat black, and the cheeks and neck gray *(podiceps, dominicus),* rufous *(ruficollis),* or black *(gigas).* The *podiceps* subgroup differs from the other two (and from all other grebes) in several ways: The ulnar origin of M. extensor longus digiti II is not confined to the extreme proximal end of the bone and the distal head of M. extensor longus digiti III is absent (Sanders, 1967); the bill is short, deep, powerful, and strongly pied in the breeding season; and the feathers of the lores, forehead, and malar region have broad, flattened tips to the rachis (Stettenheim, 1974). I consider these character states all to be advanced over those in the other three subgroups.

Members of the *ruficollis* subgroup (except *pelzelnii*) are advanced over the presumed common ancestor of the group in having an expanded, yellow-green gape and rufous on the cheeks and nape. The *dominicus* and *poliocephalus* subgroups are advanced in lacking the canal in the hypotarsus for the tendon of M. flexor perforatus digiti II (Storer, 1963b) and in having conspicuously light (ivory to orange-yellow) eyes in the breeding season. Members of the *poliocephalus* subgroup differ from all the others in having the throat and cheeks the same dark color, white, hair-like nuptial plumes on the head, and the chest rusty; and they lack mottling on the underparts.

On the basis of this morphological evidence, the *podiceps* subgroup forms one distinct assemblage, the genus *Podilymbus;* the *poliocephalus* subgroup forms another, for which the generic name *Poliocephalus* is available. The Least Grebe differs from the *ruficollis* subgroup in the hypotarsal character and in details of the breeding plumage and soft parts, but in general is closest to that subgroup. I would therefore consider the two subgroups to comprise the genus *Tachybaptus.*

These relationships are supported by some of the behavioral evidence which is available. Based on data from *rufopectus* (Storer, 1971), the *poliocephalus* subgroup is the most distinct, having unique diving and pattering displays and lacking trills. In this emphasis on visual rather than vocal displays, as in plumage characters, the *poliocephalus* subgroup may be considered convergent with the genus *Podiceps sensu stricto,* from which it differs markedly in the pattern of the downy young, courtship behavior, and type of head plumes. The species of *Podilymbus* differ from the others in having a sexually dimorphic "song" and a pivoting display. The Least Grebe resembles the members of the *ruficollis* subgroup, as far as known, in its vocal repertoire and its peculiar, presumably cryptic, resting posture; but it differs from the latter in its soliciting posture and postcopulatory displays (cf. Bandorf, 1970). The Least Grebe has presumably been isolated from its Old World relatives for a long time, and the differences between it and members of the *ruficollis* subgroup might be sufficient to place it in a separate subgenus for which the name *Limnodytes* (Obserholser, 1974) is available. However, as the number of species is small, this seems impractical.

LITERATURE CITED

BANDORF, H., 1970. Der Zwergtaucher. A. Ziemsen Verlag, Wittenberg, Lutherstadt.

BOND, R. M., 1934. A partial list of birds observed in Haiti and the Dominican Republic. Auk 51: 500-502.

CARRIKER, M. A., JR., 1910. An annotated list of the birds of Costa Rica including Cocos Island. Annals of the Carnegie Museum 6: 314-915.

CHANCE, G., 1970. Notes on a crested grebe's nest at Lake Mapourika. Notornis 17: 87-91.

COTTAM, C., and P. KNAPPEN, 1939. Food of some uncommon North American birds. Auk 56: 138-169.

CROWE, R. W., 1951. Unusual feeding method of great crested grebe. British Birds 44: 391.

DICKEY, D. R., and A. J. VAN ROSSEM, 1938. The birds of El Salvador. Zoological Series, Field Museum of Natural History 23. 609 p.

FJELDSÅ, J., 1973. Antagonistic and heterosexual behavior of the horned grebe, *Podiceps auritus.* Sterna 12: 161-217.

FRIEDMANN, H., and F. D. SMITH, JR., 1950. A contribution to the ornithology of northeastern Venezuela. Proceedings of the United Sates National Museum 100: 411-538.

FRIEDMANN, H., and F. D. SMITH, JR., 1955. A further contribution to the ornithology of northeastern Venezuela. Proceedings of the United States National Museum 104: 463-524.

GROSS, A. O., 1949. The Antillean grebe in central Soledad, Cuba. Auk 66: 42-52.

HÖLZINGER, J., and K. SCHILHANSL. 1968. Wintergewichte des Zwergtauchers *(Podiceps ruficollis)*. Anzeiger der Ornithologischen Gesellschaft in Bayern 8: 297-298.

JAMES, P., 1963. Freeze loss in the Least Grebe *(Podiceps dominicus)* in lower Rio Grande Delta of Texas. Southwestern Naturalist 8: 45-46.

LABASTILLE, A., 1974. Ecology and management of the Atitlán grebe. Lake Atitlán, Guatemala. Wildlife Monographs 37. 66 p.

MCALLISTER, N. M., 1958. Courtship, hostile behavior, nest-establishment and egg laying in the eared grebe *(Podiceps caspicus)*. Auk 75: 290-311.

MCKINNEY, F., 1965. The comfort movements of the Anatidae. Behaviour 25: 120-220.

MILLER, A. H., 1932. Observations on some breeding birds of El Salvador, Central America. Condor 34: 8-17.

OBERHOLSER, H. C., 1974. The bird life of Texas. University of Texas Press, Austin and London. 1069 p.

PALMER, R. S., 1962. Handbook of North American Birds. Volume 1. Yale University Press, New Haven and London. 567 p.

PAULSON, D. R., 1969. Commensal feeding in grebes. Auk 86: 759.

PETERS, J. L., 1931. Check-list of birds of the World. Volume 1. Harvard University Press, Cambridge. 345 p.

SANDERS, S. W. H., 1967. The osteology and myology of the pectoral appendage of grebes. Unpublished Ph.D. dissertation. University of Michigan. 281 p.

SCHMIDT, H., 1970. Parringadferden hos gråstrubet lappedykker. Naturens verden 1970: 363-374.

SIEGFRIED, W. R. 1971. Feeding association between *Podiceps ruficollis* and *Anas smithii*. Ibis 113: 236-238.

SLUD, P., 1964. The birds of Costa Rica. Bulletin of the American Museum of Natural History 128: 1-430.

SMITHE, F. B., and R. A. PAYNTER, JR., 1963. Birds of Tikal, Guatemala. Bulletin of the Museum of Comparative Zoology 128: 245-324.

STETTENHEIM, P., 1974. The bristles of birds. Living Bird 12: 201-234.

STORER, R. W., 1963a. Observations on the great grebe. Condor 65: 279-288.

STORER, R. W., 1963b. Courtship and mating behavior and the phylogeny of the grebes. Proceedings of the thirteenth International Ornithological Congress : 562-569.

STORER, R. W., 1967. The pattern of downy grebes. Condor 69: 469-478.

STORER, R. W., 1969. The behavior of the horned grebe in spring. Condor 71: 180-205.

STORER, R. W., 1971. The behaviour of the New Zealand dabchick. Notornis 18: 175-186.

STORER, R. W., 1975. The status of the Least Grebe in Argentina. Bulletin of the British Ornithologists' Club 95: 148-151.

STORER, R. W., W. R. SIEGFRIED, and J. KINAHAN, 1975. Sunbathing in grebes. Living Bird 14 (in press).

WETMORE, A., 1965. The birds of the Republic of Panama. Part 1. Smithsonian Miscellaneous Collections 150. 483 p.

ZIMMERMAN, D. A., 1957. Display of the Least Grebe. Auk 74: 390.

APPENDIX

Stomach contents of Least Grebes

RWD 14681, adult male, La Avellana, Dept. Sta Rosa, Guatemala, 10 April 1973. Stomach contents: 1 dermestid beetle, 1 probably terrestrial beetle, 2 or 3 probable true bugs, upwards of 50 ants, fish bones, many feathers.

RWD 14690, adult female, 4 mi. SW of La Avellana, 28 April 1973. Stomach contents: 2 bugs, 3 beetles (at least 2 scarabids), 5 ants, fish bones, many feathers.

RWD 14691, adult female, same locality and date. Stomach contents: about 30 shrimp, 1 crab, 5 bugs, 2 beetles, 4 flies, 13 ants, few feathers.

RWD 14999, adult male, La Avellana, Dept. Sta Rosa, Guatemala, 2 May 1974. Stomach contents: 122 ants, few feathers (most or all in pyloric plug).

RWD 15034, adult male, 6 km NW of Garita Chapina, Dept. Juliata, Guatemala, 5 May 1974. Stomach contents: 2 dragonflies, probably Libellulidae, 1 water boatman nymph, 8 hydrophilid beetles, 1 beetle, probably a weevil, 12 ants, some winged, 2 nematodes, probably parasitic, few feathers (most or all in pyloric plug).

RWD 14527, adult male, 42 miles south of Tecolutla, Veracruz, Mexico, 31 March 1973. Stomach contents: 3-4 water striders, 1 probable backswimmer, 3-4 probable gyrinid beetles, 1 scarabid, 1 weevil, 6 ants, 6 large, hairy spiders, a few probable fish ribs, few feathers (most or all in a pyloric plug).

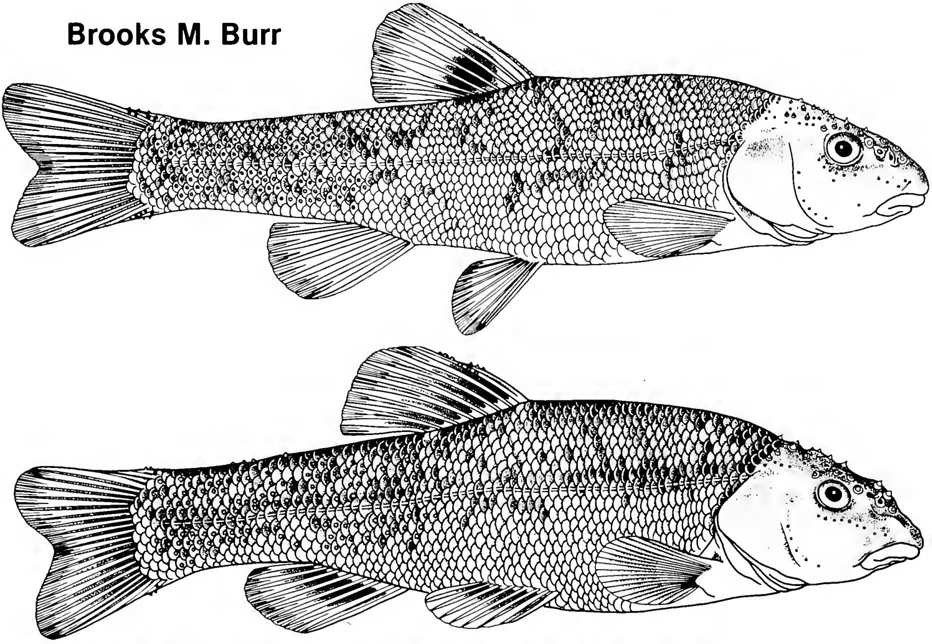
RWD 14766, first-year female, 7 miles east of Río San Pedro y Pablo, Campeche, Mexico, 2 April 1973. Stomach contents: 2 crayfish, 4 bugs (including 1 giant water bug), 2 beetles (including 1 weevil), 1 ant, moderate number of feathers.

RWD 14767, first-year male, same locality and date. Stomach contents: 2 large shrimp, 1 beetle, few feathers.

Bird Division, Museum of Zoology, The University of Michigan, Ann Arbor, Michigan, 48109.

A REVIEW OF THE MEXICAN STONEROLLER, *CAMPOSTOMA ORNATUM* GIRARD (PISCES: CYPRINIDAE)

Brooks M. Burr



TRANSACTIONS

OF THE SAN DIEGO
SOCIETY OF
NATURAL HISTORY

VOL. 18, NO. 7 30 MARCH 1976

A review of the Mexican Stoneroller, *Campostoma ornatum* Girard (Pisces: Cyprinidae)

Brooks M. Burr

ABSTRACT.—A morphological study of the Mexican stoneroller, *Campostoma ornatum*, from throughout its range revealed that the species is distinctive in the genus *Campostoma* in having very small scales, breeding tubercles in the females as well as the males, and intestinal loops that rarely coil around the bladder. *C. ornatum* is extremely variable both in meristics and morphometrics, although populations from the southern part of the range tend to be more consistent in having fewer scales and deeper bodies. Because of its extreme and rather irregular variability, from drainage to drainage, intraspecific taxa, including *C. ornatum pricei* are not recognized. *C. ornatum* displays several generalized characters and is probably close to the ancestral stock of the genus.

RESUMEN.—Un examen morfologico del "Mexican stoneroller," *Campostoma ornatum*, a lo largo de su distribución geográfica, reveló que esta especie se caracteriza en el género *Campostoma* por poseer escamas muy pequeñas, tubérculos reproductores en las hembras al igual que en los machos, y aros intestinales que raramente rodean la vejiga natatoria. *C. ornatum* es extredamente variable en ambas merística y morfometría, aunque poblaciones de la parte sur de su distribución tienden a ser mas consistentes en el sentido de que tienen menos escamas y cuerpos mas llenos. Debido a su extrema y bastante irregular variabilidad de drenaje en drenaje, taxones intraespecíficos, incluyendo a *C. ornatum pricei* no se pueden reconocer. *C. ornatum* exhibe varias características generalizadas que probablemente lo coloquen filogenéticamente cerca del antepasado de dicho género.

The genus *Campostoma* is a closely allied group presently comprising three species, all of which are morphologically similar. The wide-ranging North American *C. anomalum* (Rafinesque) is in part sympatric with *C. oligolepis* Hubbs and Greene in the upper Mississippi valley (Burr and Smith, 1976), but also occurs as far south as northeastern México. A third species, *C. ornatum* Girard occurs chiefly in west-central México and is allopatric to *C. anomalum*.

Published information on the species is primarily limited to faunal reports and checklists. An exception is Rutter's (1896) observation that in specimens from Rucker Canyon, Arizona, and the Río Conchos, Chihuahua, the intestinal loops do not encircle the air bladder, an observation of considerable interest since the generic diagnosis has largely been based on this peculiarity. This statement and the questionable status of the nominal *C. ornatum pricei* Jordan and Thoburn prompted a review of the species.

In this paper I summarize the systematics and distribution of *C. ornatum*, compare the species with other members of the genus, and discuss its geographic variation.

METHODS

Specimens were assembled from all localities known for *Campostoma ornatum*, except for a few records for which the specimens could not be located. Counting and measuring procedures followed Hubbs and Lagler (1958: 19-26) except that number of scales above the lateral line was from lateral line to lateral line just anterior to the dorsal fin. Terminology and counting procedures for the cephalic lateral line follow Illick (1956). Measurements were made with dial calipers to the nearest 0.1 mm. All measurements were converted arithmetically. Measurements are expressed in thousandths of standard length (SL) or of head length (HL). Proportional measurements were limited to adult specimens measuring 60 mm or more in SL. Gill rakers were counted on the right side of the body and were made on the first arch.

San Diego Soc. Nat. Hist., Trans. 18(7):127-144, 30 March 1976

TABLE 1. Frequency distribution of lateral line scales in selected populations of *Campostoma ornatum*.

Drainage	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	N	Mean
Río Sonora													2	2	4	3	1	2	1	3	2											20	69.8
Río Moctezuma	1		1	2	3	2	2			2	2	1	3	1	1		1															22	61.7
Río Yaqui									1			5	5	6	3	3	7	6	7	2	7	4	2				1					59	70.3
Río Papigochic									3		2	7	6	7	5	8	4	1	4	3			1	1								52	65.1
Río Casas Grandes									1	3		2	4	4	4	3	4		4	2	1											32	68.1
Río del Carmen																		1	4	4	3	1	1	2	2	2						20	74.6
Río Santa Isabel																			2		2	4	5	3	4	3	3	1		1	1	30	77.4
Río Grande												1		3	3		5	3	3	4	6	4	2	2	2							38	72.3
Río Conchos														4	3	2	5	4	6	6	4	5	2	1	1	2	2					47	72.5
Río Urique													2		2	1			4	2	3	2	2	2								20	72.5
Río Matamoros												1	1	3		3	4	6	2	2	1	1			1							25	70.5
Río Valle de Allende												2	1	2	2	3	4	2	3	1		1	1	1								23	69.2
Río Florido												1	3	1	6	4	12	2	7	4	7	4	3	2			1	1				58	71.6
Río Nazas		1	1		4	3	7	6	5	6	6	9	5	5	4	2			3													67	63.5
Río Miravalle			1		3	1	3		1	1	3		2	3	1	1																20	62.8
Río Trujillo					3	1	5	2	2	5	6	6	8	4	3	3	1	1														50	64.3

Material deposited in the following institutions was examined (abbreviations used throughout the text): Arizona State University (ASU), California Academy of Sciences (CAS), Stanford University (SU), now at CAS, Field Museum of Natural History (FMNH), Illinois Natural History Survey (INHS), University of Kansas, Museum of Natural History (KU), University of Texas, Texas Natural History Collection (TNHC), Tulane University (TU), Universidad Autónoma de Nuevo León (UANL), University of Michigan Museum of Zoology (UMMZ), and National Museum of Natural History (USNM).

MEXICAN STONEROLLER
Campostoma ornatum Girard

Campostoma ornatum Girard, 1856: 176 (original description; Chihuahua River and a tributary a few miles long, México). Girard, 1859: 41, pl. 25, figs. 1-4 (redescription; synonymy). Günther, 1868: 183 (brief description). Jordan and Copeland, 1876: 146 (listed). Jordan, 1878: 418 (listed). Jordan and Gilbert, 1883: 149 (diagnosis). Jordan, 1885: 808 (listed). Evermann and Kendall, 1894: 75, 83, 86, 89-91, 98 (listed; discussion of type). Woolman, 1894: 57, 61 (localities; tabulated measurements). Jordan and Evermann, 1896a: 205 (description; in key). Jordan and Evermann, 1896b: 243 (listed). Rutter, 1896; 259-260 (description; *C. pricei* a synonym; intestine not coiled around air bladder). Evermann and Goldsborough, 1902: 146 (Sierra Madre Mountains, Chihuahua and Colonia García, México). Meek, 1902: 41, 123 (habitat; localities in México; general range). Meek, 1903: 774, 776 (distributional pattern in México). Meek, 1904: xxxi, xxxii, xxiv, xxxviii, 41-42 (description; synonymy; in key; range; ripe female in May). Regan, 1906-1908: 149 (description; synonymy; range). Pratt, 1923: 65 (brief description; in key; Arizona). Fowler, 1924: 389 (in part). Jordan, Evermann, and Clark, 1930: 146 (in checklist). De Buen, 1940: 23 (synonymy; range). Hubbs, 1940: 10 (Terlingua Creek, Big Bend Region, Texas). De Buen, 1947: 272, 298, 319-320, 325 (synonymy; range; zoogeography). Alvarez, 1950: 46 (in key). Baughman, 1950: 130 (Texas). Jurgens and C. Hubbs, 1953: 13 (listed; range in Texas). Knapp, 1953: 51, 59 (in key; probable occurrence in Texas). C. Hubbs, 1954: 284 (Tornillo Creek, Texas). C. Hubbs, 1957a: 99 (Chihuahuan Biotic Province, Texas). C. Hubbs, 1957b: 7 (listed; range in Texas). C. Hubbs and Springer, 1957: 313 (mentioned). Eddy, 1957: 71 (key characters; figure). Moore, 1957: 138 (in key; range in United States). Miller, 1958: 214 (*C. ornatum* dispersed from Río Grande to Río Yaqui by stream capture). C. Hubbs, 1958: 7 (listed; range in Texas). Bailey et al., 1960: 13 (in checklist). Branson, McCoy, and Sisk, 1960: 220 (localities in Sonora, México). C. Hubbs, 1961: 7 (listed; range in Texas). John, 1964: 112 (Rucker Canyon, Ari-

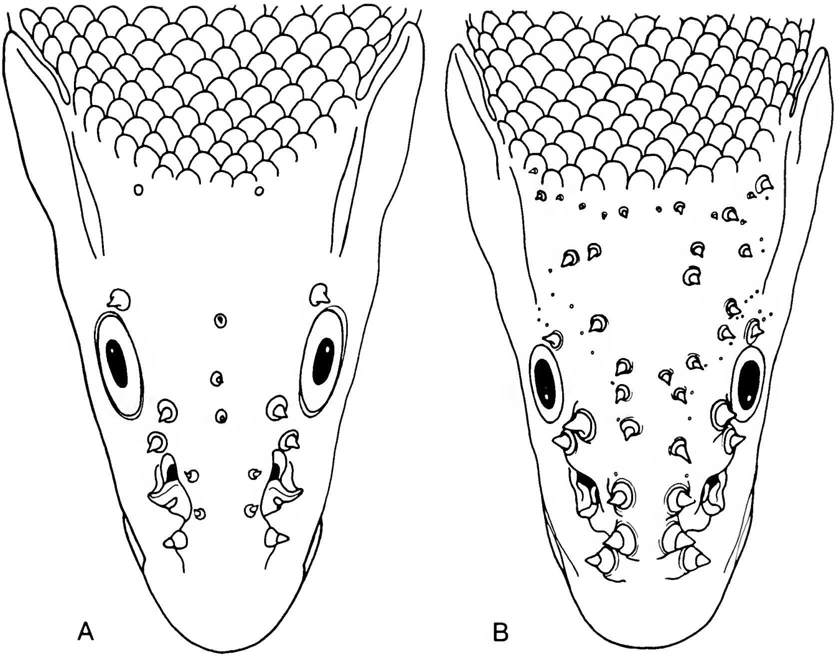


Fig. 1. Head tuberculation in breeding *Campostoma ornatum.* A) Female (UMMZ 189085) B) Male (UMMZ 161715).

zona). Miller and Lowe, 1964: 142 (range in Arizona; *C. pricei* a synonym). Anonymous, 1966: F-39 (peripherally endangered in United States). Metcalf, 1966: 139 (origins; zoogeography). Anonymous, 1968: FP-39 (peripherally endangered in United States). Minckley and Deacon, 1968: 1430 (unrealistic inclusion as an endangered species since it is only peripheral to the United States). Moore, 1968: 89 (in key; range in United States). Contreras-Balderas, 1969: 297 (Río Concepción, Sonora). Alvarez, 1970: 67 (in key; range in México). Bailey et al., 1970: 19 (in checklist). Minckley, 1971:184 (in key). Pflieger, 1971: 377 (ancestral stock). C. Hubbs, 1972: 3 (listed; range in Texas). Miller, 1972: 242 (rare in Arizona and Texas). C. Hubbs and Wauer, 1973: 376-379 (seasonal changes in Tornillo Creek, Texas). Anonymous, 1973: 69 (peripherally threatened in United States). Minckley, 1973:141 (in synonymy).

Campostoma pricei Jordan and Thoburn *in* Jordan and Evermann, 1896a: 205 (original description; Rucker Canyon, Chiricahua Mountains, southern Arizona). Jordan and Evermann, 1896b: 243 (listed). Rutter, 1896: 259-260 (synonym of *C. ornatum*). Meek, 1904: 41 (synonym of *C. ornatum*). Regan, 1906-1908: 149 (synonym of *C. ornatum*). Jordan, Evermann, and Clark, 1930: 147 (in checklist). Schrenkeisen, 1938: 156 (Arizona). De Buen, 1940: 23 (synonym of *C. ornatum*). Hubbs, 1940: 10 (reference to type-locality). De Buen, 1947: 272 (synonym of *C. ornatum*). Böhlke, 1953: 30 (holotype SU 1177). Moore, 1957: 138 (Rucker Canyon, Arizona). Miller and Lowe, 1964: 142 (synonym of *C. ornatum*). Moore, 1968: 89 (Rucker Canyon, Arizona). Minckley, 1973: 141 (in synonymy).

Campostoma ornatum pricei: Minckley, 1973: 82, 141-142 (brief description; habitat; in key; male and female figured; distribution and extinction in Arizona). McNatt, 1974: 275-276 (status in Río Yaqui, Arizona).

Types.—Girard (1856) did not designate a type for *Campostoma ornatum,* but in a later publication (Girard, 1859) cited a syntypic series with data as follows: USNM 77 (4 specimens) Chihuahua River (=Río Conchos), and a tributary only a few miles long, México, collected 1855 by John Potts. One set of pharyngeal arches (USNM 2682) is part of the syntypic series (Girard, 1859). An additional label in the jar (USNM 15388) is also present but is apparently in error. Girard's

TABLE 2. Frequency distribution of body circumferential scales in selected populations of *Campostoma ornatum*.

Drainage	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	N	Mean
Río Sonora									1	1	3	6	3	2	1	1	1	1				20	55.8
Río Moctezuma					1	3	5	4	4		2											19	50.8
Río Yaqui								1	14	11	11	11	5	4		1						58	53.9
Río Papigochic					1			1	9	9	13	2	3	6	1	2	1					48	54.2
Río Casas Grandes							1		7	6	6	8	2	2								32	53.8
Río del Carmen								1	4	3	3	4	2	1	1	1						20	54.3
Río Santa Isabel													2	1	5	4	7	4	3	3	1	30	59.9
Río Grande									5	6	10	5	6	1	2		1					36	54.5
Río Conchos									5	5	11	5	10	4	5	1	1					47	55.1
Río Urique							1	1	4	3	4	5	1	1								20	53.6
Río Matamoros									1	3	4	4	3	4	5	1						25	55.7
Río Valle de Allende									7	5	5	3	1	1	1							23	53.7
Río Florido							1	1	1	3	10	9	9	10	6	4	4					58	55.9
Río Nazas	1	2	2	7	15	13	11	8	3	1	3	1										67	49.2
Río Miravalle		3	2	4	6	2	3															20	47.6
Río Trujillo			2	1	2	7	7	7	5	7	6	3	3									50	52.5

(1859) drawing of one of the syntypes is said to be "life size" and measures about 105 mm SL. While it is not specifically designated as the type, one of the USNM series measures very close to Girard's illustration (ca. 105.5 mm SL). It is also the only specimen with the pharyngeal arches removed. The other three specimens are much larger or smaller (91-114 mm SL). Based on these data, the above-mentioned specimen is herewith designated lectotype. The other three syntypes become paralectotypes (USNM 214999).

Counts for the lectotype are as follows: lateral line scales 76; body circumferential scales 52; predorsal scales 32; and caudal peduncle scales 27. The head tubercle pattern is as in Figure 1; a black band of pigment occurs in the anal, dorsal, pelvic, and pectoral fins.

The holotype of *Campostoma pricei* Jordan and Thoburn (SU 1177) is a full nuptial male 76.7 mm SL, collected by William W. Price from Rucker Canyon, Chiricahua Mountains, Cochise County, southern Arizona. Counts for the holotype are as follows: lateral line scales 72; body circumferential scales 53; predorsal scales 32; anal rays 7, not 8 (Jordan and Evermann, 1896a). The chief differences used for distinguishing *pricei* from *C. ornatum* were head length (=.278 standard length) and snout length (=.102 standard length). In the holotype the values for head length and snout length are larger than those of other breeding males measured from Rucker Canyon; however, they are not significantly different from other populations.

Diagnosis.—A species of *Campostoma* distinguished by a combination of the following characters: lateral-line scales 54-84 (usually 58-77; Table 1); body circumferential scales 44-64 (usually 47-60; Table 2); usually with 20-23 scales above the lateral line; predorsal scales 25-40 (usually 27-36; Table 3); caudal peduncle scales 23-32 (usually 24-31; Table 4); sum of lateral-line and body circumferential scales 104-145 (usually 107-135; Table 5); gill rakers on the first arch 14-20 (Table 6). Breeding males without tubercles on the nape and anterolateral portions of the body (Fig. 1). Gravid females often with tubercles (Fig. 1). Head long with somewhat acute snout (Fig. 2). Intestinal loops rarely coiling around posterior portion of air bladder.

TABLE 3. Frequency distribution of predorsal scales in selected populations of *Campostoma ornatum*.

Drainage	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	N	Mean
Río Sonora						1	4	5	2		1	1					14	32.2
Río Moctezuma				1	2	1	2	1	1								8	30.4
Río Yaqui						7	15	14	3	5	5	1					50	32.1
Río Papigochic					1	11	14	11	3	5							45	31.4
Río Casas Grandes						4	13	6	7	2							32	31.7
Río del Carmen						1	3	3	8	3				1	1		20	33.1
Río Santa Isabel							3	4	6	5	3	6	2	1			30	34.1
Río Grande						1	5	4	2	5	2	1	1				21	33.0
Río Conchos						1	6	4	9	8	5	3	1	1			38	33.4
Río Urique						1	2	5	4	1	4	3					20	33.3
Río Matamoros						4	5	6	6	2							23	31.9
Río Valle de Allende					1	4	3	3	3	2	3	2	1				22	32.7
Río Florido						2	4	6	4	8	5	1	1	1		1	33	33.5
Río Nazas	2	2	10	11	17	15	7	3									67	28.9
Río Miravalle		1	4	2	2	4	1										14	28.5
Río Trujillo			6	8	9	10	10	4	2	1							50	29.7

Description.—Scale counts, gill raker counts, and body proportion values appear in Tables 1 to 7. General physiognomy, pigmentation, and tuberculation are shown in Figure 2, details of male and female head tubercle patterns in Figure 1. An extremely variable species of moderate size (the largest specimen examined is 114 mm SL).

Dorsal and pelvic rays number 8, with no deviations observed. Caudal rays are usually 19, sometimes 18 or 20. Anal rays number 7, rarely 8. Pectoral rays number 16 to 18. Body circumferential scales number (18) 20-23 (24), modally 22,

TABLE 4. Frequency distribution of caudal peduncle scales in selected populations of *Campstoma ornatum*.

Drainage	23	24	25	26	27	28	29	30	31	32	N	Mean
Río Sonora		1	3	2		2					8	25.9
Río Yaqui		2	1	4	9	4		1			21	26.8
Río Papigochic		2	3	5	8	7	4	3	1		33	27.3
Río Casas Grandes			5	2	3	1	1				12	26.3
Río del Carmen				5	4	3					12	26.8
Río Santa Isabel							8	5	8	5	26	30.4
Río Grande				2	5	4	3	1			15	27.7
Río Conchos				3	3	5	3	2	2	1	19	28.4
Río Matamoros		1	3	7	5	2	1	1			20	26.6
Río Valle de Allende				2	4	3	2	1			12	27.7
Río Florido		1	1	5	6	7	3	6		1	30	27.9
Río Nazas	1	1	7	9	5	5	4	1			33	26.6
Río Trujillo	2	6	13	7	7						35	25.3

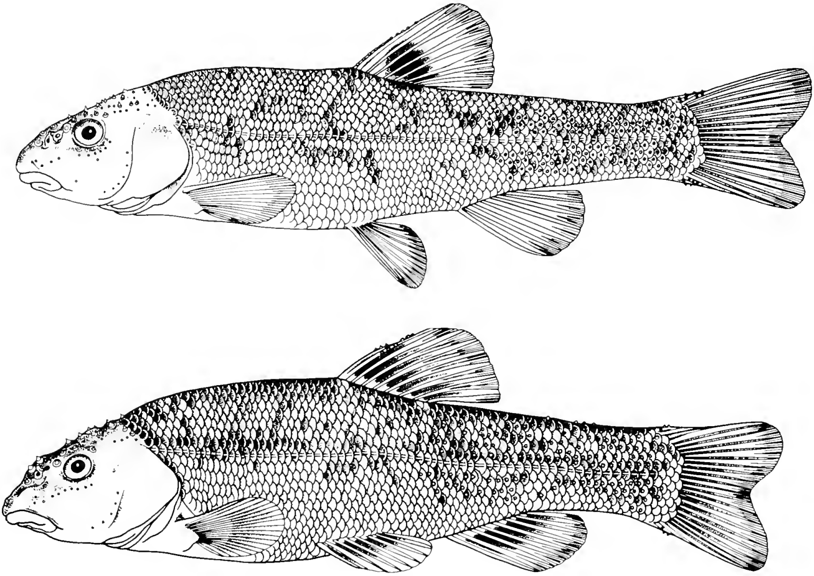


Fig. 2. Breeding adult males of *Campostoma ornatum.* Upper) UMMZ 157248, 84.0 mm SL; Río Sonora dr., 9 March 1940. Lower) UMMZ 189085, 91.5 mm SL; Río Nazas dr., 8 April 1968. Note differences in body proportions and extent of pigmentation in fins.

above the lateral line and (25) 27-34 (38) below (mode varying considerably from drainage to drainage). Caudal peduncle scales are 10 to 15 above the lateral line and 11 to 15 below. The pharyngeal tooth count from throughout the range is 0,4—4,0 in 30 specimens. Gill rakers are moderately long, well separated, and number 14 to 20.

The snout is usually acute and rounded, and projects slightly beyond the mouth. The mouth is ventral and rounded, with the lower lip having a distinct cartilaginous ridge not covered by skin. The premaxilla is protractile. The eye is small and located rather high on the head. The body is rather stout. Fins are of moderate size and angulation. The anterior rays do not exceed the length of the posterior rays in the depressed dorsal fin. The pelvic fins in breeding males usually reach the insertion of the anal fin. The posterior border of the dorsal fin is usually straight, that of the anal fin is rounded. The dorsal fin is inserted directly above or slightly behind the pelvic fin insertion.

The lateral line is straight and is usually complete, but occasionally pores are lacking on posterior scales. The cephalic lateral line is usually complete, although the supratemporal canal may be slightly interrupted at the midline or to one side. Supratemporal pore counts range from 5 to 8; the supraorbital canal pores, from 8 to 11; infraorbital canal pores, from 13 to 17; preoperculomandibular canal pores, from 9 to 11.

The intestine is variable in length (usually 150-200 mm in specimens measuring 65-70 mm SL), but in this species, contrasting with the other two, loops were found to encircle the posterior portion of the air bladder in only 12 of 60 (20%) specimens checked. Two patterns are evident: the intestine coiling around the air bladder similar to that of *C. anomalum* (Kraatz, 1924) only with the coiling less extensive; an antero-posterior folding below or to the side of the air bladder

TABLE 5. Frequency distribution of the sum of lateral line and circumferential scales in selected populations of *Campostoma ornatum*.

Drainage	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	N	Mean
Rio Sonora																1	1	1	3	4	1	1		2		2	1	1			2												20	125.4
Rio Moctezuma			2	3	3	1				2	1	2		1		1	1	1	1																								19	112.4
Rio Yaqui														1	3	3	4	5	5	3	7	3	6	3	6	4	2	2			1												58	124.3
Rio Papigochic										1			1		4	7	6	6	2	5	4	4	3			2	1		1	1													48	122.2
Rio Casas Grandes										1	1		1		2	1	5	3	4	2	3	4	2	2		1																	32	121.9
Rio del Carmen																					2		3	3	3	2	2		2			3											20	128.9
Rio Santa Isabel																											1	3	1		3	4			5	4	3	1	3			2	30	137.3
Rio Grande																1		2	2	3	1	1	5	5	3	3	3	4	2			1											36	127.0
Rio Conchos																		1	2	4	6	4	3	4	4	4	4	6	1	1				1	1	1							47	127.7
Rio Urique																1	2	1	1	1	1		3	2	2		2	3	1														20	126.1
Rio Matamoros																1	2	2			3	1	4	2	5	2			1	1		1											25	126.2
Rio Valle de Allende													1			4	2	3	1	3	3	1	2			1	1			1													23	122.9
Rio Florida													1				1		4	3	7	4	4	4	8	5	5	2	2	4	1	1					1	1					58	127.6
Rio Nazas	2	1	2	3	5	3	5	4	2	8	8	7	4	5	3	1	1	1	1	1																							67	112.9
Rio Miravalle	4	1	1	2	1		2			1	2	2	3	1																													20	110.3
Rio Trujillo				1	1	3	2	1	2	3	2	2	2	9	3	3	4	4	2	2	1	1		1																			50	114.5

with one or at most two loop folds around the air bladder but not entirely encircling it. These conditions are evidently the result of the intestine being shorter in this species than in the other two. Both intestinal conditions may occur in one sample but do not vary geographically. Rutter (1896), upon examining specimens from Rucker Canyon, Arizona, and the Río Conchos, Chihuahua, reported that in none did intestinal loops entirely encircle the air bladder. The peritoneal color ranges from dark brown to black.

Coloration is extremely variable both ontogenetically and among adults. Most adults have the characteristic mottled coloration of the genus as described by Cross (1967) for *C. anomalum*. Juveniles tend to lack heavy mottling but often have a dark lateral stripe extending from the snout to the caudal peduncle, termi-

TABLE 6. Frequency distribution of number of gill rakers on the first arch in selected populations of *Campostoma ornatum*.

Drainage	14	15	16	17	18	19	20	N	Mean
Río Sonora				4	3	4	3	14	18.4
Río Yaqui		3	3	8	4	2		20	17.0
Río Papigochic	3	5	7	4	1			20	15.8
Río Santa Isabel	2	2	7	7	2			20	16.3
Río Florido	2	2	8	5	2	1		20	16.3
Río Nazas		4	7	5	2	1	1	20	16.6
Río Trujillo	1	8	8	3				20	15.7

nating in a slight basicaudal spot. Mottling when developed in juveniles is usually dorsal (within and above the lateral stripe). Fins are usually transparent in both sexes during non-breeding seasons but a black band of pigment may appear in the dorsal fin several months prior to, and continuing through, the spawning season.

Nuptial tuberculations.—Campostoma ornatum contrasts with the two other species of *Campostoma* in having no tubercles on the nape or on the anterolateral sides of the body, in having small granular tubercles on the posterolateral sides of the body, and in having head tubercles on females.

Tubercle patterns on the head are very similar to those in *C. anomalum* (Burr and Smith, 1976: Fig. 3) and are large and erect (Fig. 1). The sides of the head (cheek and opercle) usually lack tubercles. The lower edge of the operculum, gill membranes, and the area dorsal to the upper lip are covered with minute whitish tubercles. Body tuberculation begins around the posterior edge of the dorsal fin (sometimes slightly before) and extends posterolaterally on to the caudal peduncle, often outlining the upper and lower rudimentary caudal rays. Most scales above the lateral line bear one tubercle per scale although some individuals have two per scale. The scales on the caudal peduncle below the lateral line have one tubercle per scale. The dorsal fin is tuberculate along the anterolateral edges of the rudimentary ray, and the branches of rays 2 through 4 are tuberculate. Pectoral rays 2 through 4 have a single file of tubercles basally, and the 2nd and 3rd rays have a double file distally; the 5th pectoral ray sometimes is sparsely tuberculate. The pelvic and anal fins lack tubercles.

On large breeding males (about 70 mm SL) a crescent-shaped row of 3 retrorse tubercles lies between the nostrils on a swollen portion of the snout. Another line of 2 to 4 tubercles arises anterodorsally to the eye and extends posteriad, with many small tubercles between the eyes and on the head, sometimes bordering the edge of the nape. In small specimens (40-50 mm SL) the tubercles between the nostrils and above the eye are usually the only ones present, although the pectoral fins may be almost fully tuberculate.

This is the only species of *Campostoma* in which tubercles have been reported on females. Characteristically, females of *C. ornatum* have 1 to 3 small white tubercles in a crescent-shaped row above the nostril (the snout does not become swollen) and from 1 to 4 tubercles in a line around the orbit. A few tubercles are scattered on the head and between the eyes (not as extensively as in males). No tubercles have been observed elsewhere on the fins or bodies of females. Tubercles have been recorded only on females longer than 50 mm SL and usually gravid.

Breeding coloration.—In preserved breeding males, the dorsal and anal fins often have a velvet-black medial band (Fig. 2). On the pectoral and pelvic fins black pigment is heavily concentrated on the distal edges and becomes less intense proximally. The black caudal spot lengthens transversely and often appears as a dark vertical band of pigment.

On a color slide of a breeding male (courtesy of R. R. Miller, pers. comm.), the distal half of the dorsal fin is milky white, basally the fin is orange, and medially it is velvet-black. The anal fin is similar to the dorsal fin but has less black. The caudal fin is mostly milky white, with black and orange confined to the basal one fourth. The edge of the shoulder girdle is blackened. Jordan and Thoburn, in their original description of the nominal *C. pricei* (Jordan and Evermann, 1896a), described breeding coloration as "fins all flushed with red (in spring males)." Girard (1859) stated that the fins in *C. ornatum* have black patches at their bases and are otherwise orange or yellowish brown. Apparently, breeding coloration is similar to that described for *C. anomalum* (Cross, 1967).

In breeding females only the dorsal fin develops a black band. No information is available on orange-red coloration in females.

Sexual dimorphism.—No sexual dimorphism among meristic characters was found. Males attain a greater length than females; the largest male examined measures 114 mm SL; the largest female, 80 mm SL. The dorsal, pectoral, pelvic, and anal fins are noticeably more expanded and longer in breeding males than in gravid females. In addition, the lips and the snout region of the breeding males become swollen during the breeding season. These characteristics are not expressed among females. In fully gravid females (as in ASU 6276 and UMMZ 157248) the body becomes greatly distended in depth and width.

Geographic variation.—Campostoma ornatum is noteworthy for being one of the most variable cyprinids thus far investigated in México, and yet is remarkably conservative throughout its range in such features as pharyngeal tooth number, fin ray counts, and several body proportions. Frequency distributions for meristic characters examined by drainage systems are given in Tables 1 to 6. Meristic characters were analyzed initially by river system, but have been combined into major drainages when no significant intradrainage variation was noted. Interdrainage variation in body proportions of breeding males is summarized in Table 7.

In general, mean values of meristic and morphological characters increase from south to north. The overall pattern is obscured by populations in the Río Santa Isabel (at General Trías) which have high scale numbers, and populations in the Río Moctezuma which have low scale numbers.

Gill-raker number and mottled body coloration tend to increase from east to west, whereas, body depth tends to decrease from east to west. Populations in the Ríos Nazas and Trujillo have the deepest bodies and have fewer mean numbers of gill rakers, whereas, the populations in extreme western México (Río Sonora) have the slenderest bodies and the highest mean number of gill rakers. Populations farther east than the Río Sonora, such as those in the ríos Yaqui, Casas Grandes, and Papigochic, are also heavily mottled and show a mean average increase westward in the number of gill rakers.

Scale counts are extremely variable within a stream system as well as between drainages but show some patterns, as described above. The two characters found to be the most variable were the numbers of lateral-line scales and of circumfer-

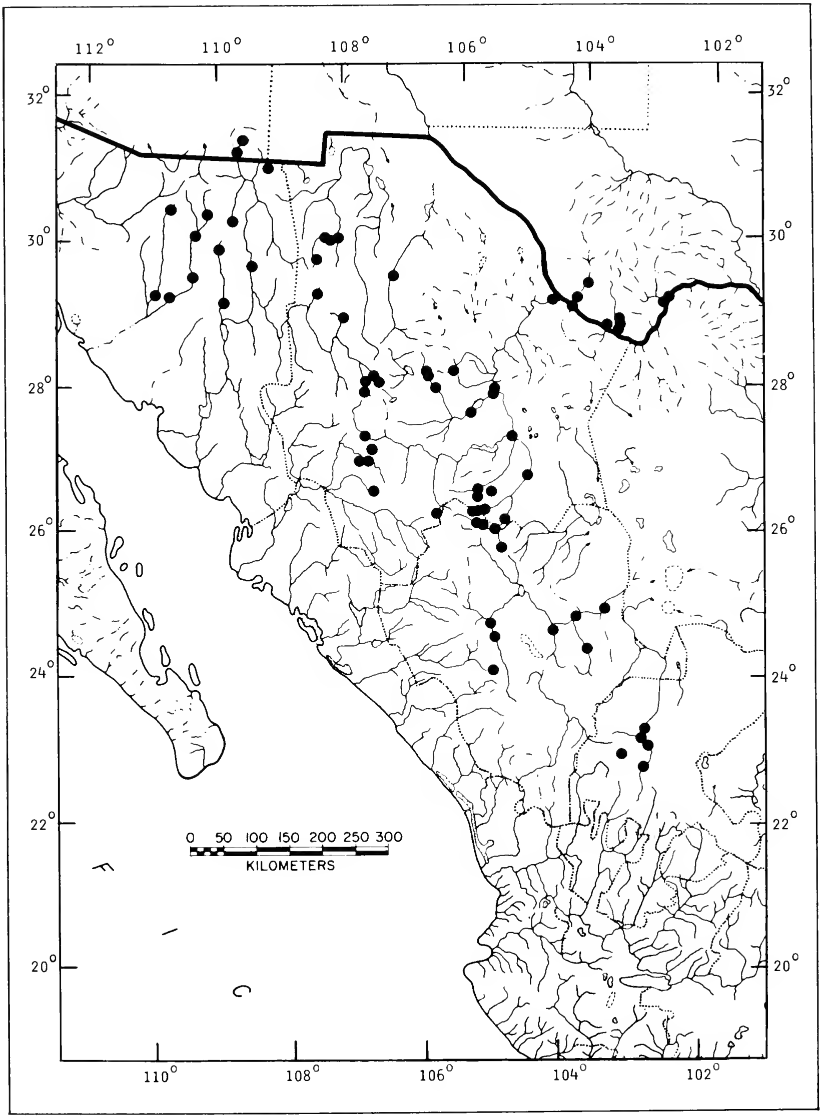


Fig. 3. The distribution of *Campostoma ornatum*. Broadly overlapping symbols are not plotted.

ential scales. The rather marked tendency for only southern populations (ríos Nazas, Trujillo, Miravalle) to have low scale numbers is obscured by the peculiar situation in the Río Moctezuma in which similar, low scale counts were found. The similarity between these geographically widely separated populations breaks down somewhat in number of body circumferential scales, number of predorsal

TABLE 7. Proportional measurements (expressed in thousandths of SL and HL) that show inter-drainage variation in full nuptial males of *Campostoma ornatum*. Range is given above, mean below.

Character	Río Nazas	Río Conchos	Río Papigochic	Río Casas Grandes	Río Sonora	Río Yaqui
N	11	12	14	11	5	7
SL (mm)	60.0-91.5 75.8	60.3-92.0 76.2	65.4-90.1 75.3	66.0-104.4 82.1	73.4-88.9 80.4	76.6-94.2 87.1
Body Depth/SL	231-263 248	209-254 231	203-263 239	216-263 236	215-246 227	209-254 230
HL/SL	253-311 283	234-298 267	261-289 281	264-296 273	265-283 271	256-284 273
Snout Length/SL	82-118 97	75-100 84	82-104 93	72-105 87	88-102 92	84-102 94
HL (mm)	16.8-26.8 21.5	15.7-24.5 20.3	18.6-24.9 21.1	17.4-28.7 22.5	19.7-23.6 21.8	20.2-26.2 23.8
Snout Length/HL	279-389 341	261-358 313	314-371 332	278-383 322	309-379 339	321-366 344
Head Width/HL	448-514 480	412-527 477	435-540 485	333-535 472	466-517 492	478-550 508
Interorbital Width/HL	170-231 199	155-218 181	175-226 195	155-256 201	174-204 191	200-218 207

scales, and number of caudal peduncle scales. The Río Moctezuma is a tributary of the Río Yaqui in which populations otherwise show typically northern scale counts. Although the more northern population in the Río Moctezuma has apparently been isolated from the Río Yaqui by an ancient lava field (of unknown geological age), the more southern population of this river transgresses this geological feature and thus its low scale numbers cannot be explained by geographic isolation.

The Río Santa Isabel population is unusual in having consistently high scale numbers; all individuals are heavily mottled, but they are intermediate in gill raker number. Again, there is no evident explanation for this combination of characters.

Southern populations of *C. ornatum* are deeper bodied and longer snouted, but this trend is disrupted by deeper bodied, long-snouted populations in the Río Papigochic. The most slender-bodied populations are those from the Río Sonora, which also have long heads and snouts. Rucker Canyon populations have rather large heads, expressed in characters measured such as bony interorbital width, head width, and head length, which in part were the primary differences used by Jordan and Thoburn to distinguish the nominal *C. pricei* from *C. ornatum* (Jordan and Evermann, 1896a). Body size was individually variable and specimens from all major drainages had similar SL measurements. The largest specimen examined (114 mm SL) was from the Río Conchos. The populations examined from the Río Grande, Río del Carmen and Río Moctezuma were all less than 66 mm SL, the majority less than 45 mm SL. Since there is some seasonal variation in population density in the Río Grande tributaries (C. Hubbs and Wauer, 1973; Gehlbach, pers. comm.) and the Río del Carmen often dries up (Meek, 1904), it may be that large adults do not ascend into these streams or perhaps the fluctuation in stream size does not produce enough resources for a substantial buildup of population size.

Coloration among adult populations from the ríos Nazas and Trujillo varies from almost no mottling to scattered dark patches of pigment both dorsally and ventrally. Populations from the ríos Yaqui, Sonora, and Casas Grandes have dark base colors and are heavily mottled. One population, from Río Sonora (UMMZ 157248), deviates considerably from the typical fin pigmentation pattern already described in that pigmentation is conspicuously lacking in all fins except the dorsal (Fig. 2). The males in this collection are highly tuberculate and the females are very ripe. The differences in coloration in *C. ornatum* are probably a response to contrasting environments as has recently been shown to be characteristic of other Mexican cyprinids (Hubbs and Miller, 1975).

Although some populations of *C. ornatum* maintain several features that initially appear to warrant taxonomic recognition, the species is subject to considerable local variation in an overall discordant pattern. Additional collections of breeding material and comparative life history studies may eventually justify a reappraisal of the status of the populations in the Río Nazas, Río Trujillo, Río Moctezuma and the Río Santa Isabel, but at present the variation defies any objective breakdown into species or even subspecies. Until more conclusive evidence is available, it is proposed that the species be treated as one highly variable entity and that use of the subspecific name *pricei* be discontinued.

Comparisons.—Campostoma ornatum differs trenchantly from *C. anomalum* and *C. oligolepis* (Table 8). The overlap in certain scale counts between *C. ornatum* and *C. anomalum* does not complicate the specific separation, since *C. anomalum* populations with the highest scale counts are generally those that approach the geographic range of *C. ornatum* where scale counts are high. *Campostoma anomalum* populations with low scale counts (the nominate *C. anomalum*) are geographically widely separated from those populations of *C. ornatum* having the lowest scale counts.

In addition to the differentiae treated in Table 8, *C. ornatum* and *C. anomalum* show subtle and average differences, best perceived after handling many specimens. *Campostoma ornatum* usually has a stouter, deeper body, a narrower head, narrower interorbital, and smaller mouth. It is also smaller.

Besides having more gill rakers, *C. anomalum* exhibits a rather high incidence of a peculiar structure of the rakers: they are Y-shaped, due to bifurcation at or near their tips. Each arch may bear from one to several anomalous rakers.

Campostoma oligolepis is readily distinghished from *C. ornatum* by its low scale numbers, its higher gill raker numbers and its unique tubercle pattern (Burr and Smith, 1976).

Distribution.—Campostoma ornatum is widepread in México, occurring on both slopes of the Sierra Madre Occidental, with its center of distribution in the states of Chihuahua, Sonora, and Durango. It is abundant in the Río Grande-Río Conchos drainages in Chihuahua and Durango (Río Florido) and the Río del Fuerte drainage in southwestern Chihuahua, as well as the streams that drain Lago de Guzman and Lago de Palos (Río Casas Grandes and Río del Carmen, respectively). In Sonora, it occupies tributaries of the Río Yaqui, Río Papigochic and the Río Sonora. Rather isolated populations occur in Durango in tributaries of the Río Nazas and Río Piaxtla, and in the state of Zacatecas in the Río Trujillo. Woolman's (1894) record for Río Lerma, Salamanca, Guanajuato is apparently in error (Meek, 1904). The species still occurs in the Big Bend Region of Texas, although it is absent during some months of the year in Tornillo Creek (C. Hubbs and Wauer, 1973) and Terlingua Creek (Frederich R. Gehlbach, pers. comm.). It is still common in Rucker Canyon and Leslie Creek, Arizona (McNatt, 1974), even though Minckley (1973) considered it extinct (specimens collected as late as 1974 have been examined from Rucker Canyon and Leslie Creek). The apparent preference of *C. ornatum* for headwater situations may account for its absence in collections from mainstream habitats.

Meek (1904) and Miller (1958) indicated that stream capture may perhaps explain the presence of Río Grande fishes in the Río Yaqui. According to Miller (1958), the Río Conchos may have been captured by the Río Papigochic (of the Yaqui system) 44.8 km (28 airline miles) south of Miñaca, Chihuahua. Also, the

TABLE 8. Summary of Primary Differences Distinguishing *Campostoma ornatum, C. anomalum,* and *C. oligolepis.*

Character	***C. ornatum***	***C. anomalum***	***C. oligolepis***
Circumferential scales	Usually 47-60	Usually 36-48	Usually 31-36
Scales above the lateral line	Usually 20-23	Usually 17-20	Usually 13-16
Predorsal scales	Usually 27-37	Usually 18-25	Usually 16-20
Lateral line scales	Usually 58-77	Usually 46-56	Usually 43-47
Sum of lateral line and circumferential scales	Usually 107-135	Usually 83-104	Usually 74-82
Tubercles on nape and antero-lateral sides of breeding males	Absent	Present	Present
Small tubercles on snout and above eye of breeding females	Present	Absent	Absent
Snout shape	Somewhat acute	More blunt and rounded	Longer and more globose
Intestinal loops coiling around air bladder	Very rarely	In majority of specimens (Kraatz, 1924)	In majority of specimens (Hubbs and Greene, 1935)
Gill rakers on first arch	14-20	21-35	19-26

Río Papigochic may have formerly formed the headwaters of the Río Casas Grandes. The circumstance that the *C. ornatum* morphotypes occurring in the Río Papigochic, Río Yaqui, and the Río Casas Grandes are very similar seems to substantiate this route of dispersal as highly probable.

Presumably, additional headwater crossovers, transfers, or migrations via periodically formed floodplains or overflow have also taken place, since *C. ornatum* (and other Río Grande types) are present in coastal drainages such as the Río Sonora, Río del Fuerte, and Río Piaxtla. It is noteworthy that portions of the headwaters of the Río del Fuerte (where *Campostoma* occurs) are presently in very close proximity to those of the Río Conchos, as are the headwaters of the Río Piaxtla and the Río Nazas. Meek (1904) stated that Lago de Mayran and Lago de Viesca (lakes drained by the Río Nazas and Río Trujillo, respectively) were probably connected at some former time and may have flowed northward toward the Río Conchos-Río Grande Basin, henceforth affording a dispersal route for *C. ornatum* into these drainages. Conant (1963) suggested that a succession of pluvial lakes during glacial stages may have permitted free water flow over a route similar to that suggested by Meek, thus allowing connections between the Río Grande fauna and that of ríos Nazas and Trujillo. Whatever the case, the lack of strong differentiation between ríos Nazas and Trujillo and the Río Conchos populations suggests that such dispersal has been relatively recent.

Although *C. anomalum* is known from tributaries of the Río Grande in Nuevo León, México (ríos Salado and San Juan; Alvarez, 1970), *C. ornatum* and *C. anomalum* have not been collected together and apparently maintain allopatric ranges.

Miller (1972) regarded *ornatum* as a threatened species in Texas and Arizona, presumably because of the restricted habitat (by reason of streams drying up) in these regions. Its depletion in numbers in recent years in Texas may also have been due to competition with *Fundulus kansae* Garman (C. Hubbs and Wauer, 1973). McNatt (1974) has summarized the information on its present status in Arizona, where he reported it to be abundant in Rucker Canyon. *C. ornatum* is recognized nationally in the United States as a peripherally threatened species (Anonymous, 1973).

In México, the species distribution has evidently undergone little change since Meek's (1904) report on the freshwater fishes of that region. *Campostoma ornatum* is presently abundant at many localities in north-central México (more than 300 specimens have been collected at several sites: KU 8411, UMMZ 182375, UANL 477, 544, 565); and all of the localities listed by Meek have been revisited by recent workers, and the species has been found to be still common. Collections with the fewest specimens were taken in the western coastal drainages such as those of rıos Sonora, Urique, and Piaxtla. Perhaps this rarity in numbers of specimens is a reflection of rather recent arrival to these drainages and the low reservoir of *Campostoma* populations that have not had time to build to suitable sizes.

Ecology.—Most Mexican stonerollers have been collected in riffles, chutes, and pools in creeks and rivers from warm, clear (sometimes slightly turbid) water and with bottom materials consisting largely of sand, pebbles, gravel, rock, and bedrock (rarely, mud). They have been taken more commonly in shallow water 10 cm to 1 m deep and apparently favor headwaters (Fig. 3). The largest collections come from gravel runs or gravel-bottom pools. Vegetation may be abundant to absent.

Nuptial males and gravid females were included in collections made from March to June in Chihuahua and Sonora and in February in Durango (Río Nazas). Males nearing full tuberculation were present in October collections made in Texas. Nuptial males ranged in size from 55-105 mm SL.

C. Hubbs and Wauer (1973) reported young individuals and breeding adults of *C. ornatum* present in January and half-grown young from May to June, in Tornillo Creek, Texas. They also remarked that the breeding season is probably in winter and spring. McNatt (1974) stated that in smaller pools in Rucker Canyon, Arizona, at least three age classes of *C. ornatum* were present. Cleared gravel areas, suggesting spawning activities, were observed in late May. The presence of tuberculate males and gravid females at different times of the year may indicate some temporal variation in spawning activities, although partially nuptial males in October and full nuptial males in February are probably only in preparation for an early spring spawning season. However, many Mexican cyprinids spawn in January and February (R. R. Miller, pers. comm.).

Cursory examination of intestinal contents suggests that the diet of *C. ornatum* is very similar to that of *C. anomalum* (Kraatz, 1923), consisting mainly of diatoms, bacteria, and algae. In the only report of predation on this species, McNatt (1974) found some in the stomachs of *Salmo gairdneri* Richardson.

Campostoma ornatum was found to be relatively free of external parasites except in one collection from the Río Trujillo (UANL 1130-51 individuals) which was heavily diseased with a monogenetic fluke. Large nemotode worms were entwined throughout the intestines of adults from Río Trujillo (UANL 1061).

Relationships.—*Campostoma ornatum* is most closely related to *C. anomalum.* The major features in which *C. ornatum* is divergent from *C. anomalum* are 1) development of smaller scales; 2) loss of tubercles on the nape; 3) development of head tubercles on females; 4) poorly developed intestinal coiling around the air bladder; and 5) more reduced body size. Of these features, 1 and 4 are clearly the primitive or generalized condition, and 2, 3, and 5 are probably primitive. *Campostoma oligolepis* displays several derived features (Burr and Smith, 1976) and is probably the most advanced member of the genus.

Specimens examined.—A list of specimens examined in this study may be obtained, for the cost of photocopies, from the author, the San Diego Natural History Museum Library, or the Carl L. Hubbs Library at Scripps Institution of Oceanography.

ACKNOWLEDGMENTS

I am grateful to Philip W. Smith and Lawrence M. Page for their helpful advice and aid, for criticism of the manuscript and numerous valuable suggestions. The drawings of *C. ornatum* were delineated by Alice Ann Prickett, University of Illinois, School of Life Sciences Illustrator. Larry Farlow, Survey Photographer, and Lloyd LeMere, Survey Illustrator, kindly executed the photographs and figures. Without the help of Robert Rush Miller, critical specimens could not have been obtained. I am deeply grateful to him for his prompt response to my requests concerning many of the aspects of this study and his enlightening comments concerning *C. ornatum*. Frederick R. Gehlbach supplied information on the depletion of Texas populations of the Mexican stoneroller. José A. Mari Mutt kindly translated the English abstract into Spanish. Field work in México was financed, in part, by a grant to Don G. Buth from the Theodore Roosevelt Memorial Fund of the American Museum of Natural History. The Mexican collecting permit was granted through the cooperation of the Mexican government. John E. Brezina and D. G. Buth ably assisted in the field.

I extend appreciation to the following curators or staff and their institutions for specimen loans and for providing laboratory assistance and/or facilities: Wendell L. Minckley (ASU, specimens sent through the assistance of R. R. Miller); William N. Eschmeyer and Tomio Iwamoto (CAS); Loren P. Woods and Robert K. Johnson (FMNH); Philip W. Smith and Lawrence M. Page (INHS); Frank B. Cross (KU); Clark Hubbs and Robert F. Martin (TNHC); Royal D. Suttkus and Michael M. Stevenson (TU); Salvadore Contreras-Balderas (UANL); Robert Rush Miller (UMMZ); Ernest A. Lachner (USNM).

LITERATURE CITED

ALVAREZ, J., 1950. Claves para la determinación de especies en los peces de las aguas continentales Mexicanas. Secretaría de Marina, Dirección General de Pesca e Industrias Connexas, México. 144 p.

ALVAREZ, J., 1970. Peces Mexicanos (claves). Instituto Nacional de Investigaciones Biológico Pesqueras, México, Serie Investigación Pesquera Estudio No. 1: 1-166.

ANON., 1966. Rare and endangered fishes of the United States, p. 1-41. *In* Endangered fish and wildlife of the United States. United States Department of the Interior, Bureau of Sport Fisheries and Wildlife, Resource Publication 34.

ANON., 1968. Rare and endangered fishes of the United States, p. 1-41. *In* Endangered fish and wildlife of the United States. Revised Edition. United States Department of the Interior, Bureau of Sport Fisheries and Wildlife, Resource Publication 34.

ANON., 1973. Threatened fishes of the United States, p. 5-72. *In* Threatened wildlife of the United States. United States Department of the Interior, Bureau of Sport Fisheries and Wildlife, Resource Publication 114.

BAILEY, R. M., E. A. LACHNER, C. C. LINDSEY, C. R. ROBINS, P. M. ROEDEL, W. B. SCOTT and L. P. WOODS, 1960. A list of common and scientific names of fishes from the United States and Canada. Second Edition. American Fisheries Society Special Publication No. 2: 1-102.

BAILEY, R. M., J. E. FITCH, E. S. HERALD, E. A. LACHNER, C. C. LINDSEY, C. R. ROBINS and W. B. SCOTT, 1970. A list of common and scientific names of fishes from the United States and Canada. Third Edition. American Fisheries Society Special Publication No. 6: 1-150.

BAUGHMAN, J. L., 1950. Random notes on Texas fishes. Part 1. The Texas Journal of Science 2: 117-138.

BÖHLKE, J. E.,1953. A catalogue of the type specimens of recent fishes in the Natural History Museum of Stanford University. Stanford Ichthyological Bulletin 5: 1-168.

BRANSON, B. A., C. J. MCCOY JR. and M. E. SISK, 1960. Notes on the freshwater fishes of Sonora with an addition to the known fauna. Copeia, 1960: 217-220.

BURR, B. M. and P. W. SMITH, 1976. Status of the largescale stoneroller, *Campostoma oligolepis*. Copeia, in press.

CONANT, R., 1963. Semiaquatic snakes of the genus *Thamnophis* from the isolated drainage system of the Río Nazas and adjacent areas in Mexico. Copeia 1963: 473-499.

CONTRERAS-BALDERAS, S., 1969. Perspectivas de la ictiofauna en las Zonas Aridas del Norte de México. International Centre for Arid and Semi-Arid Land Studies, Publication 3: 293-304.

CROSS, F. B., 1967. Handbook of fishes of Kansas. University of Kansas Museum of Natural History, Miscellaneous Publication No. 45: 357 p.

DE BUEN, F., 1940. Lista de peces de agua dulce de México. En preparación de su catálogo. Trabajos Estación Limnológica de Pátzcuaro No. 2: 1-66.

DE BUEN, F., 1947. Investigaciones sobre ictiología Mexicana. I. Catálogo de los peces de la región neartica en suelo Mexicano. Anales del Instituto de Biología Mexicana 18: 257-348.

Eddy, S., 1957. How to know the freshwater fishes. Second Edition. Sm. C. Brown Company Publishers, Dubuque, Iowa. 286 p.

Evermann, B. W. and E. L. Goldsborough, 1902. A report on fishes collected in Mexico and Central America, with notes and descriptions of five new species. Bulletin of the United States Fish Commission 21: 137-159.

Evermann, B. W. and W. C. Kendall, 1894. The fishes of Texas and the Rio Grande Basin, considered chiefly with reference to their geographical distribution. Bulletin of the United States Fish Commission 12: 57-126.

Fowler, H. W., 1924. Notes on North American Cyprinoid fishes. Proceedings of the Academy of Natural Sciences of Philadelphia 76: 389-416.

Girard, C., 1856. Researches upon the cyprinoid fishes inhabiting the fresh waters of the United States of America, west of the Mississippi Valley . . . . Proceedings of the Academy of Natural Sciences of Philadelphia 8: 165-213.

Girard, C., 1859. Ichthyology of the Boundary. *In* Report of the United States and Mexican Boundary Survey, . . . 2: 1-85.

Günther, A., 1868. Catalogue of the Physostomi . . . in the collection of the British Museum. Catalogue of the Fishes in the British Museum 7: 1-512.

Hubbs, Carl L., 1940. Fishes of the Big Bend Region of Texas. Transactions of the Texas Academy of Science 23: 3-12.

Hubbs, Carl L. and C. W. Greene, 1935. Two new subspecies of fishes from Wisconsin. Transactions of the Wisconsin Academy of Sciences, Arts, and Letters 29: 89-101.

Hubbs, Carl L. and K. F. Lagler, 1958. Fishes of the Great Lakes region. Revised Edition. Bulletin of the Cranbrook Institute of Science 26.

Hubbs, Carl L. and R. R. Miller, 1975. *Notropis tropicus*, a new cyprinid fish from eastern Mexico. The Southwestern Naturalist 20: 121-131.

Hubbs, Clark, 1954. Corrected distributional records for Texas fresh-water fishes. The Texas Journal of Science 6: 277-291.

Hubbs, Clark, 1957a. Distributional patterns of Texas fresh-water fishes. The Southwestern Naturalist 2: 89-104.

Hubbs, Clark, 1957b. A checklist of Texas fresh-water fishes. Texas Game and Fish Commission, Division of Inland Fisheries IF Series No. 3.

Hubbs, Clark, 1958. A checklist of Texas fresh-water fishes. Revised. Texas Game and Fish Commission, Division of Inland Fisheries IF Series No. 3.

Hubbs, Clark, 1961. A checklist of Texas fresh-water fishes. Revised. Texas Game and Fish Commission, Division of Inland Fisheries IF Series No. 3.

Hubbs, Clark, 1972. A checklist of Texas fresh-water fishes. Texas Parks and Wildlife Department, Technical Series No. 11.

Hubbs, Clark and V. G. Springer, 1957. A revision of the *Gambusia nobilis* species group, with descriptions of three new species, and notes on their variation, ecology and evolution. The Texas Journal of Science 9: 279-327.

Hubbs, Clark and R. Wauer, 1973. Seasonal changes in the fish fauna of Tornillo Creek, Brewster County, Texas. The Southwestern Naturalist 17: 375-379.

Illick, H. J., 1956. A comparative study of the cephalic lateral-line system of North American Cyprinidae. The American Midland Naturalist 56: 204-223.

John, K. R. 1964. Survival of fish in intermittent streams of the Chiricahua Mountains, Arizona. Ecology 45: 112-119.

Jordan, D. S., 1878. A catalogue of the fishes of the fresh waters of North America. Bulletin of the United States Geological and Geographical Survey of the Territories 4: 407-442.

Jordan, D. S., 1885. A catalogue of the fishes known to inhabit the waters of North America, north of the Tropic of Cancer, with notes on the species discovered in 1883 and 1884. United States Commission of Fish and Fisheries, Report of the Commissioner 13: 787-973.

Jordan, D. S. and H. E. Copeland, 1876. Check list of the fishes of the fresh waters of North America. Bulletin of the Buffalo Society of Natural Sciences 3: 133-164.

Jordan, D. S. and B. W. Evermann., 1896a. The fishes of North and Middle America. Bulletin of the United States National Museum 47: 1-1240.

Jordan, D. S. and B. W. Evermann, 1896b. A check list of the fishes and fishlike vertebrates of North and Middle America. United States Commission of Fish and Fisheries, Report of the Commissioner 21: 207-584.

Jordan, D. S. and C. H. Gilbert, 1883. Synopsis of the fishes of North America. Bulletin of the United States National Museum No. 16: 1-1018.

Jordan, D. S., B. W. Evermann and H. W. Clark, 1930. Check list of the fish and fishlike vertebrates of North and Middle America north of the northern boundary of Venezuela and Columbia. Reprint of Appendix X, Report of the United States Commissioner of Fisheries for 1928.

Jurgens, K. C. and Clark Hubbs, 1953. A checklist of Texas fresh-water fishes. Texas Game and Fish 11: 12-15.

Knapp, F. T., 1953. Fishes found in the freshwaters of Texas. Ragland Studios and Litho Printing Company, Brunswick, Georgia. 166 p.

Kraatz, W. C., 1923. A study of the food of the minnow *Campostoma anomalum.* The Ohio Journal of Science 23: 265-283.

Kraatz, W. C., 1924. The intestine of the minnow *Campostoma anomalum* (Rafinesque), with special reference to the development of its coiling. The Ohio Journal of Science 23: 265-298.

McNatt, R. M., 1974. Re-evaluation of the native fishes of the Río Yaqui in the United States. Proceedings of the Western Association of State

Game and Fish Commissioners 54: 273-279.

MEEK, S. E., 1902. A contribution to the ichthyology of Mexico. Field Columbian Museum, Publication 65, Zoological Series 3: 63-128.

MEEK, S. E. 1903. Distribution of the fresh-water fishes of Mexico. The American Naturalist 37: 771-784.

MEEK, S. E., 1904. The fresh-water fishes of Mexico north of the Isthmus of Tehuantepec. Field Columbian Museum, Publication 93, Zoological Series 5: 1-252.

METCALF, A. L., 1966. Fishes of the Kansas River system in relation to zoogeography of the Great Plains. University of Kansas Publications, Museum of Natural History 17: 23-189.

MILLER, R. R., 1958. Origin and affinities of the freshwater fish fauna of Western North America, p. 187-222. *In* Carl L. Hubbs (ed), Zoogeography. American Association for the Advancement of Science, Publication 51.

MILLER, R. R., 1972. Threatened freshwater fishes of the United States. Transactions of the American Fisheries Society 101: 239-252.

MILLER, R. R. and C. H. LOWE, 1964. An annotated check list of the fishes of Arizona. Part 2, 133-151. *In* Charles H. Lowe (ed), The Vertebrates of Arizona. The University of Arizona Press, Tucson, Arizona.

MINCKLEY, W. L., 1971. Keys to native and introduced fishes of Arizona. Journal of the Arizona Academy of Sciences 6: 183-188.

MINCKLEY, W. L., 1973. Fishes of Arizona. Arizona Game and Fish Department. Sims Printing Company, Inc., Phoenix, Arizona. 293 p.

MINCKLEY, W. L. and J. E. DEACON, 1968. Southwestern fishes and the enigma of "endangered species." Science 159: 1424-1432.

MOORE, G. A., 1957. Fishes. Part 2, p. 31-210. *In* W. F. Blair, et al., (eds), Vertebrates of the United States. McGraw-Hill Book Company, New York, New York.

MOORE, G. A., 1968. Fishes. Part 2, p. 21-165. *In* W. F. Blair, et al., (eds), Vertebrates of the United States. Second Edition. McGraw-Hill Book Company, New York, New York

PFLEIGER, W. L., 1971. A distributional study of Missouri fishes. University of Kansas Publications, Museum of Natural History 20: 225-570.

PRATT, H. S., 1923. A manual of land and fresh water vertebrate animals of the United States (exclusive of birds). P. Blakiston's Son & Company, Philadelphia, Pennsylvani. 422 p.

REGAN, C. T., 1906-1908. Pisces. *In* Biologia Centrali-Americana 8: 1-203.

RUTTER, C., 1896. Notes on the fresh water fishes of the Pacific slope of North America. Proceedings of the California Academy of Sciences 6: 245-267.

SCHRENKEISEN, R., 1938. Field book of fresh-water fishes of North America north of Mexico. G. P. Putnam's Sons, New York, New York. 312 p.

WOOLMAN, A. J., 1894. Report on a collection of fishes from the rivers of central and northern Mexico. Bulletin of the United States Fish Commission 14: 55-66.

Illinois Natural History Survey, Urbana, Illinois 61801

NOTES ON THE AVIFAUNA OF ISLA GRANDE AND PATAGONIA, ARGENTINA

Joseph R. Jehl, Jr. and Maurice A. E. Rumboll

TRANSACTIONS

OF THE SAN DIEGO
SOCIETY OF
NATURAL HISTORY

VOL. 18, NO. 8 9 JULY 1976

Notes on the avifauna of Isla Grande and Patagonia, Argentina

Joseph R. Jehl, Jr., and Maurice A. E. Rumboll

Recent field studies in Southern Argentina have resulted in much new information on the distribution and biology of many avian species. This paper deals largely with information obtained in Tierra del Fuego and Patagonia in the austral winters of 1971 and 1972, and the austral summer of 1973, under studies supported by the National Science Foundation.

ISLA GRANDE

Tierra del Fuego comprises all of the islands south of the Strait of Magellan. The avifauna of Isla Grande has been reviewed by Humphrey, Bridge, Reynolds and Peterson (1970). Additional general information has been contributed by Keith (1970), by Weller (1975) on waterfowl populations, and by Parmelee and MacDonald (1975) on the breeding birds of two islands in the Strait of Magellan. From 23 October and 4 November 1973, we conducted studies on Isla Grande, principally in the vicinity of Rio Grande in the northeastern part of the island (see Jehl, 1975) but were also able to transect the Argentine side of the island between the Strait of Magellan and the Beagle Channel. Because our arrival time was earlier in the austral spring than that of most other ornithologists, we were able to obtain information on arrival times and breeding seasons that has not been available previously, as well as new distributional data. Additional data gathered by Rumboll during subsequent research in the area, are also included. The data in this report pertain specifically to 1973 unless stated otherwise. Specimens collected are deposited in the San Diego Natural History Museum (SDNHM). More detailed information on localities in Tierra del Fuego may be found in Humphrey et al. (1970).

Rockhopper Penguin *(Eudyptes crestatus)*.—Single birds found dead on the beach at Viamonte on 25 October and at Rio Grande on 29 October 1973 constitute the only October records for a species which is doubtless present year-round.

Macaroni Penguin *(Eudyptes chrysolophus)*.—Humphrey et al. (1970) knew of only two specimen records (February, March). Rumboll saw a live bird, apparently an immature, captured by tourists near Viamonte on 4 March 1973.

Black-browed Albatross *(Diomedea melanophris)*.—Stiles (1974) reported six birds at Lago Fagnano, a large, inland, fresh-water lake, in December 1972 and discussed the possible significance of his observations with regard to the long-rumored existence of an albatross colony in nearby mountains. Our observations of two birds washed ashore on the eastern shore of the lake on 5 November further indicate that the species may occur there with some regularity.

Olivaceous Cormorant *(Phalacrocorax olivaceus)*.—At Ea. San José, Sr. T. Mackay showed us the remains of a colony that had been recently destroyed when beavers *(Castor canadensis)* cut down the nest trees. According to Sr. Mackay the colony normally contained 80-100 nests and had been there for many years.

Blue-eyed Cormorant *(Phalacrocorax atriceps)*.—Humphrey et al. (1970) concluded that "there are very few records indeed of *P. atriceps*" for Isla Grande, but the species is commoner in the western Strait of Magellan than they recognized (Jehl, 1973; Brown et al., 1973; see also below). We found one dead, Rio Grande, 29 October (SDNHM no. 38639), two dead at Lago Fagnano (one saved, SDNHM no. 38638) on 5 November, and saw one at Cabo Peñas, 30 October. As noted by Reynolds (in Humphrey et al., 1970), the species nests on islands in Lago Yehunin (Rumboll, pers. obs.).

Buff-necked Ibis *(Theristicus caudatus)*.—Fairly common and widespread in the northeastern part of the island. We found a nest (c/2) on the ground on an island at Ea. Los Flamencos on 31 October, along with many nests of Kelp Gulls *(Larus dominicanus)* and two nests (c/3) of Black-necked Swans *(Cygnus melanocoryphus)*. On 10 November, Sr. Mackay showed us a colony of 60-80 pairs in the woods at Ea. San José. The colony had been robbed recently, and only a few nests contained eggs; no chicks were present.

San Diego Soc. Nat. Hist., Trans. 18(8):145-154, 9 July 1976

Ashy-headed Goose *(Chloephaga poliocephala)*.—Humphrey et al. (1970) considered this goose "relatively uncommon" and Weller (1975) did not find it north of Viamonte. However, in late October it was common at Viamonte and Los Flamencos, and scattered birds were seen north to San Sebastián; many observations probably pertained to non-breeding birds. It was fairly common in forested areas at Lapataia, and on 7 November we found two nests (c/5, c/6).

Ruddy-headed Goose *(Chloephaga rubidiceps)*.—This species was once abundant on Isla Grande, and as recently as 1970 Humphrey et al. considered it common. It is now very rare as a result of control measures instituted primarily against the Upland Goose (*C. picta;* see also Weller, 1975). During our investigations, which covered a large part of the northern half of the Argentine side of the island, Rumboll counted only 30 individuals; subsequent reports (Rumboll, 1975) suggest a further decrease. The species is clearly on the verge of extirpation.

Upland Goose *(Chloephaga picta)*.—The Upland Goose remains an abundant species on Isla Grande though massive control measures (harvesting of eggs, destruction of young, shooting of adults) are certainly having important roles in limiting its population (see Humphrey et al., 1970; Delacour, 1954).

As is well known, males of this species are polymorphic, with the barred form *(C. p. dispar)* predominating in Tierra del Fuego and the white-bodied form *(C. p. picta)* in Patagonia (Delacour, 1954). Humphrey et al. (1970) concluded that on Isla Grande "the barred form . . . is by far the most abundant and the white breasted form . . . is seen seldom and always in small numbers." In our studies we found white-breasted birds fairly common in the northern part of the island; on 25 October they comprised 10-15 per cent of the hundreds of geese in the marshes near Bahía San Sebastián. Only a few kilometers farther south, however, where the land was slightly higher, they became decidedly rare and few were seen south of Ea. Sara. Yet some were present as far south as the Beagle Channel; on 7 November we saw 5 males and 2 females among the abundant *dispar* at Lago Roca.

Delacour (1954: 219) states that within this species "the females are all much alike, and individual variation is slight." To the contrary we found that females were also polymorphic and could, in most cases, be assigned by head color to *picta* (pale sandy brown) or *dispar* (warm medium brown). On 25 October we noted pair preferences among mated geese in two localities: the marshes at Bahía San Sebastián; and between the south coast of Bahía San Sebastián and Ea. Sara. Geese were assigned to white (W), intermediate (I), or barred (B) categories. Although this grouping is crude and does not fully allow for the amount of plumage variation that occurs, the results (Table 1) clearly show a strong tendency for assortive mating. In the Ushuaia area nesting had begun and it was not possible to determine which birds were mated; in one pair at Lago Roca a *picta* female was paired with a *dispar* male.

Humphrey et al. (1970) summarized evidence suggesting strong differences between *picta* and *dispar* in ecology and migration, and wondered (p. 118) "if the two phases prior to the arrival of the white man and sheep were not more separated ecologically during the breeding season." They suggested, quite reasonably, that increased habitat disturbance has allowed the forms to come into secondary contact within the past 75 to 100 years. Our data on assortative mating suggest that premating isolating mechanisms had been developed between the two forms, and these are currently being tested in northern Tierra del Fuego. The situation is a dynamic one deserving careful study especially in view of the tremendous economic importance of these geese.

White-cheeked Pintail *(Anas bahamensis)*.—Humphrey et al. (1970) knew of only one sight record on Isla Grande. Three recent sightings establish that the species probably reaches the area irregularly: one, Rio Ewan, 22 January 1975; eight, Cabo San Pablo, 2 February 1975; four, Lapataia, 27 January 1975.

Crested Duck *(Lophonetta specularoides)*.—Common to abundant in the northern part of the island as well as in the Ushuaia area. Nesting begins in early spring. We found clutches of 3, 7, and 8 eggs near Rio Grande between 25-28 October, one of which hatched on 30 October, and a pair with week-old chicks at Lapataia on 7 November. Humphrey et al. (1970) were uncertain of its breeding status. Weller (1975) reported many broods that "must have hatched in early to mid-January."

Flightless Steamer-Duck *(Tachyeres pteneres)*.—Neither Humphrey et al. (1970) nor Weller (1975) recorded this species on the northeastern coast and thus the observation of a single bird with a flock of Flying Steamer-Ducks *(T. patachonicus)* at Viamonte on 23 October is of interest.

Flying Steamer-Duck *(Tachyeres patachonicus)*.—A nest with six eggs on the shore of a small pond north of Rio Grande, on 28 October, was still being incubated on 13 November.

Andean Condor *(Vultur gyrphus)*.—In view of the many sight records for this unmistakable species in the Ushuaia area (e.g., 3-4 at Lapataia, 6 November; 3 Monte Olivia, 8 November), its designation by Humphrey et al. (1970) as "hypothetical" suggests an excessively strict standard for the acceptance of distributional data.

Red-backed Hawk *(Buteo polyosoma)*.—Humphrey et al. (1970) considered this species "common . . . throughout Isla Grande." While en route to Ushuaia on 5 November we saw several birds in the forested area, yet in nearly three weeks near Rio Grande saw only one. Hunting pressure is probably responsible for the apparent decline.

Cinereous Harrier *(Circus cinereus)*.—Humphrey et al. (1970) had no proof of nesting. We saw a pair courting at Ea. José Menendez on 27 October. One bird dropped to the ground and disappeared into the undergrowth, but we were unable to locate the nest.

Chimango Caracara *(Milvago chimango)*.—Although Humphrey et al. (1970) considered this species common everywhere, we found it so only in the wooded southern part of the island. In the north it is

Table 1. Assortative mating patterns in Upland Geese in northern Tierra del Fuego. W = white-breasted forms *(C. p. picta)*, B = barred forms *(C. p. dispar)*, I = intermediates. Data obtained 25 October 1973.

	Bahía San Sebastián Marshes[1]				*Between Bahía San Sebastián and Ea. Sara*		
	W♂	I♂	B♂		W♂	I♂	B♂
W♀	17	2	2	W♀	5	—	—
I♀	1	3	2	I♀	—	1	—
B♀	2	1	96	B♀	—	1	82

[1] Unassigned birds in the area included W♂-10, W♀-10, I♂-52, I♀-85, B♂-154, B♀-300.

decidedly rare as a result of hunting and poisoning. Near San Sebastián we found 12 dead in one small field, and carcasses strewn along the roadside were a common sight.

Crested Caracara *(Polyborus plancus)*.—The Crested Caracara, or Carancho, is thought by local inhabitants to peck out the eyes of newborn lambs, and thus is hunted mercilessly. Between 22-25 October we found more than 10 carcasses along major roadways, often in association with the remains of other predators: Black-chested Buzzard-Eagles *(Geronoaetus melanoleucus)*; Chimangos, and Patagonian Foxes *(Dusicyon culpaeus)*. Though commoner than the Chimango, and still fairly common in the northern half of the island, the Carancho seems to be decreasing.

Peregrine Falcon *(Falco peregrinus)*.—Rumboll saw two adults and a newly-fledged juvenile at Lago Escondido on 27 January 1974. This is the most convincing evidence to date that the species actually nests on Isla Grande.

Pallid Falcon *(Falco kreyenborgi)*.—The status of this rare falcon is so poorly known that all records are of interest. Rumboll saw one feeding on a large passerine (presumably *Pezites militaris*) 4 km north of Misión, near Rio Grande, on 3 May 1975. On 11 May, he saw a single bird at Ea. Condor just north of the Strait of Magellan, and 200 km north of Misión. These sightings may have been of the same individual.

Aplomado Falcon *(Falco femoralis)*.—The observation of a bird 20 km north of Lago Fagnano on 5 November is of interest because of the species' general rarity on Isla Grande and its alleged absence from the forested part of the island (Humphrey et al., 1970).

Magellanic Oystercatcher *(Haematopus leucopodus)*.—This oystercatcher breeds commonly in pastures up to 8 km inland in the Rio Grande area, but farther inland, where the land is drier, is rare and local. Hundreds of non-breeders were on the beach at Rio Grande on 24 October, and perhaps 100 were in the harbor at Ushuaia on 7 November. Nesting begins in October. On 24 and 25 October we found nests, (each c/2), and by 29 October some pairs began to act as if they had chicks.

Chilean Lapwing *(Vanellus chilensis)*.—This species, common in the northeastern part of the island, begins nesting in October. We found a nest (c/3) on 23 October and a brood on 9 November.

Black-bellied Plover *(Squatarola squatarola)*.—One at Rio Grande on 29 January 1974. There are no previous records for this species, which only occasionally winters as far south as Buenos Aires Province.

Two-banded Plover *(Charadrius falklandicus)*.—Humphrey et al. (1970) considered this plover uncommon and stated that "there are very few records for the northeastern part of the island." By contrast, we found it common on the coastal plain, with pairs nesting along the coast as well as on the shores of lakes and ponds. Nesting may begin by early October. At Laguna de los Cisnes, in Rio Grande, we found nests (each c/3) on 23 and 24 October, and newly-hatched chicks from a third nest on 28 October. Rumboll banded 2 very small chicks at Yrigoyen, in the southeastern part of the island, on 17 January 1974.

Rufous-chested Dotterel *(Charadrius [Zonibyx] modestus)*.—This species seems rare and local in the northeastern part of the island and restricted to areas of heath vegetation (Fig. 1). On 30 October we found three nests (all c/3) on the verge of hatching at Cabo Peñas. Humphrey et al. (1970) considered it common, which suggests that habitat changes and the disruption of heath communities have affected its abundance.

Tawny-throated Dotterel *(Oreopholus ruficollis)*.—Uncommon to rare in dry pastures and along old beach lines at Cabo Peñas (Fig. 2). A nest (c/3) was found at Ea. Los Flamencos on 12 November.

Hudsonian Godwit *(Limosa haemastica)*.—This species arrives by late October and winters in small numbers. Our records include: 15 on the beach at Viamonte on 23 October; 20 at Viamonte on 25 October; 10 at lakes and ponds in the Rio Grande area on 10 November 1973; and 15 at Rio Grande on 29 January 1974.

Whimbrel *(Numenius phaeopus)*.—A flock of 250 in a pasture at Viamonte on 23 October 1973 was our only observation of this species.

Greater Yellowlegs *(Tringa melanoleuca)*.—Four at Viamonte on 23 October and 1 at Rio Grande on 26 October represent the earliest records for the species.

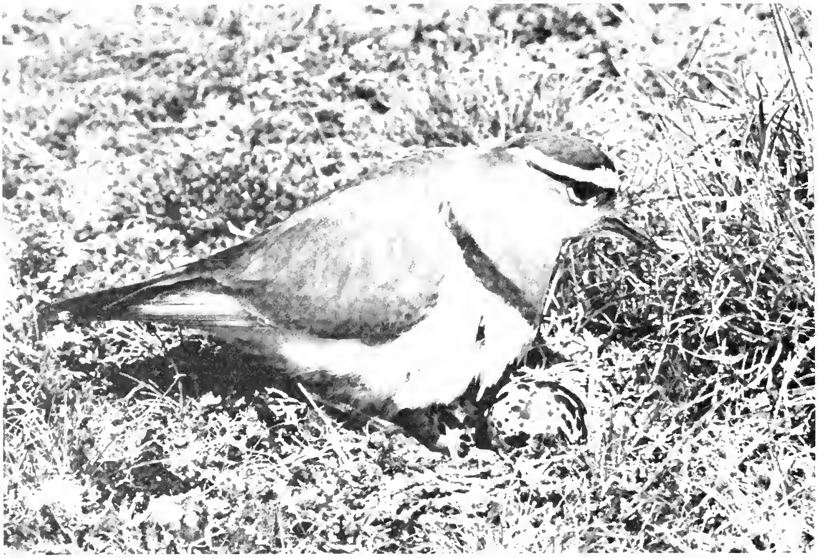


Figure 1. Rufous-chested Dotteral *(Charadrius [Zonibyx] modestus)* nesting in heath vegetation at Cabo Peñas, Isla Grande.

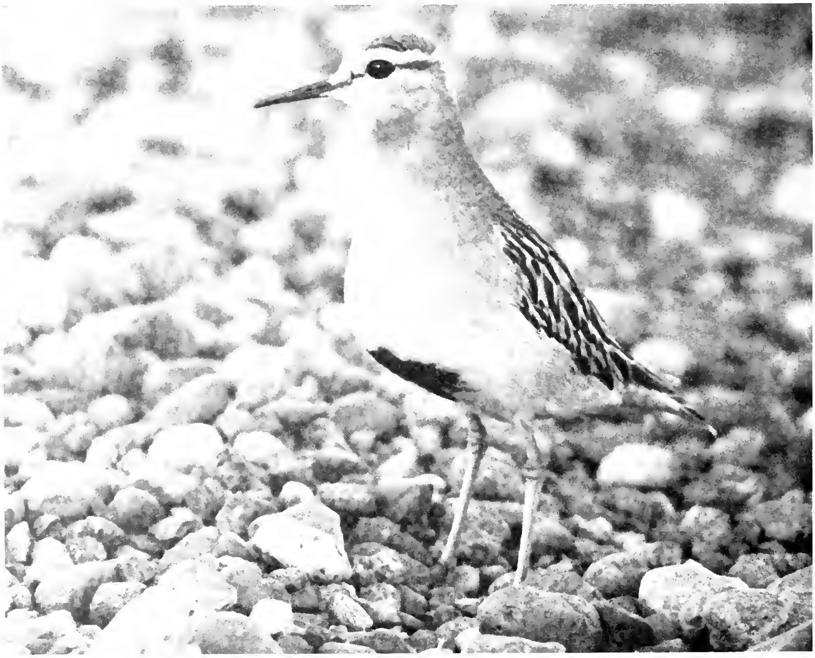


Figure 2. Tawny-throated Dotterel *(Oreopholus ruficollis)*.

Ruddy Turnstone *(Arenaria interpres).* — Meyer de Schauensee (1966) gave Cabo San Antonio, Buenos Aires Province, as the southernmost locality for this species in Argentina. On 25 October, 1973, a flock of 10, including one bird retaining traces of summer plumage, foraged on the beach at Rio Grande. The sighting of 4 at Yrigoyen on 17 January 1974, and one at Bahía San Sebastián on 28 January 1974, indicate that this species probably winters regularly in Tierra del Fuego.

Wilson's Phalarope *(Phalaropus tricolor).*—Humphrey et al. (1970) knew of only one sight record. We saw one at Laguna de los Cisnes, Rio Grande, on 24 October and three there on 26 October.

Red Knot *(Calidris canutus).*—We saw 500 on the beach at Rio Grande 23 October and 10 on the beach at Viamonte 25 October. Rumboll saw a few in the Rio Grande area on 28 January 1974. Humphrey et al. (1970) consider it "irregular" and give records from December through March.

Sanderling *(Calidris alba).*—Considered irregular by Humphrey at al. (1970). Thirty were present on the beach at Rio Grande on 25 October, and a single bird appeared at an inland pond there on 10 November 1973. Four were present at Yrigoyen on 17 January 1974.

White-rumped Sandpiper *(Calidris fusicollis).*—Humphrey et al. (1970) presented surprisingly little information on this abundant sandpiper. Large numbers of migrants were present by the time of our arrival on 23 October. On 25 October we saw 1000 feeding on kelp-covered beaches at Rio Grande, and numbers continued to increase into November as new migrants appeared. Our maximum count was 5000 at Laguna de los Cisnes on 30 October, and hundreds and often thousands could usually be found at that lake. We did not observe this species in the Ushuaia area.

Baird's Sandpiper *(Calidris bairdii).*—Common as far south as Viamonte in pasture pools, marshes, large lakes, and even coastal beaches. Flock of up to 30 were present by 23 October and numbers increased through early November, when several hundred could be seen in a day. The species is usually associated with White-rumped Sandpipers.

Pectoral Sandpiper *(Calidris melanotos).*—Our observations of this species, not previously known from Isla Grande, include: 25 in a grassy pasture at Viamonte, 24 October; 4 at Viamonte, 22 October; and 2 at Rio Grande on 27 October.

Gray-breasted Seedsnipe *(Thinocorus orbignyianus).*—This species, the commonest seedsnipe in Tierra del Fuego early in the century, is now quite rare. Sr. Len Bridges of Ea. Viamonte informed us that he had not seen any in four years at Viamonte, and we saw only one, at Ea. San José, on 11 November 1973. The reason for its decline is not understood but probably involves habitat changes resulting from overgrazing.

Least Seedsnipe *(Thinocorus rumicivorus).*—Common to abundant along the coast and up to about 15 km inland. We found newly-hatched chicks, as well as a nest that had just been started, on 9 November 1973. A small chick at Ea. La Indiana on 25 January 1975 establishes that this species nests in the southeastern part of Isla Grande, where it had not previously been known to breed.

Snowy Sheathbill *(Chionis alba).*—Up to 12 near Rio Grande between late October and mid-November 1973; a few probably present all year.

Great Skua *(Catharacta skua).*—Seen daily in the Rio Grande area, hunting along the coast as well as over pastures and along lake shores. Up to a dozen were in the harbor at Ushuaia on 7 November. All birds seen on the island were clearly *C. s. chilensis.*

Kelp Gull *(Larus dominicanus).*—A small colony had begun to form on an island in a lake at Ea. Los Flamencos on 31 October. Nest contents were: c/0-40+; c/1-14; c/2-20; c/3-14.

Black Skimmer *(Rhynchops nigra).*—An immature was seen at Cabo San Pablo on 6 Feburary 1975. Meyer de Schauensee (1966) states that the species has been recorded from Tierra del Fuego, but its occurrence was not noted by Humphrey et al. (1970).

Rock Dove *(Columba livia).*—We saw a few at Rio Grande area and one at Ushuaia, where it has become established (Keith, 1970).

Short-billed Miner *(Geositta antarctica).*—The status of this species is not well known. We found it only in flat areas at Ea. Los Flamencos where the grass was short and fine; it avoided areas of bunch grass and the undulating terrain where *G. cunicularia* was abundant.

Chocolate-vented Tyrant *(Neoxolmis rufiventris).*—Two records: one near Ea. José Menendez on 24 October, and one, carrying a small lizard (*Liolaemus* sp.) at Rio Grande, 10 November. Considered accidental by Humphrey et al. (1970) but probably commoner than the few records suggest.

Chilean Swallow *(Tachycineta leucopyga).*—A few were present on 23 October 1973, and a large influx occurred on the 27th, after which time the species was seen daily and in large numbers. On several days in late October, we watched flocks flying over shallow ponds. The birds concentrated their activities in the lee of small banks, where the surface of the water was smooth. We assumed that they were feeding on emerging insects, but the weather was cold and rainy, and no flying insects were evident. Subsequent examination of photographs shows that some birds were immersing the bill and the anterior part of the head fairly deeply into the water (Fig. 3). This was not drinking, but presumably an attempt to pluck larval insects from the upper layer of the pond. Such a feeding behavior would be advantageous to a species that must deal with the harsh weather in order to occupy the austral regions.

Blue-and-white Swallow *(Notiochelidon cyanoleuca).*—A single bird, the first arrival, appeared in Rio Grande on 29 October 1973. The species increased in early November and was almost invariably found feeding in association with sheep in pastures, rather than near open water.

Barn Swallow *(Hirundo rustica).*—Considered accidental by Humphrey et al. (1970) but probably regular. We made sightings at Rio Grande among flocks of Chilean Swallows on 27 October, 29 October, 5 November and 10 November; at Lapataia (2 birds) 6 November; and at Ea. San José, 10 November 1973.

Figure 3. Chilean Swallow *(Tachycineta leucopyga)* feeding on aquatic insect larvae; note that the bird's bill and forehead are submerged. Photo: M. Rumboll.

Cliff Swallow *(Petrochelidon pyrrhonata)*.—A single bird in a flock of Chilean Swallows at Rio Grande on 28-29 October 1973 is the southernmost record of the species and the first for Tierra del Fuego.

Patagonian Yellow Finch *(Sicalis lebruni)*.—According to Humphrey et al. (1970) this species is uncommon in the northern part of the islands. In our experience, however, it was quite rare. The few pairs we saw were all in the vicinity of gravel pits in the Rio Grande-San Sebastián area. A similar habitat preference was noted by Johnson (1967).

Comments.—Predator control measures are apparently making serious inroads on populations of Red-backed Hawks, Black-chested Buzzard-Eagles, Chimango and Crested caracaras, Upland and Ruddy-headed kelp-geese, and perhaps other species on Isla Grande. These pressures could be reversed through education. On the other hand, the pressure of habitat destruction is less easily corrected. Isla Grande is devoted to monoculture, sheep farming. Rising wool prices have encouraged farmers to increase their flocks, which, in turn, has led to serious overgrazing and habitat alterations. We suspect that our inability to find Black-throated Finches *(Melanodera melanodera)* despite some efforts, and the apparent scarcity of Red-breasted Meadowlarks *(Pezites militaris)*, may be related to the disappearance of areas of moderate to tall grass; the seeming decline of the Rufous-chested Dotterel may reflect the gradual elimination of heath habitats. On the other hand, the creation of sparsely-vegetated areas may have favored the increase of the Least Seedsnipe (at the expense of the Gray-breasted species?). The precise reasons for these changes remain to be determined. Yet, it is clear that the hand of man is having a considerable and perhaps irreversible effect on the bird fauna of Isla Grande.

PATAGONIA

Jehl made observations along the coast of Patagonia, as opportunity presented, in conjunction with pelagic bird studies in the austral winters of 1971 and 1972. His itinerary and the results of the pelagic studies are presented elsewhere (Jehl, 1974; Jehl, Rumboll, and Winter, 1973). In 1973, we made additional observations on the distribution of birds in Patagonia while en route to and from Tierra del Fuego, 17-22 October, and 14-27 November.

Magellanic Penguin *(Spheniscus magellanicus)*.—The northernmost known nesting colonies of Magellanic Penguins in Argentina are at Punta Tombo and Punta Clara, Chubut Province (Boswall, 1973). On 23 November 1973, we saw approximately 20 penguins huddled under small bushes on the

Caleta Valdes, on the Valdes Peninsula, some 240 km northeast of Punta Tombo. It was not possible to approach the area, but we think it extremely likely that the birds were nesting.

Guanay *(Phalacrocorax bougainvillii)*.—The occurrence of the Guanay in Argentina was established in 1967. Erize (1972) found 50 pairs nesting at Punta Tombo in 1969, Boswall and Prytherch (1972) estimated 60 nests in 1971, and we estimated 100 nests on 21-22 November 1973. Rumboll reports that the species has since spread northward and now nests in small numbers in colonies of *P. albiventer* on islands in Cabo Dos Bahías, Chubut Province.

Red-legged Cormorant *(Phalacrocorax gaimardi)*.—According to Meyer de Schauensee (1966) this species is found in Argentina only at Puerto Deseado. Escalante (1970) states that it is restricted to Santa Cruz Province. Our observations indicate that its range is more widespread and may be expanding. In November 1973, we observed the species between Puerto Santa Cruz (2 immatures, 16 November) and 40 km S of Comodoro Rivadavia, Chubut Province (2, 19 November). Several hundred were building nests on cliffs along the south side of Rio Deseado just west of Puerto Deseado on 19 November.

In winter, Jehl observed scattered birds, within a mile or so of shore, from 24 km S of San Julián (28 August 1972) to the vicinity of Cabo Tres Puntas, on the south shore of Golfo San Jorge (16 June 1971). The largest numbers, 300 and 150, were found at the river mouth at San Julián on 13-14 June 1971, and 28 August 1971, respectively. On 27 August 1972, Jehl saw 20 birds sitting on rocky cliffs, in an apparent colony, at Bahía de los Nodales. On 18 July 1969, R. M. Gilmore and S. L. Bowen cruised southward along the coast of Golfo San Jorge and saw a few scattered birds in the vicinity of Cabo Aristizabal (Chubut Province). Bowen reported 100 birds 8 km N of Comodoro Rivadavia. The winter range of the species thus extends for approximately 300 miles, although the bulk of the population seem to remain concentrated at river mouths in Santa Cruz province.

King Cormorant *(Phalacrocorax albiventer)*, Blue-eyed Cormorant *(P. atriceps)*.—The status of these closely similar species on the Patagonian coast is not clear, and without reliable information on distribution, questions about habitat preferences, competitive interactions, and evolution cannot be resolved.

In winter, *albiventer* (Fig. 4) is abundant in the eastern Strait of Magellan and far outnumbers the handful of *atriceps* that are present. In at-sea transects along the Patagonian coast, Jehl saw few cormorants; the majority were *atriceps*, which predominated as far north as Golfo San Jorge. Farther north, *albiventer* was by far commoner, except at Punta Leon, near Golfo Nuevo, where *atriceps* predominated on 18 June 1971. In the Golfo San José-Golfo Nuevo area, *atriceps* made up less than 10 per cent of the wintering flocks (Jehl et al., 1973). The reversal of abundance at Golfo San Jorge may be related to a sharp break in oceanographic conditions there (see Jehl, 1974).

Figure 4. King Cormorant *(Phalacrocorax albiventer)*.

In October 1973, *atriceps* and *albiventer* were equally common (about 20 of each) at Punta Delgada, on the Strait of Magellan, but along the Patagonian coast *atriceps* was the predominant, or exclusive, species through Santa Cruz Province. Observations included 10 *atriceps* (no *albiventer*) near the river mouth at Rio Gallegos, a large colony of cormorants (species uncertain) nesting on an island at San Julián, and 2500 large cormorants, predominantly *atriceps* (20:1), flying out to sea at Puerto Deseado.

In November we found only *P. albiventer* at Punta Tombo, where the colony has been estimated at 5000 birds (Boswall and Prytherch, 1972). However, Rumboll has examined a photograph taken there by Des and Jen Bartlett in late January 1974 that clearly shown an adult *P. atriceps* attending a chick.

It is Jehl's impression that *atriceps* may be slightly more pelagic than *albiventer* and prefers to feed in more turbulent waters.

Magellanic Oystercatcher *(Haematopus leucopodus)*.—The Argentine breeding range of this oystercatcher, considered by Meyer de Schauensee (1966) as restricted to Tierra del Fuego and Staten Island, is much more extensive. Zapata (1967) reported the species nesting at Rio Deseado in northern Santa Cruz Province, and we found it uncommon to rare, but widely distributed, in suitable habitat along Rte. 3 in southern Santa Cruz Province. Our only observation between the Strait of Magellan and Rio Gallegos was of a dead chick near Punta Delgada, Chile, 14 November 1973. This species was generally scarce between Rio Gallegos and the mouth of Rio Coyle, though we observed several pairs in range land 30 km N of Ea. Guer Aike that were providing target practice for the local militia; one freshly-killed and decapitated bird was found along the shoulder of this highway. Rumboll also reports that it nests along the entire valley of the Rio Santa Cruz as far west of Lago Argentino, near the base of the Andes.

The species was fairly common between Rio Coyle and Puerto Santa Cruz. Definite evidence of breeding included a nest with one egg (collected) at Hotel Lemarchand, 21 October 1973, and a pair with a large chick (wt. 75 g collected) 15 km S of Puertò Santa Cruz, 15 November 1973. We found no evidence of the species in high plateau country between Puerto Santa Cruz and San Julián, but from San Julián to El Salado it was uncommon. From there to Bahía Laura there seemed to be no suitable habitat. Our northernmost observation was of a pair, presumably breeding, near a pond at Bahía Laura.

Korschenewski (1969) stated that the Magellanic Oystercatcher occurs at Punta Tombo, Chubut Province, year-round and supposed that it might breed. However, we did not find it there on 21-22 November 1973, nor did Boswall and Prytherch (1972) in November 1971. Korschenewski did not clearly distinguish between the Magellanic and American *(H. palliatus)* oystercatchers in his report and confusion seems probable. The possibility of more northern inland breeding localities should not be discounted. The British Museum collections include four specimens taken during the breeding season (October-November 1901) at Lago Blanco, Chubut Province (identification confirmed by P.J.K. Burton). The precise locality of this lake is uncertain. Also, Sr. Juan Munoz of Puerto Madryn informed Jehl (pers. comm.) of large flocks of oystercatchers far inland, near Lago Aleusco, Chubut Province, in December 1972 and January 1973.

American Oystercatcher *(Haematopus palliatus)*. — According to Meyer de Schauensee (1966) the range of this species in Argentina extends south to Chubut and occasionally Santa Cruz province. Actually, it breeds fairly commonly along the entire coast of Santa Cruz Province south to San Julián and, we suspect, Puerto Santa Cruz. Venegas (1973) has recently reported this species at the Strait of Magellan.

Figure 5. Great Skua *(Catharacta skua antarctica)* nesting at Punta Tombo, Argentina.

Figure 6. Band-tailed Gull *(Larus belcheri)* at Puerto Belgrano, Argentina.

In Chubut Province, the American Oystercatcher is abundant on the Valdes Peninsula (see Jehl et al., 1973). We also estimated 15-18 pairs at Punta Tombo (21-22 November 1973), and several pairs at Bahía Camarones (20 November). In Santa Cruz Province we found birds at Caleta Olivia (2 pairs, 19 November), Puerto Deseado (8 pairs plus 36 non-breeders, 19 November), Bahía Laura (16 birds, 18 November) and San Julián (5 pairs, 17 November). At San Julián we saw one bird flying inland along the river carrying food and another was obviously guarding a chick. Islands in the river mouth at Puerto Santa Cruz should provide adequate habitat for this species, but we were unable to visit them.

Magellanic Plover *(Pluvianellus socialis)*.—The biology of this unusual species has been discussed elsewhere (Jehl, 1975). In January 1976, Robert W. Storer (pers. comm.) found five or six pairs nesting at Laguna Las Escarchadas, 50 km E of Calafate, in extreme southwestern Santa Cruz Province, and on 2 February 1976, Rumboll observed 17 birds including two juveniles at Ea. Tapi Aike, approximately 90 km SE of Calafate. These observations extend the breeding range of *Pluvianellus* inland nearly to the base of the Andes, and it now seems probable that the species nests throughout the valleys drained by the rios Coig, Santa Cruz, and Gallegos.

Ruddy Turnstone *(Arenaria interpres)*.—Two in Bahía de los Nodales on 27 August 1972 represented, at that time, the southernmost records for the species on the Atlantic coast.

Great Skua *(Catharacta skua)*.—At the pinguinera at Cabo dos Bahías, Chubut Province, we observed about 8 skuas on 20 November 1973 and at Punta Tombo estimated about 15 pairs plus 20 or so non-breeding birds. As reported by Olrog (*in* Boswall and Prytherch, 1972) the skuas of Punta Tombo as well as at Cabo Dos Bahías, are referable to *C. s. antarctica* (Fig. 5) and show no sign of introgression with *C. s. chilensis*. The northernmost breeding area for *chilensis* is not known but is presumably in southern Santa Cruz Province.

Band-tailed Gull *(Larus belcheri)*.—Common in the immediate vicinity of the naval base at Puerto Belgrano, 25-28 June 1971, where it was feeding on scraps from ships (Fig. 6). Scavenging on garbage is apparently an unusual behavior for this gull (Escalante, 1966). The dimensions of small series obtained on hook and line are: Culmen: 5♂, 51.2-54.4(52.6) mm; 8♀, 45.2-51.5 (47.4) mm. Bill depth at gonys: 4♂, 17.0-18.8(17.1 mm); 8♀, 16.2-18.8 (17.2)mm. Wing (chord): 5♂, 396-422 (405) mm; 8♀, 372-405 (398) mm. Tail: 5♂, 158-176 (167) mm; 8♀, 155-166 (157) mm. Tarsus: 5♂, 58.2-63.3 (60.6) mm; 8♀, 53.9-58.7 (56.9) mm. Weight: 5♂, 760-933 (840) g; 10♀, 650-715 (678) g. On all specimens the legs were bright yellow, the iris brown, the orbital ring orange-red.

Of more than 200 gulls in the area, no more than four were sub-adult, and only one was in juvenal plumage. None of the adults showed the "hooded" plumage that characterizes the Pacific population of *L. belcheri*. Escalante (1966) and Olrog (1967) have also commented on the absence of a hood in winter birds from the Atlantic coast.

ACKNOWLEDGMENTS

We are extremely grateful to our many friends on Isla Grande for sharing their homes and knowledge with us. Special thanks are due Sr. and Sra. Adrian Goodall, Sra. Clara Bridges de Goodall, Sr. Len Bridges, and Sr. Howard Reynolds of Ea. Viamonte, Sr. and Sra. Juancho Appolonaire of Ea. Maria Behety, and Sr. and Sra. Theodore Mackay of Ea. San José. Srs. Marcelo and Pablo Canevari assisted Rumboll in field work in Tierra del Fuego and are responsible for several of the records included herein.

Jehl's research in Argentina was supported by a grant from the National Science Foundation (NSF-GV-32739).

LITERATURE CITED

BOSWALL, J. 1973. Supplementary notes on the birds of Point Tombo, Argentina. Bulletin British Ornithologists' Club 93: 33-36.

BOSWALL, J. and R. J. PRYTHERCH. 1972. Some notes on the birds of Point Tombo, Argentina. Bulletin British Ornithologists' Club 92(5): 118-129.

BROWN, R.G.B., F. COOKE, P. K. KINNEAR, and E. L. MILLS. 1975. Summer seabird distributions in Drake Passage, the Chilean Fjords and off southern South America. Ibis 117: 339-356.

DELACOUR, J. 1954. The waterfowl of the world. Country Life Ltd., London.

ERIZE, F. 1972. The Guanay Cormorant *Phalacrocorax bougainvillii* nesting on the Atlantic coast of South America. Bulletin British Ornithologists' Club 95: 117-118.

ESCALANTE, R. 1966. Notes on the Uruguayan population of *Larus belcheri*. Condor 68: 507-510.

ESCALANTE, R. 1970. Aves marinas del Rio de la Plata. Montevideo, Barreiro y Ramos, S.A. 199 p.

HUMPHREY, P. S., D. BRIDGE, P. W. REYNOLDS, and R. T. PETERSON. 1970. Birds of Isla Grande (Tierra del Fuego). Preliminary Smithsonian Manual. Smithsonian Institution, Washington, D.C. 274 p.

JEHL, J. R. JR. 1973. The distribution of marine birds in Chilean waters in winter. Auk 90: 114-135.

JEHL, J. R., JR. 1974. The distribution and ecology of marine birds over the continental shelf of Argentina in winter. Transactions San Diego Society of Natural History 17(16): 217-234.

JEHL, J. R., JR. 1975. *Pluvianellus socialis:* Biology, ecology and relationships of an enigmatic Patagonian shorebird. Transactions San Diego Society of Natural History 18(3): 31-72.

JEHL, J. R., JR., M.A.E. RUMBOLL, and J. P. WINTER. 1973. Winter bird populations of Golfo San José, Argentina. Bulletin British Ornithologists' Club 93(2): 56-63.

JOHNSON, A. W. 1967. The birds of Chile and adjacent regions of Argentina, Bolivia, and Peru. Vol. 2. Buenos Aires, Platt Establicimientos Graficos. S.A.

KEITH, A. R. 1970. Bird observations from Tierra del Fuego. Condor 72: 361-363.

KORSCHENEWSKI, P. 1969. Observaciones sobre aves del litoral Patagonico. Hornero 9: 48-52.

MEYER DE SCHAUENSEE, R. 1966. The species of birds of South America. Narberth, Pa., Livingston Publ. Co.

OLROG, C. C. 1967. Breeding of the Band-tailed Gull *(Larus belcheri)* on the Atlantic Coast of Argentina. Condor 69: 42-48.

PARMELEE, D. F. and S. D. MAC DONALD. 1975. Recent observations on the birds of Isla Contramaestre and Isla Magdalena, Straits of Magellan, Condor 77: 218-220.

STILES, F. W. 1974. Black-browed Albatrosses on fresh water. Auk 91: 844-845.

RUMBOLL, M.A.E. 1975. Notas sobre Anseriformes. El Cauquen de cabeza colorado *(Chloephaga rubidiceps)*. Hornero 11: 315-316.

VENEGAS C., C. 1973. El ostrero Americano, *Haematopus ostralegus ssp.* en el Estrecho de Magallanes. Apartado Anales del Instituto de la Patagonia 4: 281-289.

WELLER, M. W. 1975. Habitat selection by waterfowl of Argentine Isla Grande. Wilson Bulletin 87: 83-90.

ZAPATA, A.R.P. 1967. Observaciones sobre ave, de Puerto Deseado, Provincia de Santa Cruz. Hornero 10: 351-378.

Natural History Museum, P.O. Box 1390, San Diego, California 92112, and Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina.

DISTRIBUTION AND BREEDING BIOLOGY OF CRAVERI'S MURRELET

Lawrence R. DeWeese and Daniel W. Anderson

TRANSACTIONS

OF THE SAN DIEGO
SOCIETY OF
NATURAL HISTORY

VOL. 18, NO. 9 18 AUGUST 1976

Distribution and breeding biology of Craveri's Murrelet

Lawrence R. DeWeese and Daniel W. Anderson

Abstract.—Craveri's Murrelets breed mostly on islands in the Gulf of California, but recent data indicate some nesting on the Pacific Coast of Baja California. Murrelet numbers build in the Gulf of California in late December. The birds probably arrive in the Gulf of California as pairs and generally occupy nests from February through May. Nests are usually found in crevices not far from high tide, and they contain an average of 1.88 eggs per clutch during years of normal productivity. Adult-chick groups varied between 1.5 and 1.3 chicks per group in 1972 and 1974. Murrelets and other seabirds nesting in the Gulf failed to produce significant numbers of young in 1973.

In the Gulf of California, murrelets feed mostly on larval fishes and small adult pelagic fishes, at or near the surface, over deep water; a limited number of invertebrates are also taken. Following the breeding season in June and July they disperse northward along the California Coast and southward along the West Coast of Mexico. This dispersal pattern is similar to that of other seabirds in the Gulf of California.

Craveri's Murrelet *(Endomychura craveri)* is the only alcid known to breed in the Gulf of California. Expeditions into the Gulf have provided most of the published information concerning the species' distribution and natural history, but detailed data are scarce. This paper reports our observations on breeding range, biology, and dispersal that we made on the species from 1971 to 1974 incidental to our other seabird studies. It attempts to synthesize the existing data available in the literature, and some miscellaneous observations from 1975 are also included.

METHODS

Murrelets were observed irregularly between February and July each year, mainly in the Midriff Region of the Gulf of California (the area where islands extend across the Gulf; Fig. 1). Their number, location, distribution, association with other species, and age ratios were routinely recorded on most trips. On occasion, nest searches were conducted, especially on islands where breeding had not been previously reported.

We were able to distinguish young from adult murrelets until the young were about three-fourths grown (Fig. 2). We collected five adult Craveri's Murrelets near Isla Las Animas in the Gulf of California on 12 and 17 April 1971 for food habits and pesticide-residue analysis. In addition, 63 sets of eggs and associated data were examined from the collections of the Western Foundation of Vertebrate Zoology (WFVZ), Los Angeles, and the Museum of Vertebrate Zoology, Berkeley.

In this report, we consider Craveri's Murrelet and Xantus' Murrelet *(E. hypoleuca)* as distinct species (A.O.U. 1957: 252-53; Jehl and Bond 1975).

BREEDING RANGE

Craveri's Murrelet has been previously reported to breed only on islands in the northern half of the Gulf of California, and on islands along the southwestern side. Records are summarized in Figure 3 and Table 1. Consag Rock (A.O.U. 1957: 253) and Isla San Jorge (van Rossem 1926) have been considered the northernmost breeding locations in the Gulf and Isla del Espiritu Santo (Grinnell 1928: 58) and Isla San Francisco (Bent 1919: 156) the southernmost. According to Bancroft (1927), the species' "center of abundance" during breeding lies north of the 28th parallel.

SAN DIEGO SOC. NAT. HIST., TRANS. 18(9):155-168, 18 AUGUST 1976

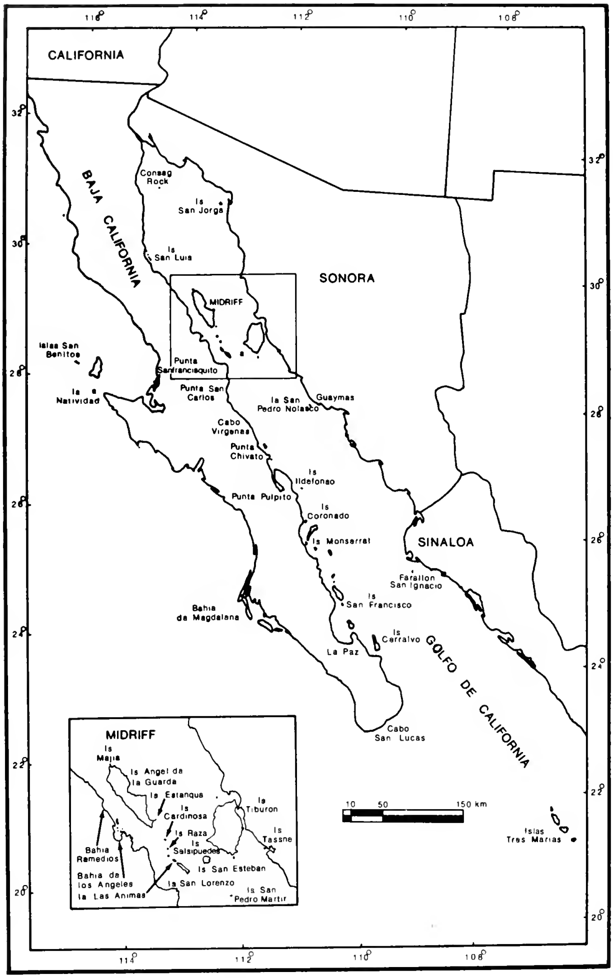


Figure 1. General map of the Gulf of California showing the major locations mentioned in the text.

Other breeding areas of Craveri's Murrelets are not so well-known. Murrelets also nest, though perhaps sparingly, on islands along the Sonora coast of the Gulf. In 1974 and 1975, we found an isolated area on Isla Tassne (Fig. 1, Table 1) with two or three active murrelet nests. We also suspect recent nesting on Islas San Pedro Martír and San Pedro Nolasco, based on our observations, and those of others, of murrelets near the island during the breeding season. A report by van Rossem (1945: 96) mentions breeding on San Pedro Martír, and the same report suggests that San Pedro Nolasco is the southernmost breeding location on the eastern side of the Gulf. There is only one island farther south (Fig. 1), Farallon San Ignacio, which we believe could have nesting murrelets. Surveys of the Tres Marías Islands, off the coast of Nayarit, have failed to reveal nesting murrelets (Stager 1957, Grant and Cowan 1964, Grant 1964).

Figure 2. A parent-chick group of Craveri's Murrelets encountered near Isla las Animas on 8 April 1972. At this age, chicks at a distance become difficult to distinguish from adults. Note the differences in the head feathers between adults and chicks.

Recently, DeLong and Crossin (Ms.) and Jehl and Bond (1975) have presented circumstantial evidence that Craveri's Murrelet breeds on islands along the west coast of Baja California. More exploration is needed at Bahía de Magdalena and the islands north of there to Islas San Benitos, where *E. hypoleuca* (2 ssp.) and *E. craveri* may breed sympatrically (Jehl and Bond 1975).

Banks (1963a) failed to find murrelets nesting on Isla Cerralvo (Fig. 1), despite intensive surveys there. His report of feral cats on Cerralvo, however, may partly explain the absence of recent nesters. Regardless, all evidence known to us suggests that there may be a gap in the breeding range of *E. craveri* around the tip of Baja California.

BREEDING BIOLOGY

Breeding buildups and the nesting season.—Murrelet eggs have been reported from 6 February through 30 April (Bent 1919: 156, van Rossem 1926). Paired birds are present in the breeding areas by late December-early January (van Rossem 1932, 1945: 96), several weeks prior to laying. In late February-early March 1973, 90% of our murrelet sightings involved paired birds (59 encounters with one or more murrelets). These observations were between Bahía de los Angeles (Area A) and Isla Monserrat, Baja California (Area F) (Table 2). During the same period in Area C where there are no nesting islands, murrelets occurred in loose groups of pairs (Table 2). Our observations thus suggest that murrelets were largely paired before they arrived in nesting areas; the loose assemblages may be a result of birds exploiting good feeding conditions. Lamb (1927) reported a high incidence of paired Xantus' Murrelets on the Pacific Coast near Natividad Island in December 1924. Marbled Murrelets *(Brachyramphus marmoratum)* also occur most frequently in pairs (J. M. Scott, pers. comm.). Sealy (1975) collected "pairs" of Marbled Murrelets, and concluded that these alcids arrive in their breeding areas already

Table 1. Records of Craveri's Murrelets used in distributional studies.

Location[1]	Date reported	Evidence	Information source
		Confirmed, possible, and suspected breeding records	
Consag Rock, GC	No data	Probably breeds	Bancroft (1927)
Is. San Jorge, GC	No data April 1925 March 1926 April 1954	Eggs seen Collections Eggs collected Eggs collected	Bancroft (1927) van Rossem (1926) N. K. Carpenter[2] C. Andersen[2]
Is. San Luis, GC	No data April 1970	Eggs seen Adult-chick groups	Bancroft (1927) This study
North end Is. Angel de la Guarda, GC	April 1972	Adult-chick groups	This study
Is. Mejia, GC	May 1974	Eggshells found	This study
Bahía de los Angeles area, GC	1926 April 1972 June 1972 March 1974	Collections Adult-chick groups Large young seen Eggs and young seen	van Rossem (1926) This study This study This study
Is. Estanque, GC	March 1962	Eggs seen	Banks (1963b)
Is. Cardinosa, GC	March 1972 April 1972 March 1974	Nest and eggs seen Adult-chick groups Nests and eggs seen	This study This study This study
Is. Raza, GC	1865 April 1875 April 1972	Collections Eggs collected Adult-chick groups	Grinnell (1928) Bent (1919) This study
Bahía de las Animas area, GC	March 1974	Adult-chick groups[3]	This study
Is. las Animas, GC	March 1972 April 1972 May 1974	Young heard Adult-chick groups Eggshells found	This study This study This study
Is. San Esteban, GC	May 1971 April 1972	Eggshells seen Adult-chick groups	This study This study
Is. Tassne, GC	March 1974	Nests and eggshells	This study
Is. San Pedro Martír, GC	April 1925 May 1973	Breeds Birds seen	van Rossem (1945) This study
Is. San Pedro Nolasco, GC	No data	Breeds	van Rossem (1945)
Is. San Marcos, GC	April 1963	Birds seen[3]	Banks (1963b)
Is. Ildefonso, GC	1909 March 1928 March 1928 April 1920's March 1930	Found breeding Eggs collected Eggs collected Collections Eggs collected	Grinnell (1928) C. C. Lamb[2] N. K. Carpenter[2] van Rossem (1926) G. Bancroft[2]
Is. Coronado, GC	April 1920's	Collections	van Rossem (1926)
Puerto Escondido, Is. Monserrat area, GC	March 1963	Birds seen[3]	Banks (1963b)
Is. San Francisco, GC	1909 March 1929 March 1930	Collections Eggs collected Eggs collected	Bent (1919) C. C. Lamb[2] G. Bancroft[2]
Isla del Ispiritu Santo area, GC	March 1887	Adult-chick groups[3]	Brewster (1902)
Bahía de Magdalena area, BWC	June 1897	Collections[3]	Anthony (1900)
Islas San Benitos, BWC	June 1968	Collections[3]	DeLong and Crossin (ms.)
		Records outside known breeding range, or breeding season	
Cabo San Lucas, GC	1859-1883	Collections	Grinnell (1928)
Is. Natividad area, BWC	No data Postbreeding	Collections Probable	Ridgway (1919) Bent (1919)
Is. de Guadalupe	June 1906	Collections	Green and Arnold (1939
Off San Diego, CA	Aug. 1914 Aug. 1915	Collections Collections	Willett (1933) van Rossem (1915)

Near Catalina Id., CA	Aug. 1928 Aug. 1932	Collections Collections	Willett (1933) Willett (1933)
Near Morro Bay, CA	Sept. 1969	Collections	McCaskie (1971)
Near Monterey Bay, CA	Aug.-Oct.	Collections	van Rossem (1926)
Off Oregon Coast	Aug. 1975	Beached carcass	Jehl (1975)
Is. San Esteban area, GC	Jan. 1932	Birds seen	van Rossem (1945)
Is. Tiburon, Bahía Kino area, GC	Dec. 1931	Birds seen	van Rossem (1945)
Off Bahía Kino, GC	Feb. 1972	Birds seen	This study
Is. San Pedro Martír area, GC	Jan. 1932	Birds seen	van Rossem (1945)
Is. San Pedro Nolasco area, GC	Dec. 1931	Birds seen	van Rossem (1945)
Near Mazatlan, Sinaloa, MWC	Winter	Birds seen	Alden (1969)
Off Guatemala, CEN	April 1973	Bird seen	Jehl (1974)

---

[1] Abbreviations used: Is. = Isla, Id. = Island, GC = Gulf of California, BWC = Baja California West Coast, CA = California Coast, MWC = Mexico West Coast, CEN = Central America West Coast.

[2] Field notes on file, Western Foundation of Vertebrate Zoology.

[3] Likely nesting areas, but not confirmed.

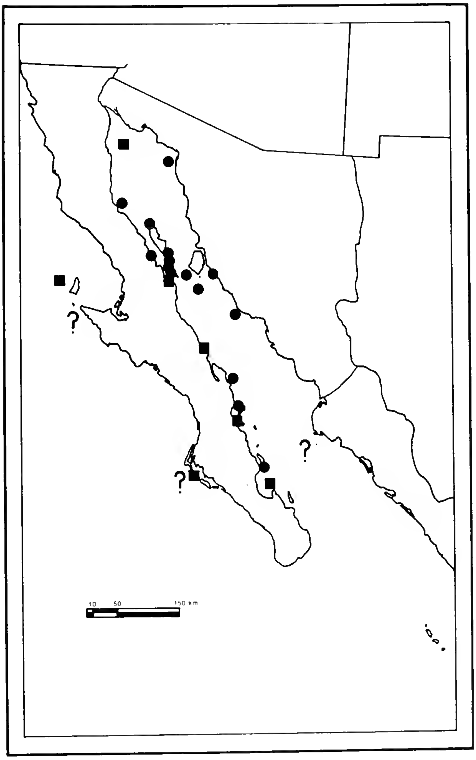


Figure 3. Breeding records of Craveri's Murrelet. Solid circles represent confirmed nesting reports, solid square represent reports that are strongly suggestive of breeding, and question marks signify areas that need further exploration.

Table 2. Pairs of Craveri's Murrelets in the Gulf of California along the east coast of Baja California from mid-February through early March of 1973.

Area[1]	No. birds observed	Birds as solitary pairs No.	Birds as solitary pairs %	Birds as multiple pairs No.	Birds as multiple pairs %	Maximum pairs per group observed
A	36	8	22	28	78	4
B	50	4	8	46	92	17
C	0	0	-	0	-	-
D	19	2	11	16	84	8
E (trip 1)	14	2	14	12	86	4
E (trip 2)	14	2	14	12	86	3
F	9	0	0	8	89	4

[1] Areas, north to south, are coded as follows: A = Midriff area, B = Punta San Francisquito through Punta San Carlos, C = Punta San Carlos to Cabo Virgenes, D = Cabo Virgenes through Punta Chivato, E = south of Chivato to Punta Pulpito, F = Punta Pulpito to Isla Monserrat.

paired. Subadults returned about the same time, but mostly as isolated individuals *(ibid).*

Our records from the northern one-third of the Gulf of California indicate that murrelets began to arrive in January and that numbers increased through April-May, depending on the year (Fig. 4). The high numbers of murrelets in April and May 1971-72 (Fig. 4) occurred at the period when adults were taking flightless young to sea. The period January through April is probably the time when most birds arrive and seclude themselves at nest sites. During 1973, murrelets apparently did not remain in the Gulf (Fig. 4) through the period when parent-chick groups would normally be observed.

Nesting, young, and productivity.—Details on the nesting of Craveri's Murrelets are briefly described by Brown (*In* Bent 1919: 154) and others. They are reported to nest in burrows or cavities (Bancroft 1927), but they may nest under large rocks or bushes (C. C. Lamb, field notes, 1929, on file at WFVZ). Both sexes incubate a reported clutch of two eggs, nest exchange is made in the dark, and adults are not found on land except when on nests (Bent 1919: 153-56). Descriptions of nest sites we found in 1974 are given in Table 3. One nest found on 17 March 1972 by J. O. Keith on Isla Cardinosa (Fig. 5) was occupied annually by nesting murrelets through 1975, when it was destroyed by a rock slide.

All previous records and most of our observations suggest that Craveri's Murrelets nest only on islands. However, on 18 May 1974, we observed a parent-

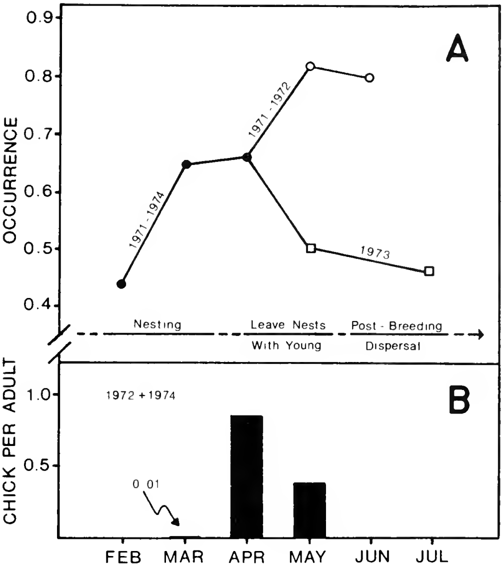


Figure 4. Occurrence patterns of Craveri's Murrelets in the Gulf of California. *A*. Relative occurrence during different years. Occurrence = transects where murrelets were encountered divided by total transects taken for the period. Transects varied in length from about 15 to 30 km. In May and June 1974, boat travel was not sufficient to obtain an adequate sample. *B*. Age ratios in 1972 and 1974; few young were seen in 1973.

Table 3. Site descriptions and contents of Craveri's Murrelet nests found during 1974.

Date	Location	Occupancy	No. eggs	Meters above high tide	Site description
24 March	Is. Cardinosa	Adult	2	3.0	Under low cliff base, nest floor of fine talus
25 March	Is. Cardinosa	Unattended[1]	2	2.7	Shallow hole in talus slope
	Is. Cardinosa	Adult	2	5.5	Under a rock, nest floor of sand
	Is. Cardinosa	Adult	2	5.5	Under a rock, nest floor of small pebbles
	Is. Cardinosa	Unattended[1]	1	5.5	Shallow hole in rocky slope
	Is. Cardinosa	Unattended[1]	2	3.0	Shallow hole in cave, nest floor of small pebbles
6 May	Is. Tassne	Unattended[1]	2	0.6	In narrow crevice
	Is. Tassne	Unattended[1]	1	0.6	In narrow crevice
	Is. Tassne	Unattended[1]	hatched shell	0.3	In narrow crevice

[1] Eggs cold or damaged.

Figure 5. *A*. Craveri's Murrelet nesting crevice found on Isla Cardinosa on 17 March 1972. The white arrow points to the location of the incubating adult. *B*. A close-up view of the adult found in that crevice.

Table 4. Location and numbers of Craveri's Murrelet chicks per adult-chick group seen in the Gulf of California in April 1972 and May 1974.

Area	No. of groups 1972	No. of groups 1974	Chicks per adult-chick group 1972	Chicks per adult-chick group 1974	Chicks per adult 1972	Chicks per adult 1974
North end Is. Angel de la Guarda	11		1.5		0.8	
Bahía de los Angeles	13	8	1.5	1.2	0.9	0.7
Islas Cardinosa and Raza	8		1.5		0.8	
Islas Salsipuedes and las Animas	15	2	1.7	1.5	0.9	1.0
Isla San Esteban	5		1.2		0.6	
Totals[1]	52	10	1.5	1.3	0.8	0.8

[1] Data include 111 adults and 93 chicks. Only three adult-chick groups seen in 1973--young per group = 1.3, and young per adult = 1.0.

chick group (2 adults and 2 chicks) with small chicks near Bahía Remedios, Baja California, within 30 m of the mainland and at least 10 km from any islands. Thus, nesting on the mainland in situations where the shoreline is isolated and protected from predators by precipitous and extensive cliffs (as at this particular area near Bahía Remedios) seems possible.

For the 63 museum sets of eggs believed to represent complete clutches, clutch size averaged 1.94 (C/1-7, C/2-53, C/3-3). Brewster (1902: 19) states that adult females collected during the breeding season off La Paz, Baja California, had two "bare incubating spaces on the belly." The three-egg clutches, thus, probably represent eggs from more than one female. In seven nests examined in 1974 (Table 3), the mean clutch size was 1.85. Excluding the three-egg clutches above, the mean clutch size, including our field data, is 1.88.

The young are protected with heavy down at hatching and move to sea 2 to 4 days after hatching (Bent 1919: 54, Bancroft 1927). Most of the young murrelets we saw at sea were one-fourth to two-thirds grown; and they were most often detected by their calls. Parent-chick groups were observed near several islands from 1972 to 1974 (Table 4), usually less than 1.6 km from shore. We could not determine the origins of these groups, and assumed that those with small young and those very near shore had bred nearby. As the season progressed, groups were found farther at sea. The young were always near adults at least until late June, when they could no longer be distinguished.

The average number of young per parent-chick group was nearly constant in the area surveyed in 1972 and 1974 (Table 4). We devoted more effort to locating parent-chick groups in 1972 and 1973. Our few observations in 1974 were due to reduced effort. In view of the data on clutch size, two parent-chick groups were not included in our analysis, one with three chicks and one with four.

Few juvenile murrelets were encountered in 1973. In April-May 1972 (the period of expected greatest frequency of emerging young), young were tallied on 49 of 71 trips (65%) (95% Confidence Limits = 63% - 77%), whereas in 1973, they were tallied on only 3 of 18 trips (16%) (95% Confidence Limits = 4% - 41%). In 1972, we also estimated, on the basis of encounters with adults only or adults plus

Figure 6. A group of Craveri's Murrelets (apparently four adults and two chicks) seen near Isla Smith on 29 June 1971. Such groups were not commonly seen. Note the dark underwing coverts.

young, that 79% of pairs in the Midriff Region produced young; in 1973, only 12% bred successfully. Productivity apparently returned to normal in 1974 (Table 4). Other seabirds in the Midriff area also produced few young in 1973 (Anderson 1973).

Attendance of chicks and the pair bond.—Craveri's Murrelets remain close to their young during the postbreeding period and apparently forage as a family unit. Two adults were seen with 81% of the broods in 1972 and solitary murrelets were rare in all years. In fact, adult murrelets were paired most of the times we saw them, except possibly during incubation when adults would be expected to be separated (Sealy 1975). Frequent observations of "twosomes" at sea during the nonbreeding period, and the high frequency of adult male-female duos collected at sea (J. R. Jehl, Jr., pers. comm.) suggest that *Endomychura* murrelets remain paired year-round. There are no data to suggest that "twosomes" observed after the breeding season represent parent-chick groups that have split to one adult and one chick, as has been reported for Common Murres *(Uria aalge)* (Scott 1973).

Feeding and food habits.—We never saw murrelets feeding in close association with other seabirds. They fed alone 74 of the 78 times we observed them in 1973 and all 25 times in 1974. (We had the same impression in 1972, although we did not record murrelet associations that year.) On the other four occasions in 1973, murrelets were feeding in the general vicinity of feeding Common Dolphins *(Delphinus bairdi)* or Eared Grebes *(Podiceps nigricollis)*.

In addition, murrelet groups rarely fed with each other and only rarely did "assemblages" of murrelets involve multiple pairs (Table 2) or multiple parent-chick groups (Fig. 6). Sometimes Craveri's Murrelets form "assemblages to exploit a local food source, but this seems rare during the breeding season. Common Murres, Rhinoceros Auklets *(Cerorhinca monocerata)*. and Tufted Puffins *(Lunda cirrhata)*, on the other hand, are frequently seen in mixed-species feeding flocks off the Oregon coast (J. M. Scott, pers. comm.), and numerous alcid species are involved in "interspecific feeding assemblages" off British Columbia (Sealy 1973).

Table 5. Identifiable food items found in five Craveri's Murrelet stomachs collected in the Gulf of California in 1971.

IDENTIFICATION[1] Common name (Scientific name)	No. individual food items	No. Murrelets
SCORPAENIDAE - rock fishes		
Rockfish (Sebastes sp.)	17	4
CLUPEIDAE - herrings		
Thread Herring (Opisthonema? sp.)	12	4
MYCTOPHIDAE - lantern fishes		
(Benthosema panamense)	8	4
CARANGIDAE - jacks		
(Caranx? sp.)	1	1
SCOMBRIDAE - mackerels		
Pacific Mackerel (Scomber japonicus)	1	1
UNIDENTIFIED FLATFISH	1	1
OTHER UNIDENTIFIED	2	1
INVERTEBRATES		
Unidentified squid	1	1
Unidentified shrimp	many	1

[1] Names are in most part from Miller and Lea (1972) and specimens were identified by J. E. Fitch (personal communication).

Fish otoliths and other undigested materials were removed from five murrelet stomachs collected in 1971 (Table 5); all otoliths except the lantern fishes were from larval fishes. The composition of these samples indicated that the murrelets had been feeding at or near the surface over deep waters (J. E. Fitch, pers. comm.).

Fish dominated, although invertebrates were also present (Table 5). The largest whole fish found in the murrelet stomachs were 40 to 70 mm long. Fish seen passed from adults to chicks were about the same size.

Predation.—The vulnerability of murrelets in their nesting cavities is readily apparent from the ease with which they can be captured. However, we found no evidence of predation on adults in nesting crevices, although we did observe some punctured eggs on Islas Cardinoas and Tassne.

Cats have been serious predators on murrelets and other alcids on some islands (Green and Arnold 1939; Hunt and Hunt 1974; Wright 1909; van Denburgh 1924), but we found no evidence of such predation in the Gulf of California. There are feral cats and rats (*Rattus* sp.) on some of the islands in the Gulf of California, and the spread of any introduced predators should be considered a threat to murrelets.

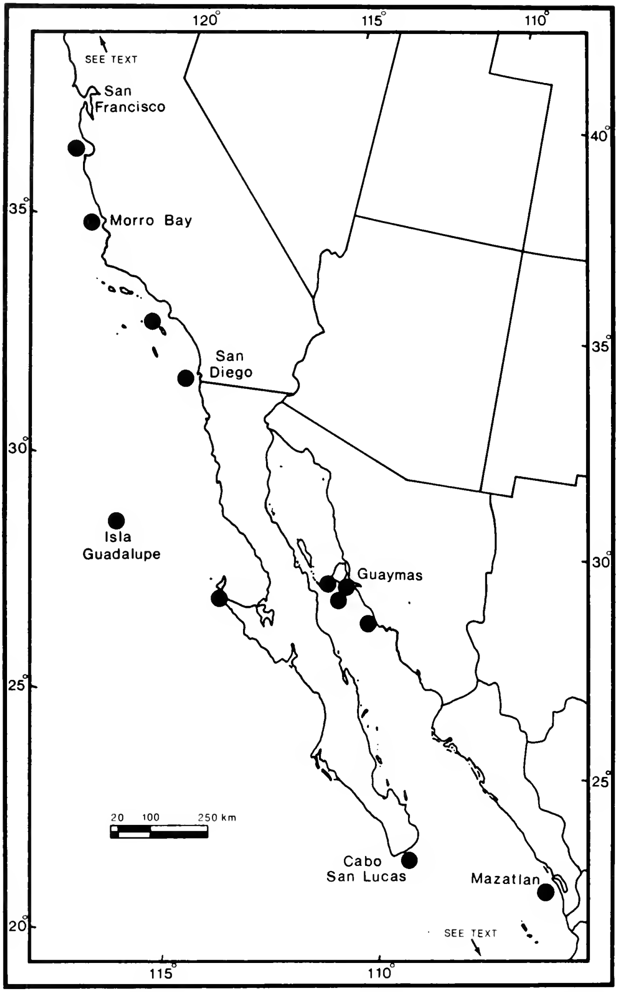


Figure 7. Summary of records of Craveri's Murrelets outside the known breeding season. Circles represent birds seen or collected.

Thoresen (1964) reported that Western Gulls *(Larus occidentalis occidentalis)* preyed heavily on Cassin's Auklets *(Ptychoramphus aleutica)* chicks on or near their nesting islands in central California. Western Gulls are also known to attack adult murrelets (Oades 1974). We never saw an attack by Yellow-footed Western Gulls *(L. o. livens)* in the Gulf, even though the gulls were numerous near murrelet nesting areas.

We found evidence of predation on adult murrelets at several Peregrine Falcon *(Falco peregrinus)* eyries; and at one eyrie, Craveri's Murrelet remains constituted 8% of the food items. On Isla Tassne, we also observed heads and wings of adult murrelets left by Barn Owls *(Tyto alba)*. Banks (1963b) also reported murrelet remains at Peregrine eyries and in the pellets of barn owls from the Gulf of California, and these two avian predators are likely the major natural predators of nesting murrelets. Most murrelets taken are probably adults captured entering and leaving their nesting cavities, or at sea during the day.

POSTBREEDING DISPERSAL

Since most research in the Gulf of California is conducted during the breeding season, little information is available on murrelets during the postbreeding period. van Rossem (1945: 96) reported them in midwinter in the Gulf. As shown in Figure 4, murrelets largely disappear from the Gulf in June and July, though perhaps never completely. Records after the breeding season are summarized in Figure 7 and Table 1.

After breeding, Craveri's Murrelets are found regularly on the Pacific Coast from northwestern Baja California to Monterey, California (Grinnell 1928, Jehl and Bond 1975); and there is one recent record for Oregon (Jehl 1975).

Grinnell and Miller (1944: 180) considered Craveri's Murrelets off California as "autumnal visitants;" they believed that in some autumns this species reached the California Coast in considerable numbers. This fall influx parallels in timing and variable intensity a similar movement of California Brown Pelicans *(Pelecanus occidentalis californicus)*, Heermann's Gulls *(Larus heermanni)*, and other species from the Gulf of California to the Pacific Coast of Baja California and California (Anderson and Anderson 1976).

Increased interest and effort by offshore observers probably accounts for the recent increase in Craveri's Murrelet sightings off the coast of California (McCaskie 1971). Likewise, the lack of Xantus' Murrelet reports off the Oregon and Washington coasts has been attributed to the scarcity of observers until 1969 (Scott et al. 1971). McCaskie (1969) suggests that the difficulty in distinguishing *E. craveri* from *E. hypoleuca* in the field probably also limited earlier reports of Craveri's off California. Since 1968, they have been reported with regularity, though in varying abundance, in late summer (McCaskie 1972).

Other areas were postbreeding distribution should be investigated are the coastal areas off mainland Western Mexico and south. Alden (1969: 58-60) stated that murrelets can be seen on "winter boat trips" as far south as Mazatlan, Sinaloa. This report is imprecise and more detail would be desirable. It is, however, apparently the only report that murrelets are common in winter outside the Gulf of California, and to the south. We suspect that the distribution of *E. craveri* may extend even farther south than Mazatlan. Jehl (1974) reported a Craveri's Murrelet off the coast of Guatemala in April 1973. This record is especially unusual because it occurred during the normal breeding season, but was obtained in a year of breeding failure for murrelets in the Gulf of California.

ACKNOWLEDGMENTS

These observations were incidental to other research in the Gulf of California supported by the U.S. Fish and Wildlife Service as sanctioned by the Dirección General de la Fauna Silvestre, Departamento de Conservación, Mexico City. We thank the following persons for assistance in our research or comments on the manuscript: D. G. Ainley, R. C. Banks, L. C. Binford, M. A. Haegele, J. R. Jehl, Jr., Ann M. Jones Bean. J. O. Keith, M. Friend, K. A. King, L. C. McEwen. J. E. Mendoza, A. R. Phillips, J. M. Scott, and M.D.F. Udvardy. We are especially grateful to John E. Fitch, California Department of Fish and Game for identification of food items from murrelet stomachs.

LITERATURE CITED

ALDEN, P., 1969. Finding the birds in Western Mexico. University of Arizona Press. Tucson. 138 p.

AMERICAN ORNITHOLOGISTS' UNION, 1957. Check-list of North American birds. 5th ed. American Ornithologists' Union, Baltimore.

Anthony, A. W., 1900. Notes on the genus *Micruria*. Auk 17: 168-169.

Anderson, D. W., 1973. Gulf of California seabird breeding failure. Smithsonian Institution Event Notification Report No. 80-73.

Anderson, D. W. and I. T. Anderson, 1976. Distribution and status of brown pelicans in the California Current. American Birds 30(1): 3-12.

Bancroft, G., 1927. Notes on the breeding coastal and insular birds of central Lower California. Condor 29: 188-195.

Banks, R. C., 1963a. Birds of Cerralvo Island. Condor 65: 300-312.

Banks, R. C., 1963b. Birds of the Belvedere expedition to the Gulf of California. San Diego Society of Natural History Transactions 13: 49-60.

Bent, A. C., 1919. Life histories of North American diving birds. United States National Museum Bulletin 107. 239 p.

Brewster, W., 1902. Birds of the Cape district, Lower California. Museum of Comparative Zoology Bulletin 41: 1-241.

DeLong, R. L. and R. S. Crossin, (Ms.) Status of seabirds on Islas de Guadalupe, Natividad, Cedros, San Benitos, and Los Coronados. Submitted to Proceedings California Academy of Sciences.

Grant, P. R., 1964. Birds of the Tres Marietas Islands, Nayarit, Mexico. Auk 81: 514-519.

Grant, P. R. and I. M. Cowan, 1964. A review of the avifauna of the Tres Marias Islands, Nayarit, Mexico. Condor 66: 221-228.

Green, J. E. and L. W. Arnold, 1939. An unrecognized race of murrelet on the Pacific Coast of North America. Condor 41: 25-29.

Grinnel, J., 1928. A distributional summation of the ornithology of Lower California. University of California Publications in Zoology 32: 1-300.

Grinnel, J. and A. H. Miller, 1944. The distribution of the birds of California. Pacific Coast Avifauna No. 27. 608 p.

Hunt, G. L., Jr. and M. W. Hunt, 1974. Trophic levels and turnover rates: the avifauna of Santa Barbara Island, California. Condor 76: 363-369.

Jehl, J. R., Jr., 1974. The near-shore avifauna of the Middle American West Coast. Auk 91: 681-699.

Jehl, J. R., Jr., 1975. A Craveri's Murrelet from Oregon. Western Birds 6: 109.

Jehl, J. R., Jr., and S. I. Bond, 1975. Morphological variation and species limits in murrelets of the genus *Endomychura*. San Diego Society of Natural History Transactions 18: 9-23.

Lamb, C. C., 1927. The birds of Natividad Island, Lower California. Condor 29: 67-70.

McCaskie, G., 1969. Southern Pacific Coast Region. Audubon Field Notes 23: 108.

McCaskie, G., 1971. Southern Pacific Coast Region. American Birds 25: 906.

McCaskie, G., 1972. Southern Pacific Coast Region. American Birds 26: 121.

Miller, D. J. and R. N. Lea, 1972. Guide to the coastal and marine fishes of California. Caliornia Department of Fish and Game, Fish Bulletin 157. 235 p.

Oades, R. D., 1974. Predation of Xantus' murrelets by western gull. Condor 76: 229.

Ridgway, R., 1919. Birds of North and Middle America. United States National Museum Bulletin 50, part 8. 852p.

Scott, J. M., J. Butler, W. G. Pearcy and G. A. Bertrand, 1971. Occurrence of the Xantus' Murrelet off the Oregon coast. Condor 73: 254.

Scott, J. M., 1973. Resource allocation in four synoptic species of marine diving birds. Unpub. Ph.D. Thesis. Oregon State University, Corvallis.

Sealy, S. G., 1973. Interspecific feeding assemblages of marine birds off British Columbia. Auk 90: 796-802.

Sealy, S. G., 1975. Aspects of the breeding biology of the Marbled Murrelet in British Columbia. Bird-Banding 46: 141-154.

Stager, K. E., 1957. The avifauna of the Tres Marias Islands, Mexico. Auk 74: 413-432.

Thoresen, A. C., 1964. The breeding behavior of the Cassin Auklet. Condor 66: 456-476.

van Denburgh, J., 1924. The birds of the Todos Santos Islands. Condor 26: 67-71.

van Rossem, A. J., 1915. Notes on murrelets and petrels. Condor 17: 74-78.

van Rossem, A. J., 1926. The Craveri murrelet in California. Condor 28: 80-83.

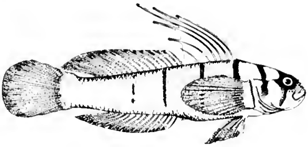
van Rossem, A. J., 1932. The avifauna of Tiburon Island, Sonora, Mexico, with descriptions of four new races. San Diego Society of Natural History Transactions 7: 119-150.

van Rossem, A. J., 1945. A distributional survey of the birds of Sonora, Mexico. Museum of Zoology Louisiana State University Occasional Paper No. 21. 379 p.

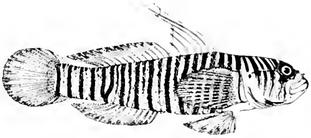
Willett, G., 1933. A revised list of the birds of Southwestern California. Pacific Coast Avifauna No. 21. 204 p.

Wright, H. W., 1909. An ornithological trip to Los Coronados Islands, Mexico. Condor 11: 96-100.

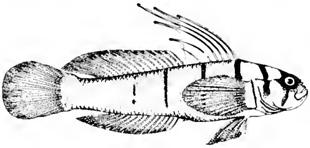
U.S. Fish and Wildlife Service, Denver Wildlife Research Center, Building 16, Federal Center, Denver, CO 80225. Present address of L. R. DeWeese: P.O. Box C, Davis, CA 95616. Present address of D. W. Anderson: Division of Wildlife and Fisheries Biology, University of California, Davis, CA 95616.

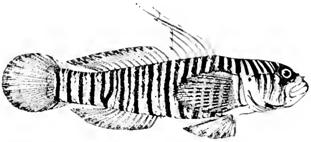


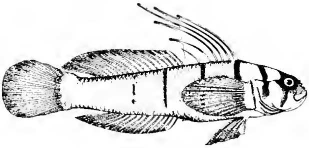
LIFE HISTORIES AND SYSTEMATICS OF THE WESTERN NORTH AMERICAN GOBIES *LYTHRYPNUS DALLI* (GILBERT) AND *LYTHRYPNUS ZEBRA* (GILBERT)



James W. Wiley

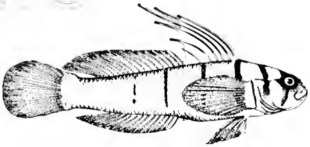






TRANSACTIONS

OF THE SAN DIEGO
SOCIETY OF
NATURAL HISTORY



VOL. 18, NO. 10 5 OCTOBER 1976

Life histories and systematics of the Western North American Gobies *Lythrypnus dalli* (Gilbert) and *Lythrypnus zebra* (Gilbert)

James W. Wiley

Abstract.—Life history investigations of *Lythrypnus dalli* and *Lythrypnus zebra* were conducted primarily on rocky reefs at Punta Banda, Baja California, Mexico, at depths of 3 to 53 m. Both species are common, but *L. zebra* tends to remain in less exposed situations and to be less numerous. Crustaceans, primarily copepods, are the major food of each species. Each species was parasitized by acanthocephalans, and by cymothoid isopods. The sex ratio among adults was 1 male to 1.61 females in *dalli* and 1:1.09 in *zebra*. Length-frequency distributions indicate two age classes in each species. Each species breeds within the first year and has a two-year life span. Males average larger than females: ripe females exceeded 22.0 mm in *dalli* and 20.7 mm in *zebra;* mature males exceeded 23.0 mm in *dalli* and 18.4 mm in *zebra*. Ripe individuals were present from March (in *dalli*) or April (in *zebra*) through October (in each species). *Lythrypnus dalli* tends to lay more eggs than *zebra* (1058 vs. 627). Eggs of *dalli* are deposited in empty mollusk shells of the reef epibiose or in unattached shells on the floor of the goby's shelter, whereas the eggs of *zebra* are attached to the roof of the shelter or to empty mollusk shells. Sexual dimorphism is evident in the fins and genital papilla.

The goby genus *Lythrypnus* is well represented in tropical and subtropical inshore waters of the eastern Pacific and western Atlantic. Most species are small, brightly colored, and have bars on the head and body. The bluebanded goby, *Lythrypnus dalli* (Gilbert), is bright coral-red with 5 to 9 blue bars on the anterior part of the body (Fig. 1). The zebra goby, *Lythrypnus zebra* (Gilbert), is cherry-red to brick-red, with 13 to 18 narrow blue bars on the head and body (Fig. 2). *Lythrypnus dalli* is readily distinguished from *L. zebra* by having higher meristic counts and fewer and wider bars on the body. Both are common inhabitants of rocky reefs along the coasts of southern California and Baja California, Mexico. Pequegnat (1964) found *dalli* to be the most abundant fish in the rock-reef formation at Corona del Mar, California, and *zebra* to be less common. Despite their abundance and the intriguing problem of niche specificity, little is known of the biology of these gobies.

STUDY AREA

Lythrypnus dalli and *L. zebra* were studied in the field simultaneously with the bluespot goby, *Coryphopterus nicholsii* (Wiley, 1973), from September 1966 through September 1969. Observations and collections were made primarily on the northeastern side of Punta Banda, Baja California, Mexico. Study reefs varied from 6 to 20 m in depth. Collections were also made in California at La Jolla, San Diego Co.; at San Clemente and Laguna Beach, Orange Co.; and at Palos Verdes and Santa Catalina Island, Los Angeles Co. Other collections were made in Baja California, Mexico at San Quintín and Islas Todos Santos.

METHODS AND MATERIALS EXAMINED

SCUBA was used in making observations and collections. Specimens were collected with "Chem-Fish" or with a slurp gun. The Punta Banda population was sampled at monthly intervals from July 1967 through September 1969 between

SAN DIEGO SOC. NAT. HIST., TRANS. 18(10):169-184, 5 OCTOBER 1976

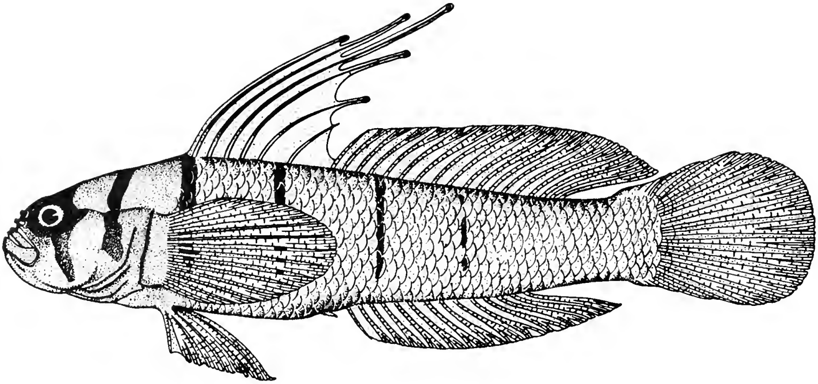


Figure 1. Bluebanded Goby, *Lythrypnus dalli* (Gilbert). Male, 38.3 mm S.L., from Punta Banda, Baja California, Mexico.

1100 and 1400 hrs. Other collections were made irregularly between September 1966 and June 1967. Methods of counting serial parts and taking measurements follow those of Hubbs and Lagler (1958), except that the caudal-ray counts follow the methodology of Ginsburg (1945). The last two ray bases of the dorsal and anal fins were counted as one ray. All measurements were taken with dial calipers to the nearest 0.1 mm. Proportions, obtained arithmetically, are presented as ranges and means. All measurements of body length are standard lengths (S.L.).

Museum specimens examined were from the collections of Stanford University (SU); California Academy of Sciences (CAS); Scripps Institution of Oceanography (SIO); University of California, Los Angeles (UCLA); and Los Angeles County Museum of Natural History (LACM).

Detailed tables of morphometric and meristic comparisons between populations of *L. dalli* and *L. zebra* have not been included in this paper, as I found no differences in the morphometrics and meristics which would warrant systematic recognition in either species. Copies of the tabular material (Tables 1-5) have been filed at the Carl Hubbs Library at Scripps Institution, Los Angeles County Museum, National Museum of Natural History—Smithsonian Institution, and the San Diego Natural History Museum. The material has also been deposited with the ASIS National Auxiliary Publications Service (NAPS)[1/].

BLUEBANDED GOBY
Lythrypnus dalli (Gilbert)

Gobius dalli.—Gilbert, 1890: 50, 73-74 (original description; off San José Island, Mexico, and Catalina Harbor, Catalina Island, California; 33 fm., 35 fm.). Eigenmann and Eigenmann, 1892: 354 (San Pedro, California). Jordan and Evermann, 1896: 458 (Catalina Harbor, Catalina Island, California; listed). Jordan and Evermann, 1898: 2230-2231 (description; Catalina Harbor, Catalina Island, California; 35 fm.). Rutter, 1904: 253 (6 specimens from San José Island, Gulf of California, Mexico; largest 1.4 inches long). Fowler, 1923: 293 (Isthmus Harbor, Catalina Island, California; listed). Koumans, 1931: 114 (description of genus *Lythrypnus* using *Gobius dalli* as type).

Lythrypnus latifascia.—Ginsburg, 1939: 54 (description of new species; holotype—Fisherman's Cove, Catalina Island, California; female—22 mm long; compared with *Lythrypnus dalli*). Ginsburg, 1945: 137 (caudal fin ray count).

Microgobius cinctus.—Nichols, 1952: 4-5, fig. 2 (description of type, paratype; Carmen Island, Gulf of California, Mexico). Birdsong, 1967: 466-467 (*Microgobius cinctus* a junior synonym of *L. dalli*).

[1/] See NAPS Document #02878 for 11 pages of supplementary material. Order from ASIS/NAPS, Microfiche Publications, P.O. Box 3513, Grand Central Station, New York, New York 10017. Remit in advance $3.00 for microfiche copy or $5.00 for photocopy. All orders must be prepaid. Institutions and organizations may order by purchase order. However there is a billing and handling charge for this service. Foreign orders add $3.00 for postage and handling.

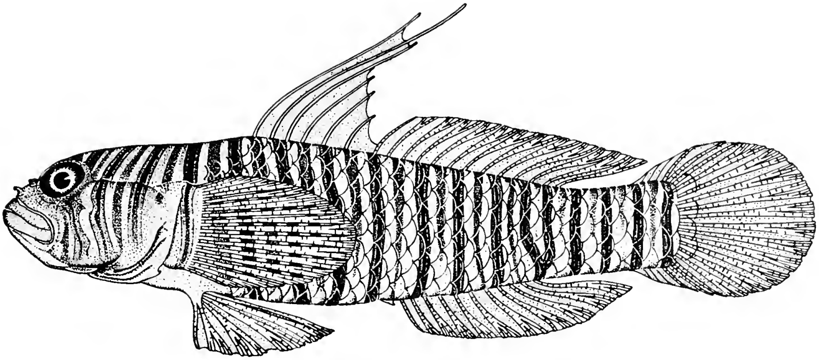


Figure 2. Zebra Goby, *Lythrypnus zebra* (Gilbert). Male 37.5 mm S.L., from Punta Banda, Baja California, Mexico.

Lythrypnus dalli.—Starks and Morris, 1907: 224-225 (Gulf of California, Mexico; Catalina Island and San Pedro, California; abundant in Catalina Harbor; description). Ulrey and Greeley, 1928: 20 (Catalina Harbor and Isthmus Harbor, Catalina Island; Gulf of California, Mexico). Jordan, Evermann and Clark, 1928: 442 (Catalina Harbor, Catalina Island, California). Ulrey, 1929: 10 (listed). Barnhart, 1936: 82, fig. 246 (description; Catalina Island, California; tide pools to about 300 feet; rare). Ginsburg, 1939: 53-54 (restriction of *Lythrypnus dalli;* description; comparison with *Lythrypnus latifascia* (n. sp.); lectotype, Gulf of California, Mexico). Fowler, 1944: 517, 582 (San José Island, Gulf of California, Mexico; listed). Ginsburg, 1945: 136-138, table II (caudal fin-ray count). Fitch, 1947: 191 (Emerald Bay, Santa Catalina Island, California; 20 feet). Hubbs and Follett, 1953: 34 (listed). Limbaugh, 1955: 121 (description; habitat; surface to 100 feet, average 30 feet; Newport Beach, La Jolla, and Santa Catalina Island, California; Los Coronados and Guadalupe Island, Mexico). Herald, 1961: 235-236, plate 101 (Catalina Island, California; fairly common; 20 feet and deeper). Roedel, 1962: 29 (common name, bluebanded goby). Pequegnat, 1964: 279, 280, table V (Corona del Mar, California; listed; population size on rock reef; habitat; most abundant fish on one reef—1,500 adults, 2,500 young). Carlisle, Turner and Ebert, 1964: 15, 28, 73, 77, table 1, Appendix A (observed on artificial reefs and offshore oil installations; spawned on Paradise Cove reef and on Redondo Beach artificial reef, California; average fish population consisted of 11.6% of the gobies *L. dalli* and *Coryphopterus nicholsii,* increased to 42.9% by December, 1960). Turner, Ebert and Given, 1969: 185-186, 208 (Appendix 3), 156 (table 5) (resident on artificial reefs at Hermosa Beach, Malibu, and Redondo Beach, California; observed on natural reefs from Santa Barbara to San Diego on mainland and at Santa Catalina, San Clemente, Anacapa, Santa Cruz, Santa Rosa, and San Miguel islands, California; intertidal to at least 180 feet; general habits). Grigg and Kiwala, 1970: 152, table 2 (Palos Verdes Point, Los Angeles County, California; listed). Macdonald, 1972: 95, 98 (range—northern Gulf of California, Bahía Magdalena, Baja California, Mexico, to Morro Bay, California; cephalic-lateralis system). Miller and Lea, 1972: 186 (description; figure; key; range—Gulf of California to Morro Bay, including Guadalupe Island; intertidal to 210 feet; length to 2.25 inches). Herald, 1972: 209 (common inshore fish of California; coloration).

Diagnosis.—*Lythrypnus dalli* has a color pattern consisting of 4-9 narrow blue bands anteriorly, becoming narrower and fainter posteriorly. Lateral scales 38-54. Pectoral rays 17-20. Anal rays 12-15.

Description.—Body short, compressed. Greatest body depth 4.0-6.2 (4.84) in standard length. Body width 7.7-14.9 (11.31) in standard length. Head high and compressed; head width 1.3-2.2 (1.91) in head length; 3.5-5.1 (4.33) in standard length; blunt, profile rounded; snout short, 1.5-2.5 (1.87) in diameter of orbit. Orbit 2.4-3.8 (3.14) in head length. Mouth moderate, very oblique; lower jaw projecting; maxillary reaching about to under center of eye, 2.1-3.1 (2.66) in head length. Jaws with an outer row of long, distant canine-like teeth, and an inner row or a narrow band of minute teeth. Four large epipores above eye along the line of the supraorbital canal. A median crest extends from the dorsal forward to between the anterior margin of eyes, not extending onto head in smaller individuals. Dorsal VI, 16-19 (17.8); first dorsal spines much produced with lengthened filamentous rays, the longest reaching to beyond the middle of the second dorsal base when depressed; 1.5-4.7 (2.79) in standard length. Dorsal fins separate. Soft dorsal rather high, the fin long, 1.9-2.5 (2.26) in standard length. Anal 12-15 (14.3), somewhat shorter than second dorsal, 2.2-3.1 (2.62) in standard length.

Pectorals 17-20 (18.8); short, 3.0-3.5 (3.3) in standard length; upper rays not free or silk-like. Caudal 17, with 3 above and 3 below segmented, unbranched rays, and 11 segmented, branched rays; rounded. Pelvics free from belly, fully united; with I, 5 rays. Scales ctenoid, of moderate size, covering entire trunk except nape; 38-54 (45.6). Color bright coral red, with 5-9 (6.3) narrow blue bands anteriorly, becoming fainter posteriorly. First bar extends from nape obliquely downward and forward ending on opercle, may be discontinuous; second blue bar runs from origin of first dorsal to behind pectoral base; third runs downward from between last two spines of first dorsal; remaining bars are under soft dorsal. Blue bars not reaching ventral outline. Marked with blue about eye: transverse interorbital blue bar, a continuation of which encircles the orbit; a blue band extends upward and posteriorly from each orbit, uniting on occiput; below orbit, a blue bar consisting of two portions, one dark triangle has its apex downward and obliquely backward across cheek, the other part upward and backward. In larger individuals, a blue streak runs along mid-dorsal line from occiput along profile to front of dorsal intersecting first body bar. Fins unmarked. Eye black. Alcoholic specimens are straw-colored with olive to dark brown bars.

ZEBRA GOBY
Lythrypnus zebra (Gilbert)

Gobius zebra.—Gilbert, 1890: 50, 73 (original description; off Santa Magdalena Island, Mexico; 36 fm.). Jordan and Evermann, 1896: 547 (west coast of Mexico; listed). Jordan and Evermann, 1898: 2226 (description; west coast of Mexico; 36 fm.). Jordan and McGregor, 1898: 284 (2 specimens from Todos Santos and Clarion islands, Mexico; coloration). Fowler, 1923: 293, 300 (Newport and Bird Rock, California).

Zonogobius zebra.—Snodgrass and Heller, 1905: 416, 425 (west coast of Lower California and Clarion Island, Mexico). Starks and Morris, 1907: 223-224 (first record north of southern part of Lower California, Mexico; specimens from San Clemente Island, California, 1 inch long; specimen from Todos Santos Islands, Mexico, 1½ inches long; description). Hubbs, 1916: 163-164 (24 specimens from San Clemente Island, California; variation from type; measurements and counts of 5 specimens; description). Ulrey and Greeley, 1928: 20 (San Clemente Island, Catalina Island and Newport, California, and Todos Santos and Guadalupe islands, Mexico). Jordan, Evermann and Clark, 1928: 441 (Pacific coast of Mexico and southern California). Ulrey, 1929: 10 (listed). Barnhart, 1936: 82 (description; Mexico to southern California; San Clemente Island, California).

Lythrypnus zebra.—Ginsburg, 1938: 115-116 (relationship between *Lythrypnus pulchellus* and *L. zebra;* differences in color patterns; the 2 populations tentatively recognized as distinct species; pectoral rays 19-20; southern California). Fowler, 1944: 517 (Mexico; listed). Hubbs and Follett, 1953: 34 (listed). Limbaugh, 1955: 120-121 (description; habitat; tide pools to 110 feet, average 27 feet; Newport Beach, La Jolla, and San Miguel, Santa Catalina, and Santa Cruz islands, California, and Los Coronados and Guadalupe Island, Mexico). Herald, 1961: 236 (description; common). Roedel, 1962: 29 (common name, zebra goby). Pequegnat, 1964: 279, table V (Corona del Mar, California; habitat; less common than *Lythrypnus dalli;* 200 individuals on reef). Best and Oliphant, 1965: 101 (Pt. Arguello, California; listed). Turner, Ebert and Given, 1969: 186, 208 (Appendix 3), 158 (table 5) (observed on Hermosa Beach, California artificial reef; resident; less numerous than *Lythrypnus dalli*). Grigg and Kiwala, 1970: 152 (table 2) (Palos Verdes Point, California; listed). Macdonald, 1972: 94-95 (range—Cedros Island, Mexico to Ventura County, California; cephalic-lateralis system indicates relationship between *Coryphopterus* and *Lythrypnus*). Miller and Lea, 1972: 186, 187 (figure; description; key; range—Clarion Island, Mexico, to Lion Rock, San Luis Obispo County, California, including Guadalupe Island, Mexico). Herald, 1972: 209 (pacific North America; life colors). Quast, 1968: table 2 (northern into central temperate; 0-130 feet).

Diagnosis.—Color pattern consisting of 13-18 narrow blue bands becoming indistinct on lower parts of sides. Lateral scales 24-30. Pectoral rays 18-21. Anal rays 9-11.

Description.—Body short and compressed. Width of body 7.1-9.0 (7.95) in standard length. Greatest body depth 4.1-5.0 (4.48) in standard length. Head high, 2.3-4.4 (3.76) in standard length; blunt, profile rounded, somewhat compressed; head width 1.1-1.6 (1.44) in head length; snout short, 1.0-1.6 (1.31) in diameter of orbit. Orbit 3.0-4.1 (3.58) in head length. Mouth moderate, 2.2-3.2 (2.70) in head length; oblique, maxillary reaching below anterior third of orbit; lower jaw projecting. Teeth in a narrow maxillary band, outer series enlarged and spaced; and in wide mandibular band with a single series, similar to the outer row in upper jaw. No ridge or crest in front of dorsal. Interorbital very narrow. Four large epipores above the eye along the line of supraorbital canal. Dorsal VI, 11-14 (12.9); first dorsal spines filamentous in adults; last soft ray of dorsal and anal longest; dorsal fins separate; length first dorsal rays 2.6-4.6 (3.76) in standard length; length second dorsal rays 2.2-2.8 (2.60) in standard length. Anal 9-11 (10.0); length anal 2.5-3.3 (2.88); anal base somewhat shorter than base of second dorsal; upper rays not free or silk-like. Caudal 17; with 3 above and 3 below segmented, unbranched rays and 11 segmented, branched rays; rounded. Pelvics free from belly, fully united; I, 5 rays. Scales ctenoid, with a row of apical spines; no scales on head, belly, or along base of spinous dorsal; 24-30 (26.1). Life colors cherry-red to brick-red ground color, with 13-18 (15.1) blue cross bars on head and sides; blue bars half as wide as interspace in large specimens, relatively much wider in smaller specimens; blue bands darker than interspaces; on middle of interspaces a very narrow blue line, becoming indistinct on lower parts of sides; area on either side of cross-bands light in color. Blue bars encircle body except for a short distance on belly and underside of head; on upperside of head and nape these bars run obliquely forward and downward, but elsewhere are vertical; on cheeks blue bars are connected by narrow cross lines, forming blue reticulations surrounding spots of the red ground color. Bars in alcoholic specimens are olive brown with darker streaks along each border and near the center.

RANGE

Lythrypnus dalli ranges from Morro Bay (35°N), California (Macdonald, 1972), south along the coast of California, the California Channel Islands, the west coast of Baja California, and into the Gulf of California (Bahía de La Paz, 24°N; Carmen Island, 26°N; Isla Angel de la Guarda, 29°N), Mexico.

Lythrypnus zebra ranges from San Luis Obispo Co. (36°N), California, south along Baja California, into the Gulf of California and the west coast of Mexico, to Clarion Island (18°N) of the Revillagigedo Group.

Limbaugh (1955) noted that both species are commoner around the offshore islands than near the mainland, and postulated that this might be due to parasitization of the mainland population by an isopod. He found that nearly all specimens collected on the mainland were infected but those collected on the islands were not. In contrast, I found a low incidence of parasitic isopods on *L. dalli* (4.3% infected, n=909) and *L. zebra* (5.1%, n=314) at Punta Banda, whereas island populations (Todos Santos and Santa Catalina) were more heavily parasitized (*L. dalli*—15.1%, n=73; *L. zebra*—24.1%, n=29).

MERISTICS AND MORPHOMETRICS

Meristic variation was studied in *Lythrypnus dalli* populations of sampled areas (Table 1[2/]). A trend toward higher dorsal and anal fin-ray counts occurred in the northern areas, whereas counts of pectoral rays and scales at midline showed an opposite trend. Fin-ray count modes of prejuveniles of *L. dalli* from Punta Banda were slightly lower than those of adults, perhaps due to delayed development of these elements.

Ginsburg (1939) and Böhlke and Robins (1960) have discussed the importance of color differences in identification of *Lythrypnus* species. Numbers of body bars and measurements of bar widths are included here with the morphometric and meristic data. Northern individuals had fewer body bars than southern gobies.

No notable trend of morphological variation was observed in the *L. dalli* populations sampled (Table 2[2/]). The ratio of standard length to body width decreases irregularly from south to north. However, the Santa Catalina Island population showed narrower bodies than other northern populations. The ratio of standard length to head length increases slightly from south to north, although the Punta Banda population did not fit this trend. A south to north decrease in the ratio of length of eye to width of body bars was also noted.

Ginsburg (1939) designated *Lythrypnus latifascia* as a new species on the basis of it having wider cross bars, higher fin ray counts (D. 18, A. 14-15, P. 18-19) and longer dorsal fin spines than *L. dalli*. Morphometric data for *L. latifascia* (UCLA, SIO, SU) are presented in Table 3[2/]. Meristic data reveal considerable overlap between *L. dalli* and *L. latifascia*, although scale counts were strongly separated; anal fin-ray counts of *L. latifascia* are somewhat lower. I found that many individuals with wide body bars have meristics which by Ginsburg's description would characterize *L. dalli;* other individuals had narrow bars and the *L. latifascia* complement of serial elements. There was a significant difference in the width of body bars number 2 and 3 ($P < 0.001$ and $P < 0.05$, respectively) between

---

[2/] Supplementary material; see bottom of page 170.

the Gulf of California *L. dalli* population and Santa Catalina *L. latifascia* specimens, but not between other sampled populations of *L. dalli* and *L. latifascia*. Means and ranges of the lengths of the first dorsal rays similarly show no distinction between *L. dalli* and *L. latifascia*. I found no behavioral or ecological differences which would support the separation into two species, and therefore have included *Lythrypnus latifascia* as a synonym of *L. dalli*.

Although only a small part of the range of *L. zebra* was examined the meristics in the sampled areas were rather uniform (Table 4[2/]). Scale count modes of Punta Banda specimens were notably higher than those of more northern populations. Prejuveniles, possibly because of delayed development, had fewer scales and body bars than adults.

The morphological data for *L. zebra* are rather uniform and no basic trend in variation of body proportions was noted (Table 5[2/]). The range of the standard length to head length ratio of the Punta Banda sample was far wider than the other populations sampled, although the ratio means were similar.

GENERAL ECOLOGY

Lythrypnus dalli and *L. zebra* were observed on the Punta Banda reefs at depths of 3 to 53 m. Limbaugh (1955) reported that *L. dalli* was found from the surface to 31 m (average depth 9.2 m) while *L. zebra* ranged from tide pools to 34 m (average depth 8.3 m). In the northern part (California) of the 2 species' sympatric range *L. dalli* is typically more numerous than *L. zebra* (Pequegnat, 1964; Turner et al., 1969; pers. obs.). Yet, at poison stations at Punta Banda, Mexico, I found *L. zebra* to be almost as numerous as *L. dalli*. Carl L. Hubbs (pers. comm.) noted that *L. zebra* was taken more commonly in poisoning operations at Isla de Guadalupe, Mexico. Apparently relative abundance of the two species varies greatly between areas, perhaps with *L. zebra* becoming proportionately commoner in southern parts of the ranges.

Both species prefer areas of rock reefs with little or moderate shell epibiose and particularly those areas that are not covered with algae or mosslike animals. The gobies remain near holes or cracks in the reef into which they retreat from

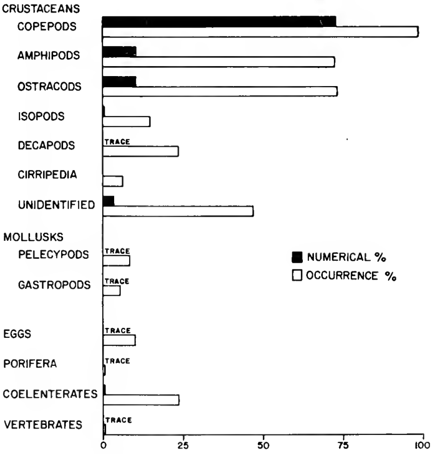


Figure 3. Analysis of 441 digestive tracts of *Lythrypnus dalli* collected at Punta Banda (NE), Baja California, Mexico, from September 1966 to September 1969.

danger. *Lythrypnus dalli* lives in crevices on the sides or upper surfaces of reefs and is commonly seen in exposed situations. *Lythrypnus zebra* prefers to remain under rocks, in caves, or far back in crevices and is less commonly observed. *Lythrypnus zebra* was frequently observed farther back in the same crevice or hole used by *L. dalli.* Pequegnat (1964) observed that *L. zebra* is characteristic of the middle-third of the reef while *L. dalli* is more often restricted to the reef base. I did not observe such distributional restrictions on the Punta Banda study reefs.

Both species are territorial and guard the shelter against intruders. In the aquarium, shelters were defended by the resident dashing out at the intruder, whereupon the latter would retreat. Occasional nip-and-chase sequences were observed in the laboratory and on the reefs.

Both species are brightly colored. *Lythrypnus dalli* appears particularly conspicuous to the human observer in its typical exposed position on a rock face. This raises the question of a possible aposematic function for the color pattern. However, during collections with Chem-Fish, poisoned individuals of *L. dalli* and *L. zebra* were frequently eaten by kelp bass (*Paralabrax clathratus*) and sheephead (*Pimelometopon pulchrum*). This suggests that these gobies are not distasteful.

FOOD HABITS

Food studies were conducted to identify the major foods, to determine if differences in seasonal utilization occurred, and to disclose any variation in the foods taken by different-sized fish. Two methods of analysis were used: numerical and

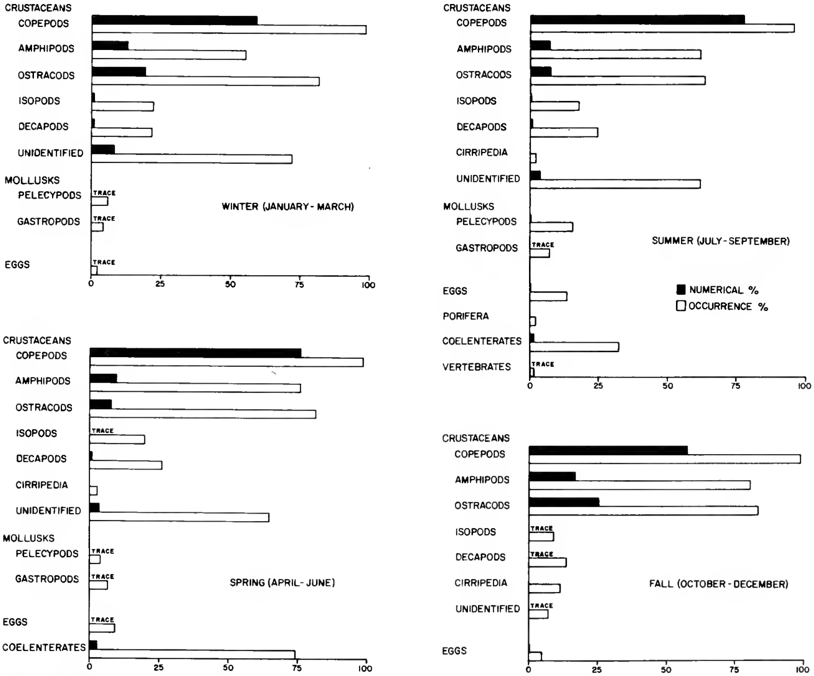


Figure 4. Seasonal analysis of the digestive tract contents of *Lythrypnus dalli.*

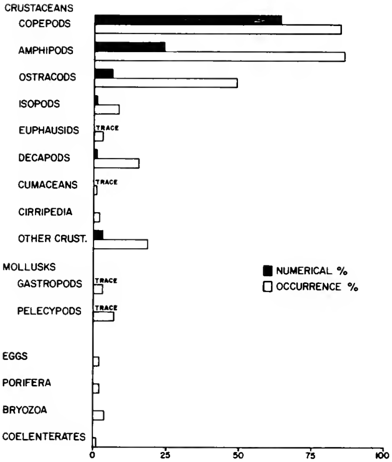


Figure 5. Analysis of 141 digestive tracts of *Lythrypnus zebra* collected at Punta Banda (NE), Baja California, Mexico, from September 1966 to September 1969.

frequency-of-occurrence. Stomach contents from 441 specimens of *L. dalli* and of 141 *L. zebra* collected at Punta Banda were analyzed.

Limbaugh (1955) reported that *L. dalli* feeds upon small crustaceans, including amphipods. I found that crustaceans comprised 98.5% of the items in the digestive tract (Fig. 3). Copepods were dominant, forming 72.4% of all items and being present in 97.2% of the stomachs examined. Ostracods and amphipods were next in importance, each forming 10.4% of the food items. Ostracods were found in 72.6%, and amphipods in 71.5%, of the stomachs examined. Other foods were generally in very small quantities. Only moderate seasonal variation was observed (Fig. 4). Copepods were found in the greatest numbers and in nearly every stomach examined during all seasons. Amphipods and ostracods became relatively more important in fall and winter. Coelenterates were taken in spring and summer, but were not found in the fall or winter samples. Occurrence of minor food classes (i.e. mollusks, eggs, vertebrates, sponges) increased during the summer season. No variation in diet between different-sized *L. dalli* was found.

Crustaceans are also the principal food item of *L. zebra* (Fig. 5), comprising 99.3% of the food items. Crustaceans were found in all stomachs examined. Copepods (63.1%), amphipods (24.2%), and ostracods (6.3%) were the most abundant crustaceans taken by *L. zebra.* Other foods (mollusks, bryozoans, and eggs) were found infrequently and in very small numbers.

Copepods were found in 85.1% of the stomachs (frequency-of-occurrence), amphipods in 86.3%, and ostracods in 49.0%. Very little seasonal variation was observed in the diet of *L. zebra.* Copepods and amphipods were the most important items during most seasons (Fig. 6). Copepods were taken more often than amphipods except in winter. Ostracods were of minor importance except in fall, when they were taken more frequently than amphipods. Several minor food classes (i.e. eggs, sponges, bryozoans, coelenterates) were noted during the summer only. No variation in diet between different-sized *L. zebra* was found, although sample size for younger individuals was too small for analysis.

Evidently, *L. dalli* and *L. zebra* depend primarily upon free-swimming or planktonic organisms and take benthic or burrowing forms only incidentally.

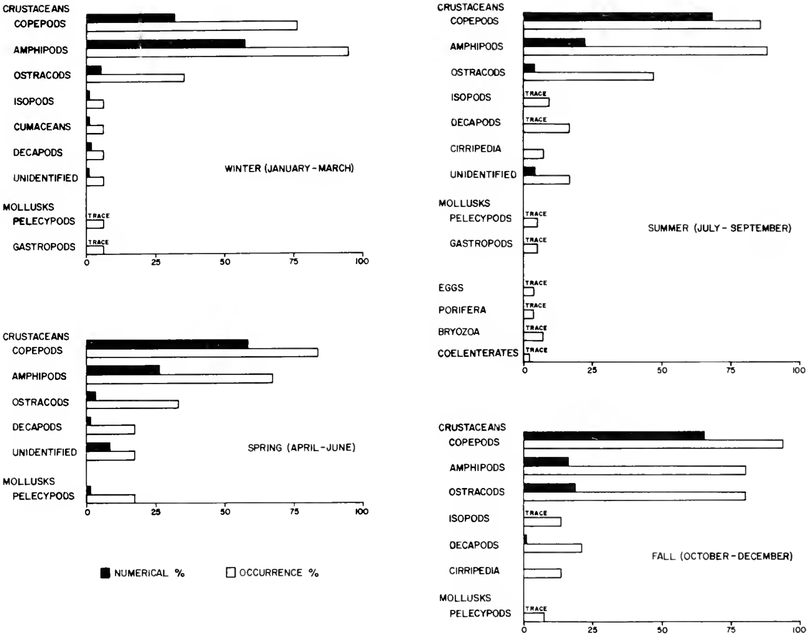


Figure 6. Seasonal analysis of the digestive tract contents of *Lythrypnus zebra.*

Feeding behavior of *L. dalli* consists of the goby swimming out from the reef about 1-5 cm, grabbing an item in midwater, and returning to its position on the reef. *Lythrypnus dalli* was also observed to selectively pick up such items as amphipods and small crabs from the substrate. The few observations that were made on the feeding behavior of *L. zebra* indicate this species takes most of its food from within the home shelter or directly in front of it. *Lythrypnus zebra* was only occasionally observed to feed in the open water in front of its shelter. In the aquarium both species preferred to take the food items (brine shrimp) as they drifted down through the water rather than pick them off the bottom.

PARASITES

Acanthocephalans are common internal parasites of both species of *Lythrypnus.* They were found in the guts of 54.5% (n=241) of *L. dalli* and 75.0% (n=106) of *L. zebra.* As many as 48 acanthocephalans were taken from one digestive tract. Other internal parasites were found infrequently. Nematodes were found in 0.7% of the digestive tracts of *L. dalli* and 3.5% of *L. zebra* guts.

Cymothoid isopods were occasionally found attached to the gills of *L. dalli* and *L. zebra* (see Range section).

POPULATION STRUCTURE

Samples from the *L. dalli* population at Punta Banda showed an adult sex ratio of 1 male to 1.61 females (228 males:368 females). In the juvenile sample (males: 13-22 mm; females: 13-21 mm), the ratio was 1:1.25 (97 males:121 females).

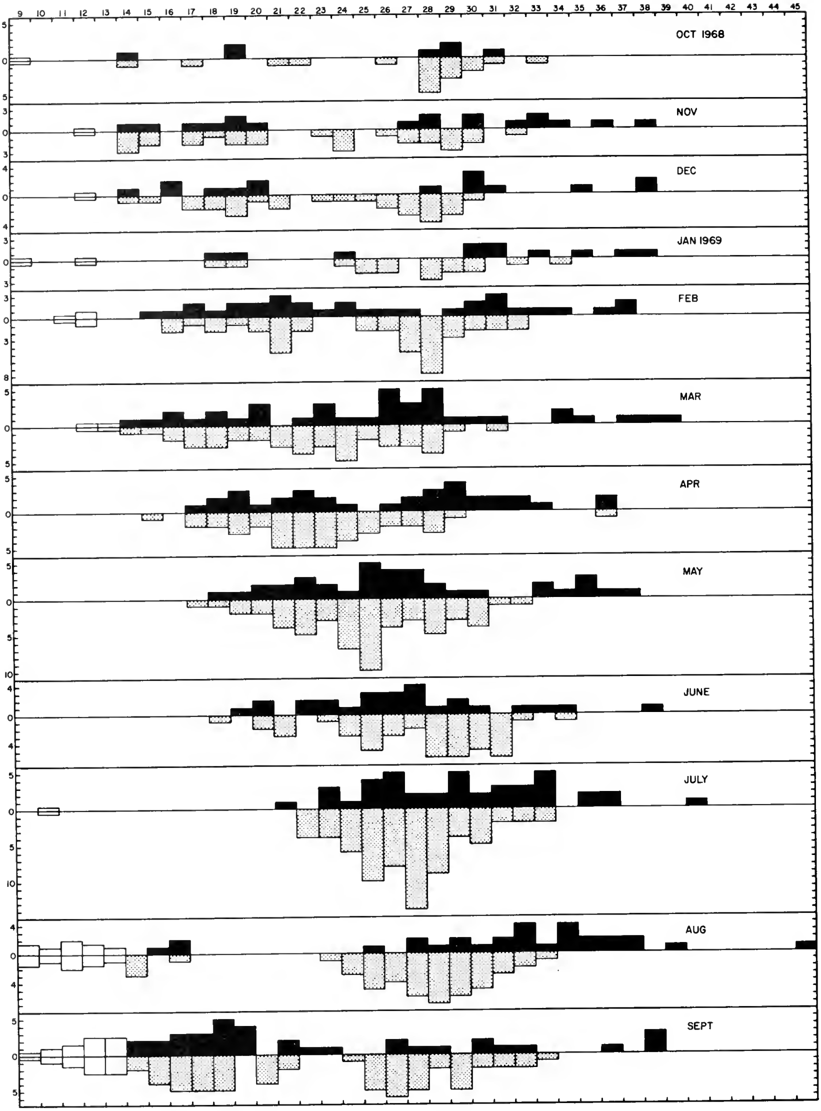


Figure 7. Length-frequency measurements of 852 specimens of *Lythrypnus dalli* taken at Punta Banda (NE), Baja California, Mexico, from October 1968 to September 1969. Clear boxes represent individuals in which sex was undetermined, solid boxes represent males, and half-tone boxes represent female individuals.

Length-frequency distributions of 852 *L. dalli* specimens indicate two age groups in most cases (Fig. 7) although overlap occurs, possibly due to the prolonged spawning period. *Lythrypnus dalli* breeds within the first year, and only a few individuals survive to the second year.

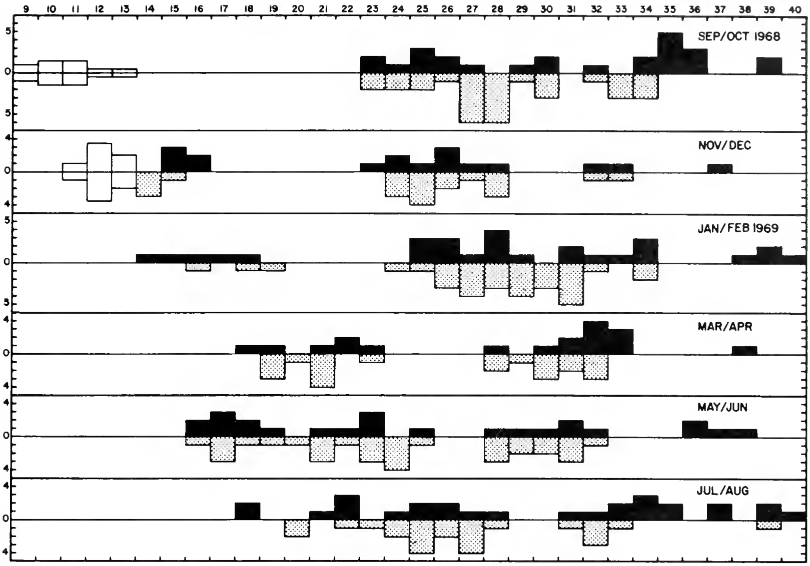


Figure 8. Length-frequency measurements of 314 specimens of *Lythrypnus zebra* taken at Punta Banda (NE), Baja California, Mexico, from September 1968 to August 1969. Legend as in figure 7.

Prejuvenile (less than 10 mm) *L. dalli* (transparent except for the bright blue bars) were observed on the Punta Banda reefs from mid-August to October. However, one 10 mm individual was observed on the reef on 17 July 1969. Pequegnat (1964) noted prejuvenile *L. dalli* on reefs at Corona del Mar, California, from September to November. The young gobies attain a length of 18-20 mm within four or five months.

The sex ratio of adult *L. zebra* collected at Punta Banda was 1:1.09 (125 males:136 females). The juvenile sample (males:14-18 mm; females:14-20 mm) showed a sex ratio of 1:1.14 (14 males:16 females).

Two age classes were indicated by length-frequency distributions of *L. zebra* (Fig. 8). *Lythrypnus zebra* breeds in the first year. Only a few individuals attain age two. Prejuveniles were not observed on the Punta Banda reefs until 14 September 1969, approximately one month later than *L. dalli* prejuveniles were observed on the same reefs.

REPRODUCTION

Nine hundred and nine *L. dalli* specimens from 9.2 to 45.3 mm were examined for reproductive condition. Ripe females were found at lengths greater than 22.0 mm on the Punta Banda and California reefs. However, female specimens from Gulf of California populations were found to be ripe at 19.0 mm and larger. Generally males from Punta Banda matured at lengths greater than 23.0 mm although two mature specimens measured 19.8 and 21.2 mm.

Ripe *L. dalli* were collected at Punta Banda from March through October (Fig. 9); the peak period of breeding activity was May through September. Limbaugh (1955) collected eggs on reefs in August and some were spawned in the lab during May. Postlarvae and young were collected by Limbaugh in March. Turner et al. (1969) reported that *L. dalli* eggs are laid in spring and early summer.

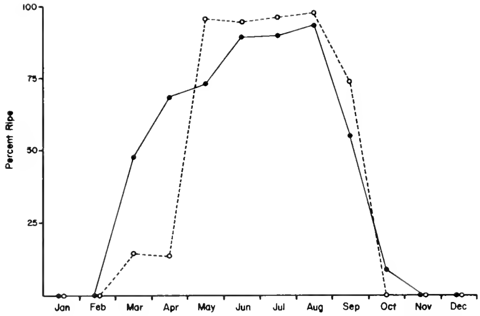


Figure 9. Monthly percentages of ripe *Lythrypnus dalli* from Punta Banda (NE), Baja California, Mexico. Based on 569 specimens greater than 23 mm S.L. taken from Punta Banda from October 1968 to September 1969. Solid dots (solid line) represent females, circles (broken lines) represent males.

They collected gravid females and their deposited eggs during August 1962.

Ripe *L. dalli* eggs ranged from 0.4 to 0.6 mm in diameter (mean 0.47 mm). Ovaries from 10 specimens contained an average of 1058 eggs (range 745-1593). Testes from 10 mature males averaged 9.2 mm long (range 8.0-10.1 mm).

Turner et al. (1969) observed *L. dalli* courtship and nest building during February 1963 in an aquarium containing three gravid females and a male. After first cleaning an area beneath a shell to receive the eggs, the male rushed at one female, nipping her genital area and jaws. Finally they locked jaws and drifted "leaf-like" about the tank. I observed similar chasing and nipping courtship behavior, but not jaw-locking displays, at Punta Banda between March and July 1968.

Spawned eggs were found in the empty mollusk shells of the reef epibiose, or, occasionally, in unattached shells on the bottom of the fish's shelter. The nest and eggs are guarded by the male only; he tends the eggs with fanning motions of the pectoral fins and rushes at intruders entering the nest territory.

Three-hundred and fourteen *L. zebra* specimens, varying in length from 9.8 to 41.5 mm, were examined for reproductive condition. At Punta Banda females were found to be ripe at lengths greater than 20.7 mm. Ripe males were found at lengths greater than 18.4 mm.

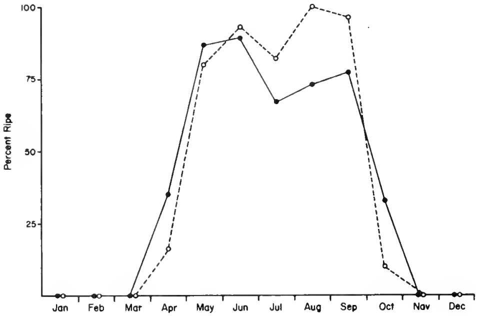


Figure 10. Monthly percentages of ripe *Lythrypnus zebra* from Punta Banda (NE), Baja California, Mexico. Based on 239 specimens larger than 19.0 mm S.L. (males) and 21.0 mm S.L. (females) taken from Punta Banda from September 1968 to August 1969. Solid dots (solid lines) represent females, circles (broken lines) represent males.

Table 6. Sexual dimorphism in fin measurements of *Lythrypnus dalli* and *Lythrypnus zebra*

	Lythrypnus dalli						*Lythrypnus zebra*					
	Males			Females			Males			Females		
Proportions	N	Range	Mean	N	Range	Mean	N	Range	Mean	N	Range	Mean
standard length / length of longest 1st dorsal ray	40	1.6-2.5	(2.12)	51	2.6-4.4	(3.46)**	19	2.6-4.0	(3.39)	20	3.2-4.3	(3.95)*
standard length / length base 1st dorsal	38	4.5-5.5	(4.95)	46	4.6-5.6	(4.98)	18	4.4-5.1	(4.80)	19	4.1-5.0	(4.57)
standard length / length of longest 2nd dorsal ray	38	2.0-2.3	(2.17)	52	2.2-2.4	(2.31)	16	2.4-2.7	(2.56)	17	2.4-2.8	(2.64)
standard length / length base 2nd dorsal	40	2.6-3.0	(2.82)	51	2.8-3.2	(3.00)	17	3.2-3.9	(3.59)	18	3.4-3.8	(3.59)
standard length / length of longest anal ray	34	2.3-2.5	(2.28)	44	2.5-2.9	(2.74)*	15	2.6-3.0	(2.80)	16	2.8-3.3	(3.02)**
standard length / length base anal	40	3.4-4.1	(3.72)	50	3.6-4.2	(3.96)	16	4.4-5.3	(4.82)	19	4.6-5.6	(5.08)

*$P<0.05$

**$P<0.001$

Ripe *L. zebra* were collected at Punta Banda from April through October, the peak of sexual activity occurring between May and September (Fig. 10). Spawned eggs were found in July, August and September. Eggs were attached to the roof of the shelter or to empty mollusk shells within the shelter. The male guards the nest and cares for the eggs.

Ripe *L. zebra* eggs averaged 0.5 mm in diameter. Collective counts of mature eggs from both ovaries of each of 10 specimens averaged 627 (range 293-1235). Testes of mature males averaged 6.1×0.9 mm (extremes 4.0×0.7, 8.6×1.3 mm) from nine individuals.

SEXUAL DIMORPHISM

Male *Lythrypnus dalli* attain a larger size than females. The mean length of 367 males and 542 females collected on the Baja California reefs was 22.8 mm; mean female length was 21.9 mm (maximum 34.0 mm), mean length of males 26.9 mm (maximum 45.3 mm). The greater size of the males may be important in nest defense.

In *L. dalli* the length of the first dorsal and anal fin-rays of mature individuals is significantly longer in males (Table 6). This dimorphism is not expressed in the length of the fin bases or in the meristic counts. The greater length of the dorsal and anal elements in males becomes evident at about 25-27 mm standard length. The tips of the first dorsal elements have bulb-like structures which are larger in males (Fig. 1). As with many species of gobies these fins are used in a variety of social displays and perhaps function in sex recognition.

Sexual dimorphism is also evident in the genital papilla (Fig. 11). *Lythrypnus dalli* can be sexed by the genital papilla at about 17 mm standard length.

Lythrypnus zebra males also attain a larger size than females. The mean length of the males collected on the reefs was 33.0 mm (maximum 43.7 mm), of females 29.4 mm (maximum 39.3 mm). The first dorsal and anal fin-rays are significantly longer in males (Table 6). *Lythrypnus zebra* can be sexed externally by the genital papilla at about 16 mm; the papilla is similar to that of *L. dalli* (see Fig. 11).

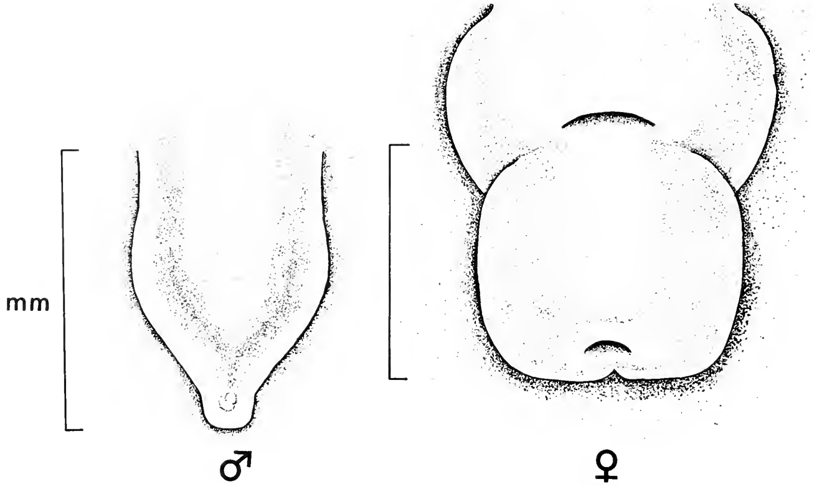


Figure 11. Sexual dimorphism in the genital papilla of *Lythrypnus dalli.* Male 37.3 mm, female 35.8 mm.

ACKNOWLEDGEMENTS

For his guidance and enthusiasm in all phases of the study I am deeply grateful to Dr. David W. Greenfield. For her encouragement, interest and assistance in the laboratory I sincerely thank Terry Arambula Greenfield. David M. Wildrick, Jack C. Turner, Dannie A. Hensley and Phillip A. Adams gave freely of their time and companionship in the field and laboratory. Dr. Carl L. Hubbs critically reviewed the manuscript and offered many suggestions, for which I am very grateful. My wife, Beth, helped in the field and provided the illustrations.

LITERATURE CITED

Barnhart, P.S. 1936. Marine fishes of southern California. University of California Press, Berkeley. 209 p.

Best, E. A. and M. S. Oliphant. 1965. A report on evaluation of fish resources of the Pt. Arguello area. Part II. Marine resources of the Pt. Arguello area. California Department Fish and Game Reports, State Fisheries Laboratory, Terminal Island, California. 129 p.

Birdsong, R. S. 1967. The goby name *Microgobius cinctus* Nichols, a junior synonym of *Lythrypnus dalli* (Gilbert). Copeia 1967 (2): 466-467.

Böhlke, J. E. and C. R. Robins. 1960. Western Atlantic gobioid fishes of the genus *Lythrypnus*, with notes on *Quisquilius hipoliti* and *Garmannia pallens.* Proceedings Academy Natural Sciences Philadelphia 112(4): 73-101.

Carlisle, J. G., Jr., C. H. Turner and E. E. Ebert. 1964. Artificial habitat in the marine environment. California Department Fish and Game, Fish Bulletin 124. 93 p.

Eigenmann, C. H. and R. S. Eigenmann. 1892. A catalog of the fishes of the Pacific Coast of America, north of Cedros Island. Annals New York Academy Sciences 6: 349-358.

Fitch, J. E. 1947. Rare fishes taken near Los Angeles. California Fish and Game 33(3): 191-192.

Fowler, H. W. 1923. Records of west coast fishes. Proceedings Academy Natural Sciences Philadelphia 75: 279-301.

Fowler, H. W. 1944. Results of the Fifth George Vanderbilt Expeditions (1941). The fishes. Academy Natural Sciences Philadelphia, Monographs 6: 57-529.

Gilbert, C. H. 1890. Scientific results of explorations by the U.S. Fish Commission steamer Albatross. Proceedings U.S. National Museum 13: 49-129.

Ginsburg, I. 1938. Eight new species of gobioid fishes from the American Pacific coast. University Southern California Publications, Allan Hancock Pacific Expeditions 2(7): 109-121.

Ginsburg, I. 1939. Twenty-one new American gobies. Journal Washington Academy Sciences 29(2): 51-63.

GINSBURG, I. 1945. Contributions to a methodology in the caudal fin ray count of fishes and its use in classification. Copeia 1945(3): 133-142.

GRIGG, R. W. and R. S. KIWALA. 1970. Some ecological effects of discharged wastes on marine life. California Fish and Game 56(3): 145-155.

HERALD, E. S. 1961. Living fishes of the world. Hamish Hamilton, London. 304 p.

HERALD, E. S. 1972. Fishes of North America. Doubleday and Co., Inc., New York. 254 p.

HUBBS, C. L. 1916. Notes on the marine fishes of California. University California Publications in Zoology 16(13): 153-169.

HUBBS, C. L. and W. I. FOLLETT. 1953. Manuscript list of the fishes of California. Unpublished. 65 p.

HUBBS, C. L. and K. F. LAGLER. 1958. Fishes of the Great Lakes region. University Michigan Press, Ann Arbor. 213 p.

JORDAN, D. S. and B. W. EVERMANN. 1896. A checklist of the fishes and fish-like vertebrates of North and Middle America. U.S. Commission Fish and Fisheries 21: 207-584.

JORDAN, D. S. and B. W. EVERMANN. 1898. The fishes of North and Middle America. Bulletin U.S. National Museum No. 47(3): 1937-2860.

JORDAN, D. S., C. H. EVERMANN and H. W. CLARK. 1928. Checklist of the fishes and fish-like vertebrates of North and Middle America north of the northern boundary of Venezuela and Columbia. Report U.S. Commission Fisheries 1928(2), Doc. No. 1055: 670 p.

JORDAN, D. S. and R. C. MCGREGOR. 1898. List of fishes collected at the Revillagigedo Archipelago and neighboring islands. Report U.S. Commission Fisheries 1898: 271-284.

KOUMANS, F. P. 1931. A preliminary revision of the genera of the gobioid fishes with united ventral fins. Drukkerij "Imperator" N. V.—Lisse. 174 p.

LIMBAUGH, C. 1955. Fish life in the kelp beds and the effect of kelp harvesting. University California, La Jolla, Institute Marine Resources Reference 55-9. 158 p.

MACDONALD, C. K. 1972. Aspects of the life history of the arrow goby, *Clevlandia ios* (Jordan and Gilbert), in Anaheim Bay, California; with comments on the cephalic-lateralis system in the fish family Gobiidae. M. S. thesis, California State University, Long Beach. xi+157 p.

MILLER, D. J. and R. N. LEA. 1972. Guide to the coastal marine fishes of California. California Department Fish and Game, Fish Bulletin 157. 235 p.

NICHOLS, J. T. 1952. Four new gobies from the eastern and western Pacific. American Museum Novitates no. 1594: 1-5.

PEQUEGNAT, W. E. 1964. The epifauna of a California siltstone reef. Ecology 45(2): 272-283.

QUAST, J. C. 1968. Fish fauna of the rocky inshore zone. Pp. 35-55. *In* Utilization of kelp-bed resources in southern California. North, W. J. and C. L. Hubbs (eds.). California Department Fish and Game, Fish Bulletin 139. 264 p.

ROEDEL, P. M. 1962. The names of certain marine fishes of California. California Fish and Game 48(1): 19-34.

RUTTER, C. 1904. Notes on fishes from the Gulf of California with the description of a new genus and species. Proceedings California Academy Sciences, Ser. III: 251-253.

SNODGRASS, R. E. and E. HELLER. 1905. Shore fishes of the Revillagigedo, Clipperton, Cocos and Galapagos islands. Proceedings Washington Academy Sciences 6: 333-427.

STARKS, E. C. and E. L. MORRIS. 1907. The marine fishes of southern California. University California Publications in Zoology 3(11): 159-251.

TURNER, C. H., E. E. EBERT and R. R. GIVEN. 1969. Man-made reef ecology. California Department Fish and Game, Fish Bulletin 146. 221 p.

ULREY, A. B. 1929. A check-list of the fishes of southern California and Lower California. Pan-Pacific Research Institute, Journal 4(4): 2-11.

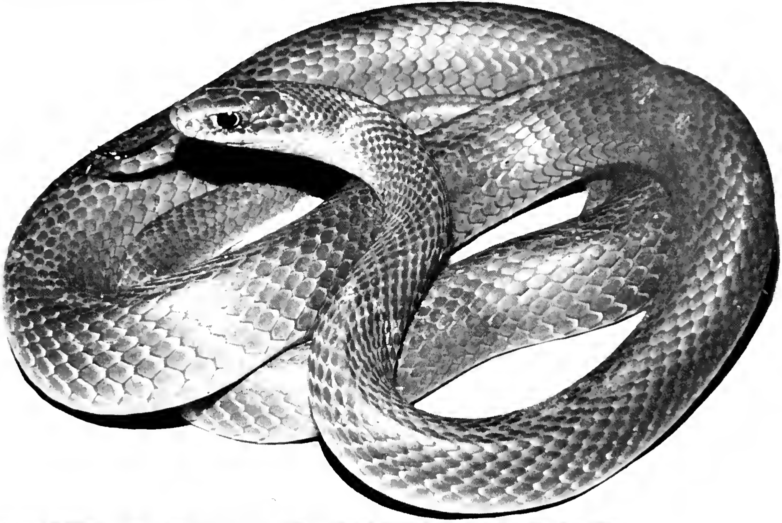
ULREY, A. B. and P. O. GREELEY. 1928. A list of the marine fishes (Teleosti) of southern California, with their distribution. Bulletin Southern California Academy Sciences 27(1): 1-53.

WILEY, J. W. 1973. Life history of the western North American goby, *Coryphopterus nicholsii* (Bean). Transactions San Diego Society of Natural History 17(4): 187-208.

California State University, Fullerton, California 92631. Present address: U.S. Forest Service, P.O. Box 21, Palmer, Puerto Rico 00721.

AXIAL MYOLOGY OF THE RACER *COLUBER CONSTRICTOR* WITH EMPHASIS ON THE NECK REGION

Gregory K. Pregill



TRANSACTIONS

OF THE SAN DIEGO
SOCIETY OF
NATURAL HISTORY

VOL. 18, NO. 11 25 JANUARY 1977

Axial myology of the Racer *Coluber constrictor* with emphasis on the neck region

Gregory K. Pregill

ABSTRACT.—Little is known about the evolution of the occipito-vertebral joint in limbless vertebrates and how the neck has been affected by the loss of a shoulder girdle. Snakes are perhaps the most specialized limbless vertebrates. The neck region of *Coluber constrictor,* an advanced species, is described. An account of the cervical skeleton describes features of the occipito-vertebral joint and the bony elements that are associated with muscles of the anterior trunk. A description of the neck myology follows to (1) explain the change in relationship of the various trunk muscles as they approach the head and (2) state precisely which muscles insert on the skull and how each facilitates cranial mobility. M. obliqus capitus magnus and M. rectus capitus anterior are prime movers in head flexion and extension and have no trunk counterparts. They are described for the first time in snakes. The neck muscles of *Coluber constrictor* then are compared among several related genera to assess variation. Finally, the major features of neck morphology are analyzed. Evolutionary implications are discussed and a comparative study with other snakes and lizards is proposed.

In the evolution of land vertebrates the cranial-atlas-axis complex and its associated musculature has played an important role in facilitating cranial mobility. The transformation of the generalized first vertebra into the atlas in early amphibians provided an occipito-vertebral articulation that permitted vertical or horizontal movement of the head independent of the trunk. Subsequent specialization in the reptiles of the second vertebra as the axis allowed rotation of the head. Still greater freedom of movement was effected by a reduction in the number of freely articulating ribs on those vertebrae immediately behind the axis. The general pattern of evolution of these skeletal elements and their associated muscles now is well known, but there remain a number of curious specializations in the cervical region that are not yet fully understood. Among the departures from the usual plan are those amphibians and reptiles in which the limbs and girdles have become reduced or lost entirely.

Cranial mobility in tetrapods is a response to an increased horizon resulting from an elevated body, but in limbless vertebrates such as snakes the body is flush with the substrate so that head mobility must be adapted not only for orientation within the environment but for other functions as well—feeding, climbing and burrowing, for example. In snakes the structural significance of the occipito-vertebral region is not easily recognized because the shoulder girdle has been lost and the vertebral skeleton and its associated muscles have become dedifferentiated. That is, the neck and trunk are no longer structurally and functionally independent. For example, the muscles of the neck have either joined with or been replaced by the long muscles of the trunk. The effect of this change on cranial mobility is unknown. The significance of the neck region in the evolutionary transition is obvious, but on the whole it has been ignored in previous studies on snake morphology.

It has been inferred erroneously from the studies on the trunk myology of snakes by Nishi (1916) and Mosaur (1935) that the neck is simply the most anterior portion of the trunk which abruptly terminates (or begins) at the head. Neither Nishi nor Mosaur included the cervical region in their analyses. Although

SAN DIEGO SOC. NAT. HIST., TRANS. 18(11):185-206, 25 JANUARY 1977

more recent papers by Auffenberg (1958, 1961, 1962, 1966), Gasc (1967) and Ludicke (1962) have renewed interest in snake myology, their work pertains to the trunk and does not include study of the neck region. In this paper I have attempted to ascertain the effect of the absence of an appendicular skeleton on the neck morphology in a colubrid snake. Although the emphasis is descriptive, functional properties are discussed where appropriate.

The classification of higher snakes (caenophidians) is unstable and in particular, the composition of the family Colubridae has undergone extreme changes in recent years (see Bailey, 1967; Dessauer, 1967; Dowling, 1967; Rossman, 1967; Underwood, 1967a). In its most restricted sense the family is composed of advanced snakes having the following characters: asymmetrical hemipenes; a simple sulcus spermaticus passing over to the left hand side of the hemipenis; a simplex retina; a vidian canal that generally is short; and a levator anguli oris muscle that usually is absent (Underwood, 1967b). In following Underwood's classification I am not arguing the higher taxonomic catagories of snakes, but only informing the morphologist as to the identity of the animal studied. Thus, *Coluber constrictor* was chosen because (1) throughout all taxonomic rearrangements the species always has been considered among the most advanced species of snakes, (2) the overall anatomy of the genus is known fairly well, (3) an adequate sample of preserved specimens was available for dissection, and (4) the genus serves as the type of the family.

MATERIALS AND METHODS

This study is based on dissection of the trunk and neck muscles of forty preserved snakes. There were twenty *Coluber constrictor mormon* (Baird and Girard) representing 11 adults and nine sub-adults and juveniles of both sexes. Adults of five other colubrid genera and one natricid genus dissected for comparison included: *Lampropeltis getulus californiae* (4), *Elaphe g. gutta* (3), *Drymarchon corais erebenus* (3), *Pituophis melanoleucus anmectens* (1), *Chionactis occipitalis annulata* (3). Natricidae: *Thamnophis sirtalis* (6).

Dissections were made with the aid of a binocular microscope. At the beginning of the study a few specimens of *Coluber* were completely dissected individually. Once a technique was established specific muscles of several snakes could be examined simultaneously. Skeletal material of each species was at hand to facilitate the location of muscle origin and insertion and to aid in osteological description.

The illustrations accompanying the text depict muscles as they were exposed, but by necessity the figures are semi-diagrammatic to emphasize important topographical relationships. The muscle descriptions define the adult, but include pertinent comments on juveniles. The juvenile condition and subsequent ontogeny is summarized in the discussion at the end of the paper. The terminology of the trunk musculature is from Mosaur (1935), the facial muscles from Haas (1973), and names of certain occipito-vertebral muscles are my own.

OSTEOLOGY OF THE NECK REGION

Attention to neck osteology is focused on two areas—the occiput and the anterior vertebral column. Together with the muscles these bones produce movement of the head independent from the rest of the body and make up the vaguely defined neck of the snake. The occipital region of the skull is relatively simple and will be discussed in a later section. The vertebral column is more complex. There is no differentiated cervical region. Furthermore, the whole vertebral column lacks the regionalization characterizing higher tetrapods, which possess distinct cervi-

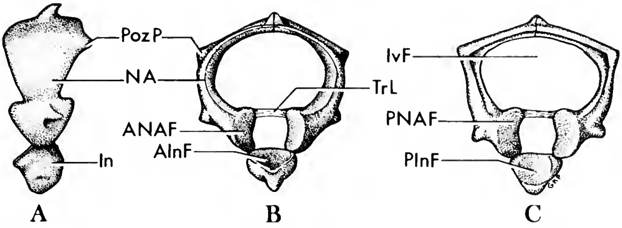


Figure 1. Atlas, *Coluber constrictor:* A, lateral; B, anterior; C, posterior. AInF, anterior intercentral facet; ANAF, anterior neural arch facet; In, intercentrum; IvF, intervertebral foramen; NA, neural arch; PInF, posterior intercentral facet; PNAF, posterior neural arch facet; PozP, postzygapophysial process; TrL, transverse ligament.

cal, thoracic, lumbar, sacral and caudal regions. Snake vertebrae traditionally are viewed as either "presacral" or "caudal." Although there have been many attempts to define cervical vertebrae only the atlas and axis are distinctive. The study of snake osteology has a lengthy history and the current knowledge of the subject is summarized by Hoffstetter and Gasc (1973).

The vertebral column of snakes is unique among limbless vertebrates and eludes stereotyping. For example, between successive vertebrae there are five points of articulation instead of three and the column functions more as a cable than a hinge (Auffenberg, 1962). Johnson (1955) concluded from a statistical survey on vertebral morphology in snakes that vertebral structure is conservative, varying minimally across major phyletic lines, despite extreme variation in adaptive modes within these lines. His conclusions are consistent with Mosaur's (1935) findings on trunk muscles. So it is not surprising that almost any description of snake vertebrae, regardless of species, is fairly applicable to any other. For example, the description by Williams (1959) of the occipito-vertebral joint in *Cylindrophis rufus,* an oriental burrowing snake, could be used for *Coluber.*

The morphology of snake vertebrae is further characterized by a reduction in surface area available for muscle attachment. Muscles originate and insert on structures such as hypapophyses, neural spines and accessory processes on the zygaopphyses. These structures are present in the neck, but differ on each of the first three vertebrae. The atlas, axis and anterior trunk vertebrae of *Coluber constrictor* are described briefly below as they relate to each other and with the skull.

Atlas.—The first vertebra, or atlas, is a more or less ring-shaped structure consisting of three bones (Fig. 1). Laterally and dorsally are two thin neural arches loosely sutured to each other mid-dorsally. Ventrally the ring is completed by the single intercentrum ligamentously attached to the pedicel of each neural arch. Each neural arch bears large elliptical facets on the anterior and posterior surface of the pedicel that articulate with the occipital condyle in front and the axis behind. On the lateral surface of each pedicel is a short median transverse process. A second process projects from the dorsolateral angle of the arch as a small conical protuberance analogous to the postzygapophysial process of the trunk vertebrae. From their pedicels the arches curve dorsally and become wider in the anterposterior plane. The arches meet at the dorsal midline to enclose the intervertebral foramen (neural canal). There is no neural spine dorsally, but a small midsagittal crest instead.

The atlas intercentrum is a single midventral element bearing articular facets on its anterior and posterior surfaces similar to those on the arch pedicels. A basal prominence, or hypaophysis, is present, but it is much smaller than the hypapophyses of other vertebrae.

With the three bones joined in a ring, the anterior face of the atlas forms a midventral cotyle for the reception of the occipital condyle. The posterior face mirrors the anterior face and forms a concavity that receives the odontoid process of the axis. The two concavities complete a canal, or foramen septi, which is

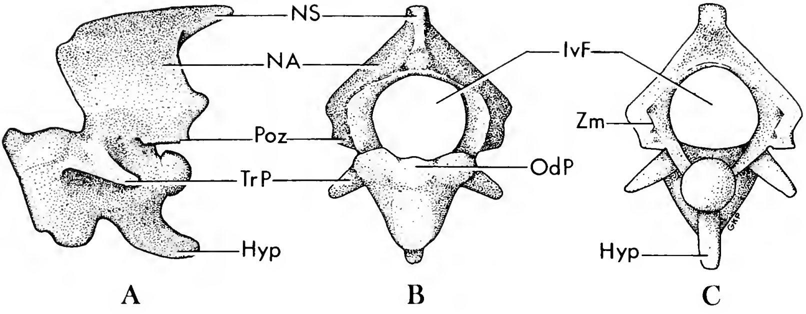


Figure 2. Axis, *Coluber constrictor:* A, lateral; B, anterior; C, posterior. Hyp, hypapophysis; IvF, intervertebral foramen; NA, neural arch; NS, neural spine; OdP, odontoid process; Poz, postzygapophysis; TrP, transverse process; Zm, zygantrum.

separated from the intervertebral foramen above it by the ligamentum transversum (transverse ligament). The ligament spans the dorsomedial surface of the arch pedicels.

Axis.—The axis of *Coluber* (Fig. 2) consists of an anterior cone-shaped odontoid process flattened on its dorsal surface; an intercentrum below the odontoid, a median centrum (body) terminating caudally in a ball-like condyle, and a pair of neural arch halves fused middorsally in a strong spinous process. The neural arch bears a pair of postzygapophyses and a weakly developed zygantrum for articulation with the third vertebra. Two hypapophyses are present on the ventral surface of the axis. The anterior one is a basal outgrowth of the intercentrum. The better developed posterior hypapophysis arises from the centrum and slopes backward.

The axis articulates with the atlas by two lateral facets on the odontoid and by the vertical anterior face of the intercentrum. The odontoid is received by corresponding facets on the atlas neural arch pedicels while the intercentrum fits flush with the opposing face on the atlas intercentrum. The articulation permits little vertical movement, but slightly more rotational and horizontal movement. Moreover, the tip of the odontoid barely makes contact with the depression on the occipital condyle (fovea dentis of Williams, 1959). Thus, articulation between the skull and the vertebral column is primarily by the atlas.

Anterior trunk vertebrae.—The 15 to 20 vertebrae immediately caudal to the axis (Fig. 3) differ little from the others of the trunk. Neural spines, accessory processes and hypapophyses become smaller towards the skull; thus there is a gradual reduction in over-all size of each vertebra so that the column tapers as it approaches the head. Only the third vertebra is at all peculiar. It lacks free ribs but is otherwise only slightly modified in possessing elongate, bilobed parapophyses without articular facets for ribs. Romer (1956) considered these processes to be composed of short fused ribs and hence referred to it as a "cervical" vertebra.

The occiput.—The occipital region of the skull consists of four bones; a dorsal supraoccipital, a pair of lateral exoccipitals and a ventral basioccipital. Only the exoccipitals and basioccipital contribute to the formation of the occipital condyle, but all four serve as sites of attachment for the cervical musculature. Most characteristic are the crest and processes. On the dorsal aspect of the occiput is a prominent transverse crest formed by the median supraoccipital sutured on either side to exoccipitals. The crest rises perpendicular to the roof of the foramen magnum forming a depression for the insertion of the dorsal cervical muscles.

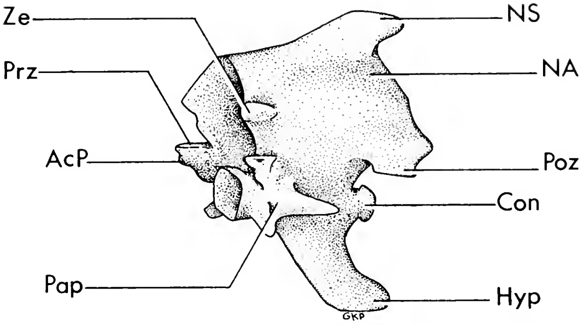


Figure 3. Anterior trunk vertebra, *Coluber constrictor:* Three quarter view, anterior is to the left. AcP, accessory process; Con, condyle; Hyp, hypapophysis; NA, neural arch; NS, neural spine; Pap, parapophysis; Poz, postzygapophysis; Prz, prezygapophysis; Ze, zygosphene.

Laterally the crest of the exoccipitals angles ventrad and caudad becoming smaller as it approaches the basioccipital below. Where these two bones are sutured anterior to the occipital condyle, they form the knob-like paraoccipital process.

The basioccipital forms the ventral plate of the occiput. Posteriorly it terminates as the single median element of the occipital condyle. On its cranial border is a low crest bearing a central, caudally directed process bordered on each side by a small hump. The ventral cervical muscle inserts over the entire surface of the bone. Positions of the crests and processes on the occiput suggest the pattern of insertion for the cervical musculature. These elements are strongest dorsally and ventrally and weakest laterally. Likewise, muscle insertion is mostly dorsal and ventral. Consequently, the occipito-vertebral joint allows more movement in the vertical plane than in the horizontal.

THE MUSCLES

Previous studies on snake myology have been directed toward two broad areas of ophidian biology, namely taxonomy and the evolution of limbless locomotion. These areas, of course, are not mutually exclusive, but express the problems that seemed most obvious to the investigators. The number of such studies exclusive of head musculature is surprisingly few. The more recent and comprehensive of these include papers by Mosaur (1935), Auffenberg (1958, 1961, 1962, 1966), Gasc (1967) and Ludicke (1962).

Mosaur's paper remains the classic. His tripartite classification of snakes based on trunk musculature is basicaly sound. He recognized little inter-familial variation and concluded that there are three basic types of muscle arrangements, as typified by boids, colubrids and viperids. Auffenberg (1958, 1966) subsequently demonstrated that Mosaur's scheme, although useful as a general application, was over-simplified and of little help in more specific taxonomic problems. Auffenberg examined a number of henophidians (Booids) such as *Eryx, Tropidophis, Xenopeltis* and *Cylindrophis.* He suggested that the variation observed in the axial spinal muscles indicated certain phyletic tendencies toward the colubrid type of arrangement. He called this "myological colubridization." The fact remains that the colubrid pattern is the most derived. In the Colubridae, certain muscles such as the M. supracostalis dorsalis have been lost, whereas others have lost their osseous connections and become associated with adjacent muscles. This is most evident in the fast moving terrestrial racers such as *Coluber.*

In his evolutionary analysis of trunk muscles, Auffenberg (1961) recognized several steps leading to the advanced condition found in racers. He described the events of two major trends that suggest myological evolution from a simpler and presumably more primitive type to the complex or more advanced. These trends are: (1) the tendency for median muscle elements to become associated with more lateral ones and (2) the association of posterior myological elements with anterior ones resulting in lengthening of functional units by the fusion of shorter muscles. This is the most conspicuous feature of colubrid muscles and is most noticeable in the sacrospinalis complex. In most henophidians the M. spinalis-semispinalis is a single muscle arising from the neural spine by a tendonous arch. In contrast, the same muscle in colubrids has split posteriorly into lateral and medial elements, each of which arises independently of the other. Moreover, the lateral element arises not from an osseous connection, but instead from the medial tendon of the M. longissimus dorsi. Thus, one muscle originates from the terminal tendon of the other, this results in a linkage of separate elements into long myological chains. Furthermore, each chain of elements is overlapped segmentally by similar ones. This myological macramé is significant functionally because it insures uniform and synchronous flexion over long sections of the body.

In the cervical region the trends in myological evolution have occurred concomitant with elongation of the body and loss of the pectoral girdle. Because this paper is concerned with description of the most advanced condition, it is important for the reader to understand that the relationships and arrangements of neck muscles have been obscured by evolutionary change and are not always obvious.

The descriptions that follow are of the muscles of the neck region. Most neck muscles are simply continuations of those of the trunk; however, there are some that are exclusively cervical. Furthermore, many of the trunk muscles have been modified in the neck. For these it will be necessary to first describe them as they appear in the trunk and then describe their modifications in the neck region. Mosaur (1935) has given a thorough account of the trunk myology so I will not provide descriptions as detailed as his. The descriptions given here should give the reader sufficient information to understand the morphological changes that occur in the neck.

Organization of muscle groups.—Organizing the various trunk and neck muscles into meaningful categories is difficult. This is particularly so in colubrid snakes in which the different muscles may be related structurally but not functionally.

Mosaur recognized four main groups of ophidian skeletal muscles; (1) muscles between vertebrae, (2) muscles between vertebra and rib, (3) muscles between ribs and (4) integumentary muscles. This study adds two more groups of muscles—those between the trunk and head, and those muscles continuous with the cervicals but not reaching the head. Of course, several of the muscles may fall into more than one category. For example, the M. longissimus dorsi connects articular processes of vertebrae with spinous processes of vertebrae by its medial tendon giving rise to the M. semi-spinalis. Its lateral tendon, however, connects articular processes with ribs via the M. retractor costae biceps. Table 1 summarizes the main neck muscles inserting on the skull.

The descriptions presented will be organized more or less within Mosaur's categories, but in a different sequence. First will be the cervical muscles themselves (trunk to head) as they are most germane. This group includes the facial muscles and occipito-vertebral muscles. Second will be the modified trunk muscles in the neck region: the axial spinal muscles, subvertebral muscles and other vertebral costal muscles. Third will be the costal muscles and the last category

TABLE 1. Occipito-vertebral muscles of *Coluber constrictor.*

Muscle	Origin	Insertion on occiput	Action
spinalis capitus	neural spines of V2, V3, V4	supraoccipital crest	dorsal extension of head
semispinalis cervicus	anterior medial tendons of longissimus	exoccipital crest	dorsal extension of head and neck
spinalis-semispinalis	2 heads: tendon of multifidus; medial tendon of longissimus	supraoccipital crest	dorsal extension of head and neck
longissimus dorsi	accessory process	exoccipital crest and paraoccipital process	abduction of head and neck
retractor costae biceps	lateral tendon of longissimus	paraoccipital process	abduction of head and neck
obliqus capitus magnus	neural spines of V2, V3, V4	exoccipital	rotation and dorsal extension of head
rectus capitus anterior	hypapophyses of VII to axis	pars ventral: basioccipital pars dorsal: paraoccipital process, basioccipital	ventral flexion of head and neck

includes the miscellaneous muscles elements. The important connective tissue and fascia will be explained following the descriptions of the muscles in *Coluber.*

FACIAL AND OCCIPITO-VERTEBRAL MUSCLES

Facial Muscles.—The four muscles of this group are the Mm. constrictor coli, cervicomandibularis, neurocostomandibularis and retractor quadrati. All insert on the head, but function primarily in feeding and not in cranial mobility. They are considered here because all have their origins on the neck and must be removed to expose the cervical and vertebral muscles that lie beneath them.

The facial muscles have been described for a variety of snake genera. All of the studies that discussed them dealt with jaw mechanics or comparative cephalic anatomy. Haas (1961) discussed the phylogenetic implications of snake head muscles and also provided the most recent complete summary of the subject in Squamata (Haas, 1973). His terminology is employed here except for the M. constrictor coli which he calls the M. sphinctor coli.

M. constrictor coli (Fig. 4): This is the most superficial muscle of the neck region. It is entirely subcutaneous throughout its length and is destroyed easily if the skin is not removed carefully. The M. constrictor coli appears as a wide band or collar just behind the head and is mostly aponeurotic.

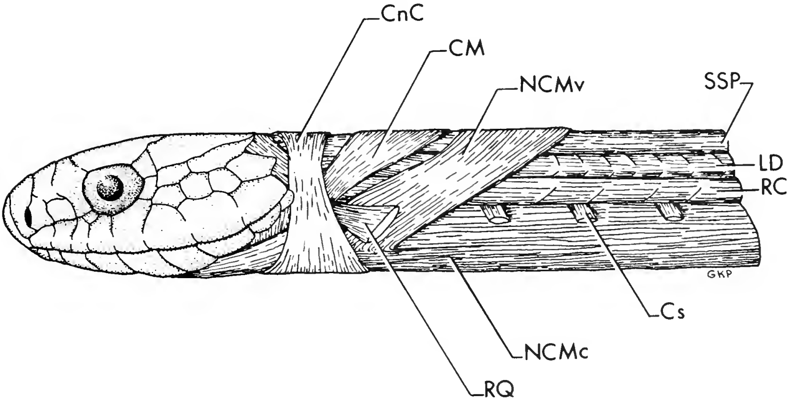


Figure 4. Facial and superficial neck muscles of *Coluber constrictor:* Left lateral view. CM, M. cervicomandibularis; CnC, M. constrictor coli; Cs, M. costocutaneous superior; LD, M. longissimus dorsi; NCMc, M. neurocostomandibularis—costal head; NCMv, M. neurocostomandibularis—vertebral head; RCB, M. retractor costae biceps; RQ, M. retractor quadrati; SSP, M. spinalis-semispinalis.

It originates on the dorsal fascia and runs lateroventrad to insert partly on the hyoid, but principally on the ventral fascia that covers the cartilagenous rib tips. The anterior edge of the muscle barely crosses the posterior corner of the quadrato-mandibular joint. The extent of the posterior edge is variable, but in most individuals it reaches the first or second rib. The muscle has few fibers which are confined to its lateroposterior margin. The fibers extend just past the level of the maxillary ligament.

M. cervicomandibularis (Figs. 4 and 5): Removal of the M. constrictor coli exposes two large flat muscles covering the lateral surface of the neck and superficial to all others in the area. The more anterior of these is the M. cervicomandibularis. The posterior muscle is the M. neurocostomandibularis. The former arises by an aponeurosis from the dorsal fascia between neural spines of the third through fifth vertebrae. Muscle fibers are directed obliquely anteroventrad and converge to form a thin aponeurotic tendon. The tendon inserts on the capsule of the jaw joint. Fibers on the caudal edge may coalesce with the vertebral head of the M. neurocostomandibularis, but the two usually can be separated.

M. neurocostomandibularis (Figs. 4 and 5): This large muscle originates on the neck by two widely separated heads and inserts on the mandible by a single head. It arises by a dorsal "vertebral head" and a ventral "costal head." The vertebral head is attached by an aponeurosis to the dorsal fascia that covers the sixth through ninth vertebrae. The muscle fibers sweep downward and cranially as a wide flat sheet somewhat thinner than the M. cervicomandibularis which it parallels. The dorsal head of the M. neurocostomandibularis inserts on an inscriptional tendon that it shares with the costal head. This inscription is located in a more or less transverse plane behind the quadrato-mandibular joint. A second, more anterior tendonous inscription was found in approximately one third of the individuals.

The costal head forms the ventral origin of the M. neurocostomandibularis. This head arises by a series of narrow slips, each attached to the distal end of an anterior rib. The number of these slips is difficult to ascertain because the more posterior ones interlace with fibers of the M. costocutaneous inferior. In *Coluber* the single slips usually are confined to the second through sixth ribs (over half the specimens examined). In some individuals slips also arise from ribs seven and eight; in others they are confined to ribs two to four. The shorter first rib is not a site of attachment. The individual muscle slips are arranged in cranially directed straps. The posterior elements form a single superficial strap overlapping the anterior elements which form a deeper one. The anterior strap inserts on the tendonous inscription deep to the vertebral head. The superficial sheet inserts on the inscription above the deeper strap, although some of its medial fibers pass over the inscription and fuse with the terminal belly that inserts on the mandible.

Insertion of the M. neurocostomandibularis on the mandible is by a flat sheet of muscle originating from the tendonous inscription that unites the vertebral and costal heads. The muscle sheet runs craniad along the ventral surface of the neck and gives rise to a broad aponeurotic tendon. The tendon inserts on the ventral surface of the posterior half of the lower jaw.

The M. neurocostomandibularis has been described in several ways. In their study of *Elaphe,* Albright and Nelson (1959) treated the vertebral and costal heads as described here, *i.e.,* two parts of a single muscle. Cowan and Hick (1951) described a third head in *Thamnophis,* the pars hyoideus, which I could not identify in *Coluber.* Langebartel (1968) argued that the heads of origin and the insertion portion are separate muscles because each receives different nerve supplies. Haas (1973) considered it one muscle. Whatever the history, the parts of the M. neurocostomandibularis are joined to produce a common action.

M. retractor quadrati (Fig. 4): The M. retractor quadrati often is listed as a head muscle in studies on snake feeding mechanisms. To call it a head muscle or cervical muscle is not important. After the head and neck are skinned, the origin of the muscle is free and can be seen fanning out from beneath the M. cervicomandibularis and crossing over the vertebral head of the M. neurocostomandibularis. It originates as fibers attached to the integument caudal to the lateroposterior border of the M. neurocostomandibularis. The muscle begins as a truncate bundle of fibers directed anterodorsally. This portion is brief, for the muscle narrows almost immediately as it passes superficial to the M. neurocostomandibularis and disappears under the belly of the M. cervicomandibularis. Here it gives rise to a well-developed tendon. The tendon continues in the same anterodorsad direction along the medial surface of the quadrate. It inserts on the posterior process of the proximal end of this bone.

Occipito-vertebral muscles.—In *Coluber constrictor* there are four muscles peculiar to the cervical region that insert on the skull. Three of these are dorsal extensors: the Mm. spinalis capitus, semispinalis cervicus, obliqus capitus magnus; and one is a ventral flexor, M. rectus capitus anterior. None has been described for snakes although their probable homologues are known in some lizards (e.g., *Iguana:* Evans, 1939; *Ctenosaura:* Oelrich, 1956). In fact, they are named here for the analogous muscles described in these genera. Two of the muscles are large and conspicuous. These are the M. obliqus capitus magnus and M. rectus capitus anterior. The Mm. spinalis capitus and semispinalis cervicus are less distinct, but should be considered separately.

M. spinalis capitus (Figs. 5, 8 and 9): As viewed dorsally this is the most anteromedial of the cervical muscles. Medial to it are neural spines of the axis and third and fourth vertebrae. Laterally is

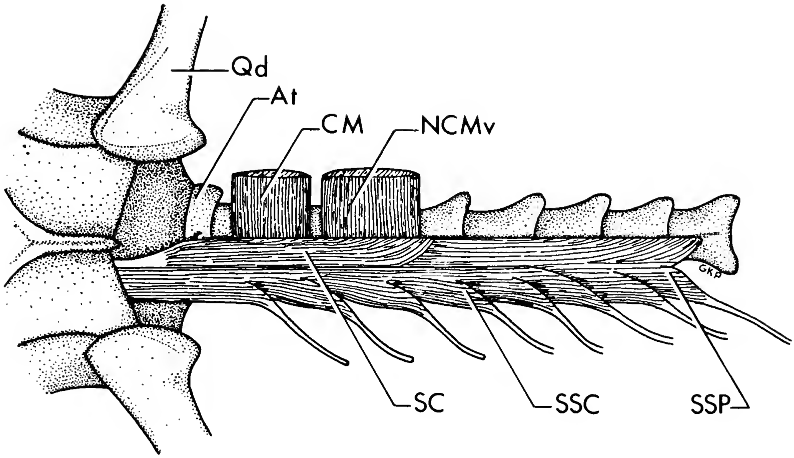


Figure 5. Spinal cervical muscles of *Coluber constrictor:* Dorsal view. M. neurocostomandibularis and M. cervicomandibularis have been cut and deflected dorsally. At, atlas; Cm, M. cervicomandibularis; NCMv, M. neurocostomandibularis—vertebral head; Qd, quadrate; SC, M. spinalis capitus; SSC, M. semispinalis cervicus; SSP, M. spinalis-semispinalis.

the M. semispinalis cervicus and deep is the M. obliqus capitus magnus. The muscle could be considered part of the axial spinal muscle M. spinalis-semispinalis. Its origin, however, is unlike any other muscle found in the neck or trunk.

The muscle originates partly as fibers directly from the fascia above the ligamentous sheath enclosing the terminal tendons of the M. spinalis-semispinalis. Most of it arises as small slips attached by very short medial tendons. The tendons are fixed to the posterior-dorsal angle of the neural spines of the axis and third and fourth vertebrae. They are visible only on the ventral surface of the muscle and become progressively thinner caudally. In smaller specimens and juveniles only the axis tendon may be present so that the majority of the muscle arises directly as fibers. The fibers of the small slips fuse and are directed towards the head in a narrow strip terminating in a short tendon. The tendon inserts on the supraoccipital crest.

The muscle is separated laterally from the M. semispinalis cervicus by the terminal tendon of a M. spinalis-semispinalis muscle passing through the fibers to the nuchal ligament. The deeper fibers of the M. spinalis capitus and M. semispinalis cervicus intermingle with each other and are difficult to separate. The result is a muscle whose origin is clear enough, but otherwise difficult to define.

M. semispinalis cervicus (Figs. 5, 8 and 9): The M. semispinalis cervicus essentially is the anterior termination of the M. semispinalis column of the trunk. Its status as a separate muscle could be argued, but because its position and relationship is unique, a different name seems warranted. It lies lateral to the M. spinalis capitus, medial to the M. longissimus dorsi and superficial to the M. obliqus capitus magnus.

The individual slips comprising the muscle arise from the medial tendons of the M. longissimus dorsi. Usually these are the seven most anterior medial tendons of that muscle. However, the number of tendons varies from five to nine. In the trunk, the individual muscles arising from the medial tendons of the M. longissimus dorsi become the Mm. semispinalis, which join with more medial muscle elements (Mm. spinalis) to form the column of the M. spinalis-semispinalis. In the neck region they do not join medial components, but coalesce with each other distally. Separation of the individual slips is possible, but the deeper and more anterior fibers may fuse with the M. spinalis capitus. The entire muscle inserts on the dorsomedial aspect of the exoccipital crest by two or three short tendons.

M. obliqus capitus magnus (Figs. 7-9): This muscle is exposed by removing the M. spinalis capitus and M. semispinalis cervicus and by pulling the M. longissimus dorsolaterally. Its thick fleshy appearance makes it one of the more conspicuous muscles of the neck. It overlies the neural arches of the third vertebra, axis and atlas, and the roof of the foramen magnum. Deep and medial to it are fibers of the M. multifidus.

The muscle originates posteriorly by a weak tendon attached to the dorsal fascia of the fourth vertebra, but most of it arises as fibers from the neural spines of the third vertebra and axis. Near the occiput the muscle becomes thickened laterally and ventrally because the more superficial fibers

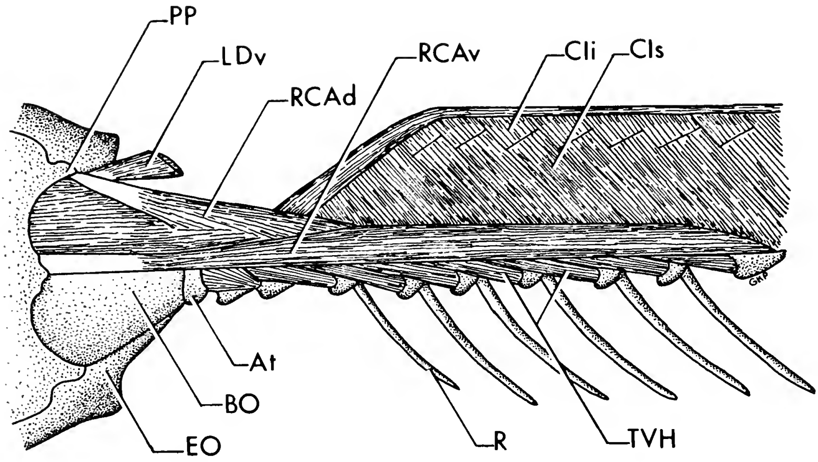


Figure 6. Ventral cervical muscles of *Coluber constrictor:* M. rectus capitus anterior and costal muscles have been removed from the left side to expose the M. transversohypapophyseus. At, atlas; BO, basioccipital; CIi, M. costalis internus inferior; CIs, costalis internus superior; EO, exoccipital; LDv, M. longissimus dorsi—ventral head; PP, paraoccipital process; R, rib; RCAd, M. rectus capitus anterior pars dorsalis; RCAv, M. rectus capitus anterior pars ventralis; TVH, M. transversohypapophyseus.

are bent at almost right angles to the horizontal. In cross section it would appear wedge-shaped. Thus, the muscle is blunt anteriorly but tapered caudally. The ventrolateral edge of the muscle is free, and the muscle can be lifted up and away from the neural arches if the insertion on the exoccipital is cut. However, the deeper medial muscle fibers above the axis do not easily separate from those of the M. multifidus.

The M. obliqus capitus magnus inserts over a wide area of the exoccipital. Dorsally the muscle swings away from the vertebral midline near the atlas and fills most of the depression formed by the roof of the foramen magnum and the crest of the exoccipital bone by a ligamentous connection and a short wide lateral tendon.

M. rectus capitus anterior (Figs. 6, 9 and 10): The muscle forms a long, well-developed column on the ventral surface of the vertebral column from the eleventh vertebra forward to the basioccipital. It is the only subvertebral muscle inserting on the skull and is therefore the primary flexor of the head and neck. A similar muscle was described by Albright and Nelson (1959) as the M. transversohypapophyseus. However, the M. rectus capitus anterior and M. transversohypapophyeus are both present in colubrids and from their description it is not clear as to which muscle they are referring. Apparently they have confused the former with the latter and in doing so did not properly describe either.

The M. rectus capitus anterior has two heads; a pars ventralis and a pars dorsalis. The pars ventralis is the longest and most ventromedial portion of the M. rectus capitus anterior. Lateral to the pars ventralis is the M. costalis internus superior, medial to it are the vertebral hypapophyses, dorsal are the pars dorsalis and M. transversohypapophyseus. Ventral to the pars ventralis is the esophagus. The muscle originates as fibers from the hypapophyses of the eleventh vertebra and those craniad to the axis. In some cases, the anterior muscle fibers arise by short tendons. Fibers from successive hypapophyses intermingle with each other cranially to form a long thick muscle column. The pars ventralis inserts on the prominent median basioccipital process by a long wide tendon. The length of the insertion tendon varies. It may extend caudad (buried deep in the fibers) to the fifth or sixth vertebra, or it may be short and superficial and extend only as far back as the axis. There is also variation in the width of the muscle at its anterior end. In fully adult specimens it is narrow and difficult to separate from the *pars dorsalis.* These individuals have long insertion tendons. In subadults and juveniles the anterior end of the pars ventralis is wide and noticeably overlaps the pars dorsalis. They have short insertion tendons.

The relationship of the pars dorsalis to the pars ventralis is complicated. Fibers from both intermingle near the occiput and cannot be completely separated. Furthermore, the pars dorsalis has two heads; a longer lateral head and a shorter medial head. The lateral head originates from the hypapophyses dorsal to the pars ventralis, but reaches caudally only as far as the forth vertebra. Its fibers fuse as they swing laterally away from the pars ventralis. Near the level of the axis (its most anterior origin) the lateral head gives rise to a stout tendon that inserts on the paraoccipital process, ventral to the insertion of the ventral head of the M. longissimus dorsi. Thus, it assists in lateral head movement.

The medial head of the pars dorsalis arises in common with the lateral head near the latter's anterior limit, and additionally by a tendon from the basal prominence of the axis intercentrum. The belly of the muscle fans out between the lateral head and the pars ventralis and inserts onto the basioccipital, covering it entirely.

MODIFIED TRUNK MUSCLES IN THE NECK REGION

Axial spinal muscles.—When the superficial cervical muscles have been cut and deflected and the underlying fascia removed, the axial spinal muscles are exposed. Most conspicuous are the three longitudinal columns that extend the length of the trunk. These three muscle columns represent the sacro-spinalis complex of higher vertebrates (Mosaur, 1935). The most medial and dorsal column is the M. spinalis-semispinalis complex. The most ventral and lateral column is the M. retractor costae biceps and the middle column is the M. longissimus dorsi. All three insert on the occiput and have a relationship to one another in the neck different from that of the trunk. In the trunk they are directly connected to one another by lateral and medial tendons of the M. longissimus and act as dorsal and lateral flexors of the vertebral column. They are more indirectly connected in the neck region and act as extensors and flexors of the head. The deep axial spinal muscles are the M. multifidus and M. digastricus dorsalis.

M. spinalis-semispinalis (Figs. 4, 5, 8, 9 and 12): This column of muscles is the most dorsal and medial of the epaxial trunk muscles. It lies against the vertebral neural spines superficial to the fibers of the M. multifidus. Lateral and ventral to it is the column of the M. longissimus. Mosaur described the repetitive nature of this muscle in the trunk of *Masticophis.* The arrangement in *Coluber* is in agreement.

In the neck region the M. spinalis-semispinalis interacts closely with two other muscles that insert on the occiput. These are the M. spinalis capitus and M. semispinalis cervicus. Their relationships are quite complicated and require an understanding of the trunk musculature to dissect them properly. I will review the M. spinalis-semispinalis as it occurs in the trunk and then discuss its termination on the skull.

In the trunk the two parts of the M. spinalis-semispinalis are clearly distinct in the Colubridae because the muscle has two heads of origin. The medial head is the M. spinalis. It originates as fleshy fibers from the tendons of the M. multifidus which lies deep to it. The M. spinalis is partly concealed laterally by the long slender tendons that cross it obliquely dorsocraniad. The fibers run craniad and slightly laterad for about three segments before fusing with fibers of the lateral head, the M. semispinalis.

The lateral head, or M. semispinalis, originates from the medial tendon of the M. longissimus. This tendon passes craniad for approximately five segments before it gives rise to the spindle-shaped muscle belly of the semispinalis. The muscle belly is directed cranially and somewhat dorsally for another four segments, and then joins the medial head. The common muscle that results continues its course anteriorly for another two to three segments and finally gives rise to a long slender tendon. The tendon passes obliquely craniad and dorsad, crossing superficially to the medial spinalis muscles, and then travels dorsal along the neural spines. Here it is enclosed in a tough, ligamentous sheath along with terminal tendons from other spinalis-semispinalis muscles. The individual tendon finally inserts on the posterior dorsal aspect of a neural spine some 13 to 15 segments anteriorly from the point of origin. Thus the total length of a single muscle is quite long, about 18 to 20 segments. Dissection of the muscle is complicated because (1) there are as many individual muscles as there are trunk segments and (2) each muscle is overlapped caudally by the muscle that immediately precedes it.

In the neck region the M. spinalis-semispinalis is modified considerably. The modification is a result of (1) the interlacing of other axial muscles (see Mm. spinalis capitus, semispinalis cervicus, multifidus) and, (2) the necessary shortening of the terminal tendons and muscle fibers to accommodate termination of the muscle column on the skull.

The two heads of the muscle continue to arise as they do in the trunk up to the region of the sixth or seventh vertebrae. It should be apparent that the insertion tendons of individual muscles in the neck cannot run 13 to 15 segments as they do in the trunk. In fact, the most anterior individual muscle with a tendon of this length begins at about the sixteenth vertebra. Muscles originating anterior to this one are not as long, and they have insertion tendons that become progressively shorter, about one half segment length shorter for each segment cranially. Accordingly, the tendon inserting on the axial neural spine is only seven to eight segments in length. The tendon inserting on the axis is the most anterior one to be enclosed in the ligamentous sheath, but there are two other tendons that insert farther forward. The tendon next in sequence does not insert directly on the atlas as expected, but to the nuchal ligament that covers the atlas. This tendon is very thin and passes superficially through fibers of the M. spinalis capitus and M. semispinalis cervicus; it acts as a shallow

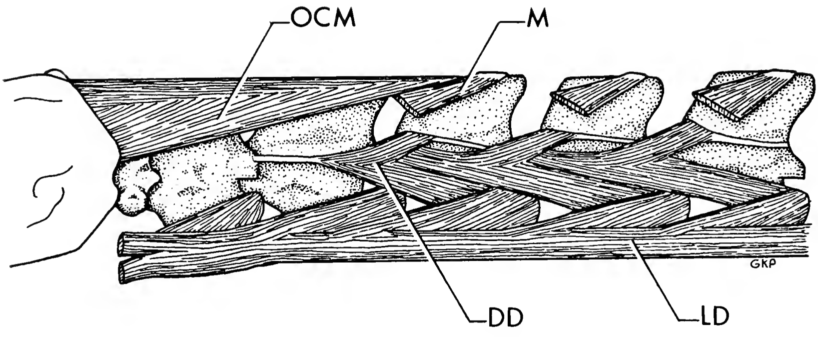


Figure 7. Some deeper cervical muscles of *Coluber constrictor:* Left lateral view. M. longissimus dorsi has been pulled ventrolaterally to expose M. digastricus dorsalis. DD, M. digastricus dorsalis; LD, M. longissimus dorsi; M, M. multifidus; OCM, M. obliqus capitus magnus.

inscription between these two muscles. The tendon is between five and six segments in length. Careful dissection will show that the spinalis portion from which it arises is made up of fibers originating from two or three multifidus muscles instead of one as in the trunk.

One more tendon remains and it represents the most anterior extent of the spinalis-semispinalis muscle column. It inserts on the supraoccipital crest medial to the insertion of the M. spinalis cervicus. The tendon is short, only four or five segments in length, and passes directly through the fibers of the M. semispinalis cervicus. Its association with this muscle is nearly inseparable and the tendon even collects some of its fibers.

The variability of the spinalis-semispinalis muscle in the neck is moderate. The arrangement described is typical of most of the material examined, but the presence of more than one tendon inserting on the supraoccipital crest occurred in several instances, particularly in larger specimens. Also, the coalescence of the two anteromost muscles with the M. spinalis capitus and M. semispinalis cervicus is such that it is nearly impossible to clearly distinguish their boundaries. The most important point is that the column does not terminate abruptly on the skull but, instead, it terminates by a short, thin tendon that represents a gradual reduction in fiber and tendon length of the most anterior muscles in the column.

M. longissimus dorsi (Figs. 4 and 6-11): The M. longissimus dorsi is the intermediate column of axial spinal muscles. In the trunk the muscle column arises by as many slips as there are body segments; each slip arises from a short tendon attached to the cranial circumference of a vertebral accessory process. Successive slips overlap one another caudally to form a muscle column ventrolateral to the M. spinalis-semispinalis and dorsomedial to the column of the M. retractor costae biceps. At the anterior end of each slip is an aponeurotic tendon. The tendon bifurcates almost immediately into medial and lateral tendons. The medial tendon courses anteromediad for five segments, passing through the intermuscular septum and gives rise to the lateral head of the M. spinalis-semispinalis. The longer lateral tendon runs anterolaterad for about eight segments and gives rise to the medial head of the M. retractor costae biceps. This is the arrangement of the M. longissimus dorsi throughout the trunk. Individual slips continue to arise as far craniad as the axis. Because there is no accessory process on the axis, this slip is attached to the process of the postzygapophysis, in common with the rudimentary accessory process of the third vertebra.

Modification of the M. longissimus in the neck region begins near the twentieth vertebra. From this point craniad, the individual muscles and their medial and lateral tendons become gradually shorter. At the level of the tenth vertebra the medial tendons are only three or four segments long and the lateral tendons one or two segments. The muscle slips arising anterior to the tenth vertebra no longer terminate in a bifurcate tendon; they fuse with one another at their anterior ends. Slips from the ninth vertebra to the fifth vertebra join those arising from the fourth vertebra to the axis by a tough tendonous inscription which runs obliquely anterodorsad through the muscle column near the level of the third vertebra. The inscription divides the whole column into dorsal and ventral heads; however, the heads are not distinct because the inscription does not pass completely through the fibers. Thus, the M. longissimus actually inserts on the skull by two heads. The dorsal head more or less represents the termination of slips from the fifth through ninth vertebrae and inserts by a short wide tendon onto the narrow lateral angle of the exoccipital crest. The ventral head is formed by fibers from slips originating from the axis to the fourth vertebra. This head runs farther cranially than the dorsal head because it passes ventral to the latter and inserts on the more cranially placed paraoccipital process.

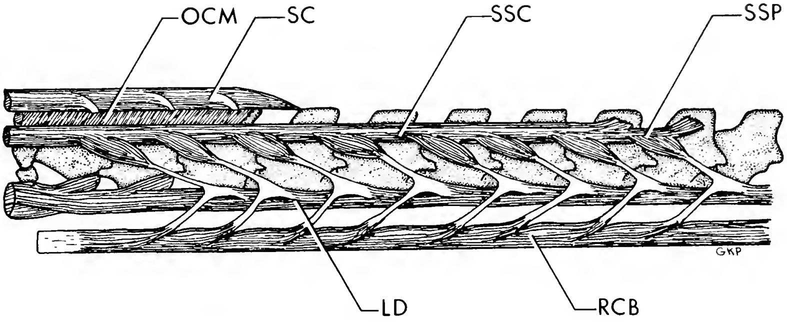


Figure 8. Axial spinal muscles in the neck region of *Coluber constrictor:* Left lateral view. M. longissimus dorsi and M. retractor costae biceps have been pulled ventrolaterally to expose tendons. M. spinalis capitus has been deflected dorsomediad. LD, M. longissimus dorsi; OCM, M. obliqus capitus magnus; RCB, M. retractor costae biceps; SC, M. spinalis capitus; SSC, M. semispinalis cervicus; SSP, M. spinalis-semispinalis.

The anterior structure of the M. longissimus dorsi is further complicated by the presence of the M. retractor costae biceps. The latter closely overlaps the M. longissimus laterally and inserts in common with the ventral head.

M. retractor costae biceps (Figs. 4, 8, 10 and 12): Following the long axis of the trunk laterally is a wide column of muscle, the M. retractor costae biceps. The column lies ventrolateral to the M. longissimus dorsi and dorsomedial to the M. supracostalis lateralis. Mosaur (1935) described the M. retractor costae biceps as a modified ileocostalis muscle and therefore part of the vertebral costal muscle group. The muscle is discussed here because of its close association with the M. longissimus dorsi, particularly in the neck.

In the trunk, the individual slips of the M. retractor costae biceps originate from the lateral tendons of the M. longissimus. Each tendon ends in a thin band of muscle that Mosaur termed the medial belly of the M. retractor costae biceps. The medial belly runs craniad, passing over four ribs, then narrows into a short tendon. The tendon continues anteriad and slightly ventrad for another two segments before joining a lateral belly. The lateral belly passes over four more ribs, finally giving rise to a terminal tendon that inserts on a rib shaft some twelve segments anteriorly. The total length of an individual muscle is more than twenty segments, and each is overlapped closely by the caudally adjacent segment. I was not able to separate the medial and lateral bellies from their adjacent counterparts as Mosaur described them, but the tendons connecting the medial and lateral bellies were found easily.

In the neck region the M. retractor costae biceps is best considered in two parts—(1) the insertions of the terminal tendons from the lateral bellies and (2) the termination of the column of muscle fibers (medial and lateral bellies) that arises cranial to the lateral belly that gives rise to the most anterior terminal tendon.

The anterior terminal tendons can be exposed by pulling the ventral side of the muscle column dorsally and away from the body. The tendons are arranged in an overlapping fashion, but each can be separated and followed to its respective rib. All ribs, including the shorter first rib articulating with the fourth vertebra, bear an insertion tendon. Three other tendons insert even farther anteriorly. These attach to the transverse processes of the third vertebra, axis and atlas. As pointed out, the insertion tendons in the trunk are approximately twelve segments in length. However, those that begin anterior to the sixteenth vertebra become gradually shorter so that the tendon inserting on the transverse process of the atlas is only six or seven segments in length. The precise site of this transition in length is variable and may be difficult to determine.

Remaining are the muscle fibers that arise from the lateral tendon of the M. longissimus cranial to that lateral belly the tendon of which inserts on the atlas transverse process. This column is simply a continuation from the trunk and represents a fusion of fibers from individual slips too far anterior to bear terminal tendons. In other words, cranial to the eighth vertebra, the medial and lateral bellies form a single column without insertion tendons. The column becomes very thin near the third vertebra and terminates as an aponeurosis. The aponeurosis is continuous with the tendonous fascia surrounding the ventral head of the M. longissimus dorsi, and thus inserts in common with it on the paraoccipital process.

The attachment of the M. retractor costae biceps to the skull is tenuous and indirect; therefore, the muscle does not function significantly in cranial mobility.

M. multifidus (Figs 7, 11 and 12): This is the deepest of the dorsal spinal muscles. It connects successive vertebrae. It is exposed in the trunk by removing the M. spinalis-semispinalis and in the neck by removing the Mm. spinalis capitus, semispinalis cervicus and obliqus capitus magnus. Throughout the trunk each muscle arises by a tendon from a vertebral neural spine. The muscle is directed obliquely anterolaterad. The deeper fibers insert on the posterior border of the neural arch of the second vertebra, whereas the more superficial fibers insert on the fourth vertebra anterior. This repetitive arrangement continues uninterrupted throughout the trunk. The series inserts most anteriorly on the atlas. No fibers insert on the skull.

In the neck region the M. multifidus appears basically as it does in the trunk. Only the two most anterior muscles are modified. They are shorter and their fibers are directed more laterally. The muscle originating from the neural spine of the fourth vertebra mostly passes over the third vertebra and inserts partly on the axis lamina and partly on the atlas. The fibers inserting on the atlas do so mainly by a short tendon attached to the caudal process above the postzygapophysis. The succeeding and most anterior multifidus muscle is peculiar. It originates by a tendon from the axis neural spine. The muscle fibers are directed almost completely in a lateral direction. They cover the neural arch of the axis and insert on the postzygapophysial process of the atlas. Superficial fibers interlace with those of the M. obliqus capitus magnus which overlies them.

M. digastricus dorsalis (Figs. 7, 11 and 12): Mosaur (1935) described the complicated arrangement of this muscle in the Colubridae and noted that it probably represents the M. interarticularis superior of boids. Gasc (1967) insisted that this was indeed the case and that the muscle is not a digastricus at all, but simply an interarticularis muscle that has lost part of its osseous connection. It is exposed by removing the M. spinalis-semispinalis and by pulling the M. longissimus dorsi ventrally. It is also of the repetitive type with all the segments together forming a narrow longitudinal muscle column. Individual segments arise by two heads. A medial head, which is covered in part by fibers of the M. multifidus, originates by a tendon fixed to the postzygapophysis. A lateral head arises in part by a tendon attached to the accessory process and in part by fibers from a tendonous raphe shared with the medial side of the M. longissimus dorsi. The two heads join and extend over three segments to insert by a tendon onto the postzygapophysis of a more cranial vertebra.

The muscle is modified only slightly in the neck region. Beginning from the twelfth to fifteenth vertebrae and continuing cranially, the lateral head arises more from the raphe shared with the M. longissimus and less on its own from the accessory process. The most anterior insertion of the M. digastricus dorsalis is on the postzygapophysis of the axis.

Subvertebral muscles.—There are two subvertebral muscles—the M. transversohypapophyseus and the M. costovertebrocostalis. They are intimately associated, and are best understood if dissected concurrently.

M. transversohypapophyseus (Figs. 6, 12): This ventral spinal muscle, peculiar to colubrids, is restricted approximately to the fifty anterior vertebrae in *Coluber constrictor*. In colubrid snakes that have well-developed hypapophyses throughout the trunk, the muscle extends to the vent (Mosaur, 1935). Ventrally it is covered by the aponeurotic origin of the M. costalis internus superior, which, if deflected, will expose the tendonous slips of the individual muscles. In the neck, the M. rectus capitus anterior must also be removed. The single slips arise by a fleshy connection from the cranial circumference of a transverse process and, as a narrow band of muscle, runs anteriorly for three or four segments and inserts by a tendon onto the posterior angle of a vertebral hypapophysis. The caudal muscles overlap the cranial ones, interlacing as they do so.

In the neck, the M. transversohypapophyseus inserts as far cranially as the atlas. I found no evidence of it inserting on the skull, but there are a few peculiarities of the muscle in this area. First, the muscles that originate from the third and fourth vertebrae are shorter than those of the trunk. They insert by a common tendon onto the basal protuberance of the atlas intercentrum. Second, several individuals (6 of 18) showed the curious condition of a second, more lateral tendon inserting on the ventrolateral margin of the axis centrum. Third, there are additional anterior fibers arising from the third vertebra and the axis. Together with two or three tiny tendons, they insert on the dorsal border of the atlas intercentrum. Their arrangement gives a crescent-shaped appearance to this angle of the atlas-axis articulation. I am unsure what muscle these fibers represent. They may be part of the M. costovertebrocostalis but they seem associated more closely with the M. transversohypapophyseus.

M. costovertebrocostalis (Fig. 11): Exposing this muscle can be a memorable exercise in patience and dexterity. It is small and occupies the intercostal space around the ventrolateral surface of the vertebra, the transverse process and rib heads. Medial to the M. costovertebrocostalis is the hypapophysis, lateral is the M. intercostalis quadrangularis, dorsal is the M. tuberculocostalis and ventral the aponeurosis of the costalis internus superior and the M. transversohypapophyseus. The muscle originates on the ventrolateral margin of the centrum and runs caudally, inserting on the ventral tubercle of the capitulum costae of the succeeding rib. Mosaur (1935) described two heads to this muscle—a dorsal head joined to a ventral head by a short raphe. In the anterior trunk I could not identify separate heads, only the single muscle. This would support Auffenberg's assumption that

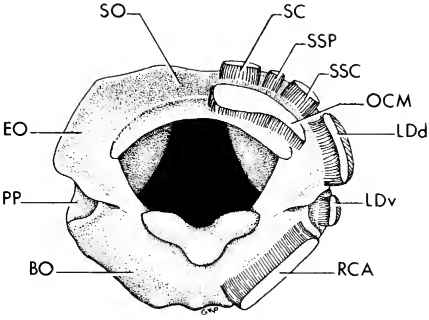


Figure 9. Cranial view of occiput of *Coluber constrictor:* Insertions of occipito-vertebral muscles are shown on the right side. BO, basioccipital; EO, exoccipital; LDd, M. longissimus dorsi—dorsal head; LDv, M. longissimus dorsi—ventral head; OCM, M. obliqus capitus magnus; PP, paraoccipital process; RCA, M. rectus capitus anterior; SC, M. spinalis capitus; SO, supraoccipital; SSC, M. semispinalis cervicus; SSP, M. spinalis-semispinalis.

the ventral head of the muscle has been replaced by the M. transversohypapophyseus in those colubrids bearing well-developed hypapophyses (Auffenberg, 1958).

In the neck, this muscle is found anteriorly as far as the fourth vertebra and it inserts on the capitulum costae of the rib articulating with it. It is shorter than its trunk counterparts.

Other vertebral-costal muscles.—Two miscellaneous vertebral-costal muscles are the M. interarticularis inferior intertendinosus and M. levator costae.

M. interarticularis inferior intertendinosus (Figs. 10 and 11): This thin column of muscle is at first difficult to locate because of its proximity to the ventromedian side of the M. longissimus. To expose it, the M. retractor costae biceps must be removed and the M. longissimus dorsi pulled gently dorsad. The individual muscles form a narrow column of intermingling fibers. Each arises from an accessory process, in common with the M. longissimus. The fibers are sent craniad where some of them insert onto succeeding accessory processes. Most of the muscle inserts on the tendon of a levator costae muscle. The deeper fibers insert on the succeeding tendon, but the more superficial ones will reach to the fourth tendon ahead.

In the neck, the main column reaches as far craniad as the accessory process of the third vertebra and the tendon of the most anterior levator costae muscle. Anterior to this insertion, a small segment of the muscle column connects the first three vertebrae. This smaller element originates from the prezygapophysis of the third vertebra and passes craniad where most of its fibers terminate on the neural arch pedicle of the axis. A narrower collection of fibers passes below these and forward into the

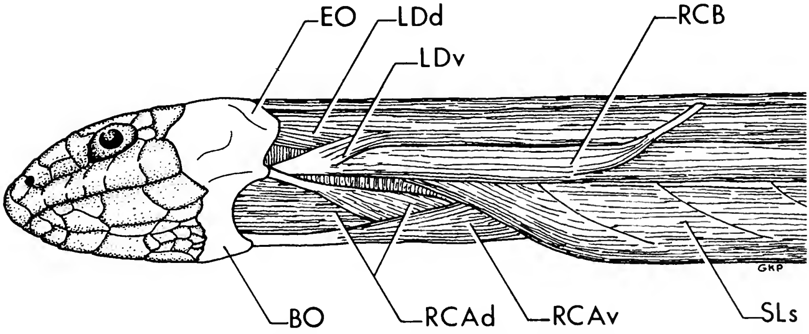


Figure 10. Occipito-vertebral muscles of *Coluber constrictor:* Ventrolateral view. Note insertion of M. retractor costae biceps in common with ventral head of M. longissimus dorsi. BO, basioccipital; EO, exoccipital; LDd, M. longissimus dorsi—dorsal head; LDv, M. longissimus dorsi—ventral head; RCAd, M. rectus capitus anterior pars dorsalis; RCAv, M. rectus capitus anterior pars ventralis; RCB, M. retractor costae biceps; SLs, M. supracostalis lateralis superior.

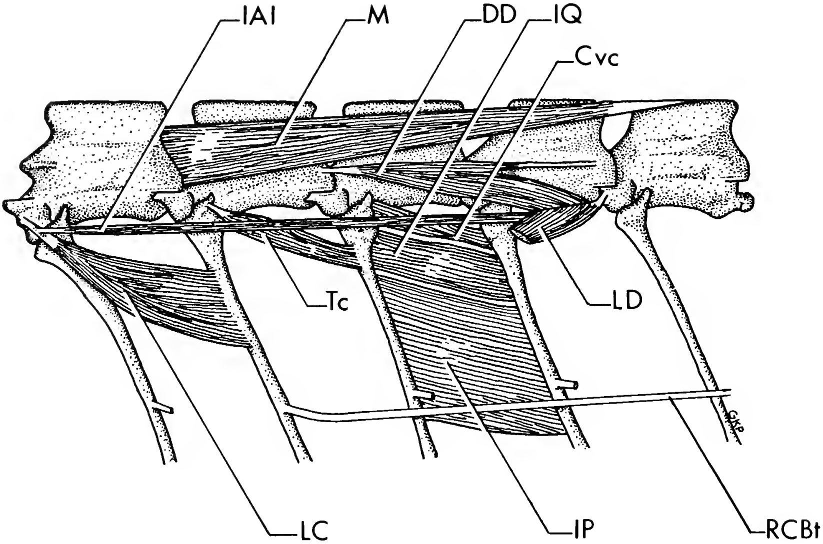


Figure 11. Deep muscles of the trunk and neck of *Coluber constrictor:* Lateral view (modified from Gasc, 1967). Cvc, M. costovertebrocostalis; DD, M. digastricus dorsalis; IAI, M. interarticularis inferior intertendinosus; IP, M. intercostalis proprius; IQ, M. intercostalis quadrangularis; LC, M. levator costae; LD, M. longissimus dorsi; M, M. multifidus; RCBt, terminal tendon of M. retractor costae biceps; Tc, M. tuberculocostalis.

posterolateral wall of the atlas neural arch.

M. levator costae (Fig. 11): The belly of this muscle is exposed by pulling the column of the M. retractor costae biceps dorsally and medially. Its tendonous origin remains concealed by the column of the M. interarticularis inferior intertendinosus, which covers it laterally. The muscle is more or less diamond-shaped and occupies the vertebral portion of the intercostal space lateral to the M. tuberculocostalis. Its origin is by a strong tendon arising from the caudal circumference of the accessory process. The tendon crosses over the rib articulating with the same vertebra and passes into the muscle fibers. The fibers are directed caudally and ventrally, following the lateral body contour. They insert on the cranial border of the adjacent caudal rib shaft near the insertion of the terminal tendon of the M. retractor costae biceps.

The M. levator costae is attached to all of the ribs in the neck region. There is slight but noticeable modification of the muscle acting on the first rib. It is the most anterior levator costae muscle and arises from the diminutive accessory process of the third vertebra. The muscle belly is shorter and narrower than those of the trunk and adheres closely to the terminal bundle of the costal muscles on its cranial side. Its deeper fibers insert on the shaft of the first rib, whereas the superficial fibers pass over it and join those from the same muscle that insert on the second rib.

COSTAL MUSCLES

The costal muscles will be considered in two groups. The first group includes two muscles occupying the intercostal space on the upper one-third of the rib shafts. These are the M. tuberculocostalis and M. intercostalis quadrangularis. Their close association with neighboring vertebral-costal muscles (Mm. levator costae, costovertebrocostalis) warrants brief but separate descriptions of each.

The second group includes the other costal muscles. They are found on the lower two-thirds of the rib shafts forming a fleshy stratum that (1) connects successive ribs and (2) forms throughout the trunk a covering on the inner and outer surfaces of the ribs. These muscles are the Mm. intercostalis proprius, supracostalis lateralis superior and inferior, and costalis internus superior and inferior. Their relationships will be summarized in a single description.

M. tuberculocostalis (Fig. 11): Lying just beneath the M. levator costae is a small, somewhat cylindrical muscle, the M. tuberculocostalis. Its origin is by a short tendon attached to the caudal circumference of the dorsal rib tubercle. Fibers run obliquely laterad and caudad to insert on the

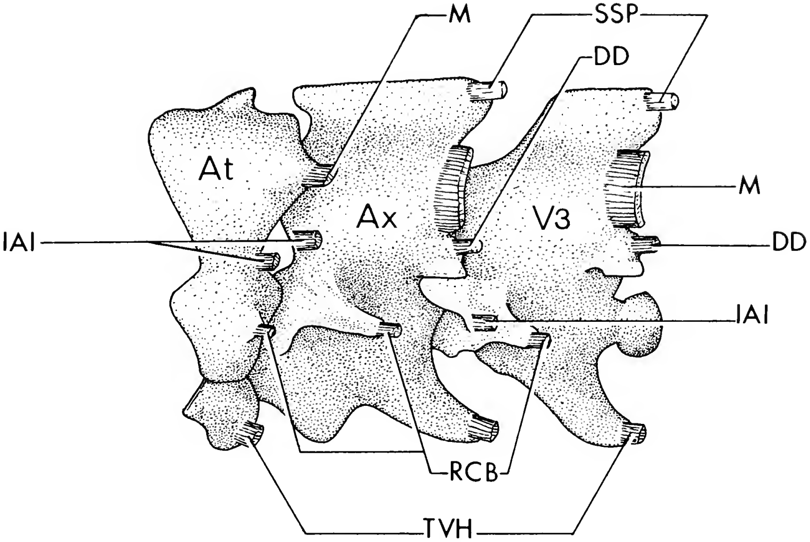


Figure 12. Most anterior three vertebrae of *Coluber constrictor* showing muscle insertions: Left lateral view. At, atlas; Ax, axis; DD, M. digastricus dorsalis; IAI, M. interarticularis inferior intertendinosus; M, M. multifidus; RCB, M. retractor costae biceps; SSP, M. spinalis-semispinalis; TVH, M. transversohypapophyseus; V3, third vertebra.

cranial border of the following rib shaft just below the neck.

The muscle is found anteriorly as far as the intercostal space between the first and second rib.

M. intercostalis quadrangularis (Fig. 11): This is a ventral median costal muscle that lies just lateral to the M. costovertebrocostalis. It arises from the medial surface of the ventral tubercle of the rib and passes caudad and laterad to insert on the anterior surface of the succeeding rib. The longer fibers of the muscle are directed at an oblique angle ventrally, thereby giving the muscle a quadrangular shape.

The muscle is found anteriorly as far as the intercostal space between the first and second rib.

Other costal muscles (Figs. 4, 6, 10-12): The remaining costal muscles are the Mm. intercostalis proprius, supracostalis lateralis superior and inferior, and costalis internus superior and inferior. The M. intercostalis proprius is a wide, single muscle sheet that connects successive ribs, filling the ventral two-thirds of the intercostal space. Fibers pass from the posterior border of one rib and insert on the cranial surface of the succeeding caudal rib. The muscle begins in the neck region from the first rib.

Along the trunk, on the lateral and medial surfaces of the ribs, are the Mm. supracostalis lateralis superior and inferior, and costalis internus superior and inferior. Both pairs of muscles form a fleshy covering on the outer and inner surfaces of the ribs that, in effect, envelopes the M. intercostalis proprius.

Segments of the M. supracostalis lateralis superior and inferior arise from the lateral surface of each rib. The muscle fibers run caudad, spanning up to fifteen ribs before inserting on the cranial circumference of a rib shaft. Fibers from successive segments interlace with each other, obscuring the origins.

Segments of the M. costalis internus superior arise from an aponeurosis attached to the hypapophysis of the vertebrae. Together the segments form a muscle of considerable thickness, which runs at an oblique angle downward and craniad. The separate elements insert on the fifth rib ahead, caudal to the origin of the M. costalis internus inferior. The inferior portion is essentially a ventral continuation of the superior, although its segments span only three ribs.

In the cervical region the M. supracostalis lateralis and M. costalis internus have a unique relationship. They wrap around the cranial surface of the first rib and join each other in a fleshy bundle. This bundle runs obliquely anterodorsad, parallel to the first rib, and narrows into a wide tendon. The tendon inserts on the transverse process of the atlas.

MISCELLANEOUS MUSCLES

Several axial muscles found during the dissection, but not relevant to the study, are mentioned here for the sake of completeness.

Mm. costocutanei superiores and inferiores: These two muscles are the principal elements causing movement between the trunk and the skin. They have been described thoroughly in snakes by Buffa (1904) and Mosaur (1935) and are summarized briefly here.

The individual slips of the M. costocutaneous superior (Fig. 4) arise from the lateral side of the ribs and pass outward between the M. retractor costae biceps and M. supracostalis lateralis superior. The fibers form flat bundles directed backward and laterad. They insert on the lateral and ventrolateral scale rows.

The segments of the M. costocutaneous inferior are similar to the M. costocutaneous superior. They are attached to the cartilagenous rib tips, run caudad and insert on the sides of the ventral scales and the first three or four scale rows.

Both of these muscles reach the cervical region where they maintain a close alliance with the hyoid and its associated muscles (see Langebartel, 1968 for a full description of hyoid musculature).

Mm. obliqus abdominis internus, transversus abdominis: These two muscles form a double-layered sheet across the ventral aspect of the trunk. The M. transversus abdominis lies deep to the M. obliqus abdominis internus. Muscle fibers of the former arise from the medial surface of the ribs near their distal ends. They constitute a thin sheet that extends posteriad and mediad to the linea alba. The latter muscle arises and inserts in common with the M. transversus abdominis, but its fibers are directed craniad. The two sheets terminate anteriorly at the hyoid cornu.

M. rectus abdominis: This muscle stretches between successive rib cartilages and follows exactly the long axis of the body. It is not particularly distinct from the M. intercostalis proprius and some of its fibers even mingle with those of the M. supracostalis lateralis inferior.

Connective tissue and fascia.—In *Coluber* there is a well-developed system of intermuscular fascia that furnishes structural and functional stability to the intricate muscle architecture. The formation of fascial tunnels through which the long muscles extend solves numerous packaging problems that result when the muscles are flexed and the body bends and curves. Such tunnels enclose the muscle columns of the axial spinal series throughout the trunk and neck. The fascia surrounding the column of the M. spinalis-semispinalis is particularly tough. Medially and dorsally this fascia is continuous with the ligamentous sheath enclosing the terminal tendons of that muscle. Additional fibrous connective tissue stretches the length of the trunk along the dorsal midline above the ligamentous sheath. It connects both M. spinalis-semispinalis columns on either side of the neural spines.

A ventral fascia also covers the subvertebral muscles and provides a membrane for the inner body wall.

Other important connective tissue separates the columns of the M. longissimus and M. spinalis-semispinalis as a *septum intermusculare dorsi mediale* (Mosaur, 1935). The septum is formed from the medial tendons of the M. longissimus that pass through it and by the fascia that connects these tendons in a vertical plane (Type A of Mosaur). In some colubrid snakes like *Lampropeltis, Rhinocheilus* and *Drymarchon* the medial tendons of the M. longissimus fuse with the septum (Type B of Mosaur) and do not pass through to the M. semispinalis (see section on Neck Muscles in Other Colubrid Snakes for more detail).

Finally, a *ligamentum nuchae* (nuchal ligament) is present in *Coluber,* though I found no mention of it elsewhere for snakes. The structure appears as a thick fibrous sheet separating the spinalis capitus muscles anteriorly on either side of the dorsal midline. The nuchal ligament arises from the midsagittal crest of the supraoccipital bone and reaches posteriorly between these muscles covering the atlas neural arch. It attaches deeply to the neural spine of the axis, but superficially the ligament continues caudad with the dorsal fascia of the neck.

NECK MUSCLES IN OTHER COLUBRID SNAKES

The description of *Coluber* is more meaningful if its range of morphological variation encompasses that found in related genera. Mosaur (1935) concluded that the trunk muscles of most colubrid snakes have an arrangement referable to that of *Masticophis.* From an admittedly small sampling I conclude similarly—most colubrid snakes have cervical muscles similar to those of *Coluber.*

The following genera selected for comparison were placed in the Colubridae by Underwood (1967b). Three are medium sized terrestrial forms: *Lampropeltis getulus californiae* (Blainville), *Elaphe g. guttata* (Linné) and *Pituophis melanoleucus anmectens* (Baird and Girard). Another is the large terrestrial snake *Drymarchon corais erebenus* (Cope). The small desert species *Chionactus occipitalis annulata* (Baird) provides a contrast to these generalized types by its commitment to a subterranean existence (see Norris and Kavanau, 1966). The common garter snake *Thamnophis sirtalis* (Linné), placed by Underwood (1967b) in the closely related family Natricidae, was examined for intrafamilial similarity.

The muscles described for *Coluber constrictor* are present in the above snakes with the exception of the M. constrictor coli in *Pituophis* and *Chionactus*. Variation in most muscles is unremarkable and involves minor differences such as the appearance of additional tendons or the interlacing of adjacent muscles. The more obvious are discussed below according to muscle or muscle group.

Dorsal cervical muscles: The M. spinalis capitus and M. semispinalis cervicus are the most variable muscles, mainly because of the intermuscular septum. Recall that the septum divides the column of the M. spinalis-semispinalis from the column of the M. longissimus dorsi and receives the medial tendons of the latter muscle. The tendons either pass directly through the septum to the belly of the Mm. semispinalis (Type A of Mosaur), or they fuse with the septum, and the belly of the Mm. semispinalis arises independently from the medial surface of the septum (Type B of Mosaur). *Coluber, Elaphe, Pituophis* and *Thamnophis* are Type A. *Drymarchon, Lampropeltis* and *Chionactus* are Type B. In the neck of Type A snakes the M. semispinalis cervicus arises as it does in *Coluber.* In the neck of Type B snakes the M. semispinalis cervicus originates from the medial surface of the intermuscular septum as a bundle of fibers continuous to the anterior limit of the septum. The septum reaches cranially to the fourth or fifth vertebra. The individual slips of the muscle are less distinct in these genera than in the Type A snakes. It would seem that the origin of the muscle by a well-defined tendon is probably the more advanced condition.

There is also modification in the M. spinalis capitus. In each genus it originates from the dorsal fascia above the ligamentous sheath enclosing the terminal tendons of the Mm. spinalis-semispinalis. In *Coluber* and *Thamnophis* this is by tendonous slips attached to the neural spines, but in *Elaphe, Drymarchon* and *Pituophis* only a single tendon arising from the axis neural spine is present. The rest of the origin is fibrous. In these snakes, particularly *Pituophis,* the muscle is wider and quite difficult to separate from the M. semispinalis cervicus lateral to it. Interestingly both these muscles are better developed in *Chionactus.* In fact, the axial muscles throughout the trunk of this snake are exaggerated.

M. rectus capitus anterior: This muscle is present in each genus as a pars ventralis and a pars dorsalis. The two parts are best exhibited in *Drymarchon, Pituophis* and *Lampropeltis.* They partly coalesce anteriorly in *Coluber, Thamnophis* and *Elaphe* and are almost inseparable in *Chionactus.* There is little difference in the pars dorsalis, but in *Elaphe* and *Drymarchon* there is a second tendon from the lateral head of the muscle that inserts just caudal to the one inserting on the paraoccipital process of the skull.

Slips of the pars ventralis of *Drymarchon* originate by conspicuous tendons. In the other snakes the slips have a fibrous origin. The pars ventralis of *Chionactus* deviates by reaching posteriorly to the eighteenth vertebra, whereas in the other genera the extent of the muscle is invariably restricted to the eleventh or twelfth vertebra.

M. longissimus dorsi and M. retractor costae biceps: Coluber is unique in that the column of the M. retractor costae biceps terminates cranially as an aponeurosis continuous with the fascia surrounding the ventral head of the M. longissimus. This connection is fleshy in the other genera and conceals the dorsal/ventral division of the M. longissimus. The bulk of the muscle inserting on the paraoccipital process in these snakes is from the M. retractor costae biceps. The ventral head of the M. longissimus is still present, but it is not as distinct as it is in *Coluber.* For *Elaphe, Drymarchon* and *Pituophis* the most anterior medial tendon of the M. longissimus passes through the muscle column and completes the division. This tendon inserts on the postzygapophysial process of the atlas.

M. constrictor coli: This muscle is present in each genus with the exceptions of *Pituophis* and *Chionactus.* However, its apparent absence in them may be a technical artifact. Only one poorly preserved specimen of *Pituophis* was dissected. Although the condition of most muscles was reasonably diagnostic, the M. constrictor coli may have deteriorated. *Chionactus,* on the other hand, is such a small snake that the muscle could have been overlooked. In the other genera the muscle is as described for *Coluber.*

Fascia: The intermuscular connective tissue is abundant but irregularly distributed. This is worth mentioning because where there is less connective tissue dissection of muscles is considerably easier. Of course, there may be a functional significance worth exploring because the fascia provides mechanical support. The dorsal fascia is thick and fibrous in *Pituophis, Drymarchon* and *Lampropeltis.* It is thinnest in *Coluber* and *Thamnophis.*

Summary of Generic Comparison: Examination of additional colubrid genera supports the conclusion that *Coluber* is typical of the family. The following conclusions apply to the neck muscles in the group as a whole.

1. The myology of the neck region in generalized colubrid snakes approximates that found in *Coluber constrictor.* Variation is limited largely to fiber bulk, number of tendonous origins and fibrous association with adjacent muscles.
2. Of the species compared, *Thamnophis* is the most similar to *Coluber.* I consider the familial ranking of the Natricidae questionable. Underwood (1967b) distinguishes the Colubridae from the Natricidae essentially on hemipenal characters. His classification is used here for the sake of consistency to this presentation and to underscore the prevalence of a Coluber-like myology among higher, non-venomous snakes.

3. The myology of *Chionactus* is the most aberrant of the species compared. It has a long M. rectus capitus anterior and a general bulkiness about the axial musculature which seem related to the species burrowing habits.

4. The value of cervical myology as a taxonomic tool at the subfamily and generic level remains to be tested. Currently it appears weakened by the remarkable similarity of muscles found in genera showing diverse life styles and which are taxonomically distinct on other grounds. The muscle architecture of colubrid snakes represents a persistence of common features found throughout the family.

DISCUSSION

When the shoulder girdle was lost in snakes so was the thoraco-cervical boundary, and evidently the body musculature has obliterated any trace of its former position. The anterior trunk muscles are of no help in delimiting the cervical region because each is modified so subtly. For example, muscles associated with the first rib bear nearly the same relationship to each other as they do in the trunk. Moreover, modification of some muscle groups is inconsistent with others. The long muscles (Mm. spinalis-semispinalis, longissimus dorsi, retractor costae biceps) become shorter anteriorly in a graduated sequence, but some of the briefer intervertebral series (Mm. digastricus dorsalis, interarticularis intertendinosus) tend to lengthen. Also, all but two of the occipito-vertebral muscles are continuous with the trunk (Table 1). Thus the terms M. spinalis capitus and M. semispinalis cervicus are at present more convenient than real. One is left with the impression that modification of the trunk musculature in the cervical region reflects accommodation to structural uniformity. Fortunately there are two muscles that prove a neck exists at all. The M. obliqus capitus magnus and M. rectus capitus anterior have no trunk counterparts and they function exclusively for movement of the head and neck. These muscles have probably been retained from a tetrapod ancestry, but I am uncertain as to how they have been modified.

This study of *Coluber* provides several points relevant to understanding the structural evolution of the cervical region in snakes.

1. The skeleton tells us little about the structural history, other than there was intense selective pressure for consistent design.

2. Dissection of adults and juveniles suggests that during ontogeny size increase imposes mechanical demands on the muscles in the form of an increase in the number of tendonous origins and proportionately longer muscles. There is also a corresponding enlargement of the crests and processes of the occipital bones and vertebrae, which should be taken into account by investigators attempting identification of snake vertebrae by statistical analysis.

3. The muscle architecture of colubrids is conservative yet amazingly adaptable, being suitable for sand burrowing as shown by *Chionactus* and perhaps for climbing as well, as in the arboreal colubrids (e.g., *Chrysopelea* or *Oxybelis*) which depend on body rigidity rather than short radius arcs in locomotion (Auffenberg, 1962).

4. Moderate interspecific variation in muscle patterns is tolerable so long as functional units are maintained.

5. The origin of the M. rectus capitus anterior in snakes lacking hypapophyses is unknown. Vertebral hypapophyses are a classic systematic character in snakes, but one which has been difficult to apply. They are varyingly present in both primitive and advanced species (Malnate, 1972). Perhaps correlation with this muscle will help clarify the meaning of the character.

6. Muscles of the neck region can be organized into three groups: (1) those inserting on the occiput that originate anterior to the twelfth vertebra, (2) those inserting on the occiput as a termination of repetitive elements from the trunk, and (3) those muscles continuous with the trunk that do not insert on the occiput, but terminate on the atlas, axis or third vertebra. The most well-defined cervical

muscles are the M. obliqus capitus magnus and M. rectus capitus anterior. They are restricted to the neck and are probably homologous to the same named muscles described for *Iguana* by Evans (1939) and *Ctenosaura* by Oelrich (1956).

7. The description of *Coluber* is representative of most snakes in the family Colubridae, but the myology may vary slightly in species with special adaptive requirements. Variation of muscle relationships in a species is minor and attributable to ontogenetic change and individual variance.

The functional properties of the neck are more difficult to assess. Because efficient lateral undulatory locomotion is a primary concern of snakes (and indeed a major reason for their success), synchronous and uninterrupted flexion are best accomplished by the head and neck acting functionally as one. Movement at the occipito-vertebral joint is probably more important for feeding and defensive action than for routine cruising and the articulation is typical of most squamates in that versatility is nearly restricted to vertical movement. In colubrids other uses of the head and neck (such as for burrowing) are behavioral adaptations in which any structural modifications are secondarily acquired—for example, the longer M. rectus capitus anterior pars ventralis of *Chionactus*.

Further research into the neck morphology of snakes and its relationship to that of other limbless reptiles may help clarify functional properties. The problem is to determine the morphological events in cervical evolution that accompanied limb reduction and loss of the shoulder girdle. The current theory on snake origins states that snakes were derived from limbless or nearly limbless burrowing lizards and that "proto-snakes" subsequently emerged from below ground and diversified (Bellairs and Underwood, 1951; Underwood, 1967b). Logically the next step would be to examine snakes having musculature that is less complicated than the Colubridae, for example boids. Ultimately lizards must be investigated. The published accounts on the myology of limbless species are few and mostly concerned with head musculature; description of body morphology has been generally neglected. In light of the numerous studies on reptilian head morphology (see Gans and Parsons, 1973) it is unfortunate that so many of these ignored the neck region.

ACKNOWLEDGMENTS

The guidance of Dr. Richard E. Etheridge was incomparably profound and valuable insights were also provided by Dr. Jason A. Lillegraven, Dr. Richard D. Estes and Dr. David M. McArthur, all of San Diego State University. Suggestions and criticisms were also offered by Dr. Thomas H. Fritts of the San Diego Natural History Museum. Dr. Linda Trueb of the Museum of Natural History at The University of Kansas generously donated her time and resources to many phases of the manuscript. Other assistance was provided by Mr. Jacques A. Gauthier and Ms. Ann L. Pregill. The cover photo is courtesy of J. T. Collins.

LITERATURE CITED

ALBRIGHT, R. G. and E. M. NELSON, 1959. Cranial kinetics of the generalized colubrid snake *Elaphe obsoleta quadrivittata*. I. Descriptive morphology, and II. Functional morphology. Journal of Morphology 105: 193-291.

AUFFENGERG, W., 1958. The trunk musculature of *Sanzina* and its bearing on certain aspects of the myological evolution of snakes. Breviora, Museum of Comparative Zoology No. 82.

AUFFENBERG, W., 1961. Additional remarks on the evolution of trunk musculature in snakes. American Midland Naturalist 65: 1-19.

AUFFENBERG, W., 1962. A review of the trunk musculature in the limbless land vertebrates. American Zoologist 2: 183-190.

AUFFENBERG, W., 1966. The vertebral musculature of *Chersydrus* (Serpentes). Quarterly Journal of the Florida Academy of Science 29: 183-190.

BAILEY, J. R., 1967. The synthetic approach to colubrid classification. Herpetologica 23: 155-161.

BELLAIRS, A. d'A. and G. UNDERWOOD, 1951. The origin of snakes. Biological Reviews of the Cambridge Philosophical Society 26: 193-237.

Buffa, P., 1904. Richerche sulla muscolature cutanea dei serpenti e considerazioni sulla locomozione di questi animali. Dall'l stituto di Zoologia e Anatomia Comparata della R, Univerista di Padova p. 145-225.

Cowan, I. and W. Hick, 1951. A comparative study of the myology of the head region in three species of *Thamnophis*. Transactions of the Royal Society of Canada 45: 19-60.

Dessauer, H. C., 1967. Molecular approach to the taxonomy of colubrid snakes. Herpetologica 23: 148-152.

Dowling, H. C., 1967. Hemipenes and other characters in colubrid classification. Herpetologica 23: 138-142.

Evans, F. G., 1939. The morphology and functional evolution of the atlas-axis complex from fish to mammals. Annals of the New York Academy of Science 39: 29-104.

Gans, C. and T. Parsons, eds., 1973. Biology of the Reptilia Vol. 4, Morphology D, Academic Press, New York.

Gasc, J. P., 1967. Introduction a l'étude de la musculature axiale.des squamates serpentiformes. Mémoires du Muséum National D'Histoire Naturelle, Paris Série A 48: 69-124.

Haas, G., 1961. Remarques concernant les relations phylogeniques des diverses familles d'ophidiens fondées sur la différenciation de la musculature mandibulaire. Problēms Actuels de Paléontologie (Évolution des Vertebres) 104: 215-241.

Haas, G., 1973. Jaw muscles in Rhynchocephalia and Squamata, p. 285-490. *In*, Gans, C. and T. Parsons (eds.), Biology of the Reptilia Vol. 4, Morphology D, Academic Press, New York.

Hoffstetter, R. and J. Gasc, 1965. Vertebrae and ribs of modern Reptilia, p. 201-310. *In*, Bellairs, A. d'A. and T. S. Parsons (eds.), Biology of the Reptilia Vol. 1, Morphology A, Academic Press, New York.

Johnson, R. G., 1955. The adaptive and phylogenetic significance of vertebral form in snakes. Evolution 9: 367-388.

Langebartel, D. A., 1968. The hyoid and its associated muscles in snakes. Illinois Biological Monographs No. 38.

Ludicke, M., 1962. Ordung der Klasse Reptilia, Serpentes. *In*, W. Kukenthal, T. Krumbach, J.-G. Helmcke, H. von Lengerken and D. Starck (eds.), Handbuch der Zoologie Band 7, Halfte 1, Lieferung 5, Walter de Gruyter, Berlin.

Malnate, E. V., 1974. Observations on the vertebral hypapophyses and associated musculature in some snakes, with special reference to the Colubridae. Zoologische Mededelingen 47: 221-239.

Mosaur, W., 1935. The myology of the trunk region in snakes and its significance for ophidian taxonomy. University of California at Los Angeles, Publications in Biological Sciences No. 1: 81-120.

Nishi, S., 1916. Zur vergleichenden Anatomie der Eigentlichen (genuinen) Ruckenmuskeln. Morphologie Jahrbuch 50: 167-318.

Norris, K. S. and J. L. Kavanau, 1966. The burrowing of the western shovel-nosed snake, *Chioncatus occipitalis* (Hallowell) and the undersand environment. Copeia p. 65-644.

Oelrich, T. M., 1956. The anatomy of the head of *Ctenosaura pectinata* (Iguanidae). Miscellaneous Publications Museum of Zoology, University of Michigan No. 94.

Romer, A. S., 1956. Osteology of the reptiles. University of Chicago Press, Chicago.

Rossman, D. A., 1967. Introduction to the symposium on colubrid snake systematics. Herpetologica 23: 137.

Underwood, G., 1967a. A comprehensive approach to the classification of higher snakes. Herpetologica 23: 161-168.

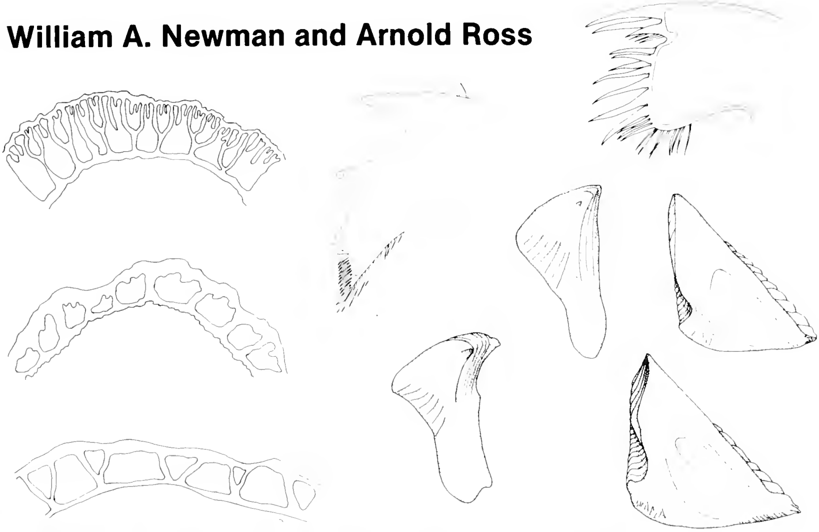
Underwood, G., 1967b. A contribution to the classification of snakes. British Museum (Natural History), London, 179p.

Williams, E. E., 1959. The occipito-vertebral joint in the burrowing snakes of the family Uropeltidae. Breviora, Museum of Comparative Zoology No. 106.

Museum of Natural History, The University of Kansas, Lawrence, Kansas

A LIVING *TESSEROPORA* (CIRRIPEDIA: BALANOMORPHA) FROM BERMUDA AND THE AZORES: FIRST RECORDS FROM THE ATLANTIC SINCE THE OLIGOCENE

William A. Newman and Arnold Ross



TRANSACTIONS

OF THE SAN DIEGO
SOCIETY OF
NATURAL HISTORY

VOL. 18, NO. 12 24 February 1977

A living *Tesseropora* (Cirripedia; Balanomorpha) from Bermuda and the Azores; first records from the Atlantic since the Oligocene

William A. Newman and Arnold Ross

ABSTRACT.—*Tesseropora* occupies a central position in the evolution of the Tetraclitinae, and likely the Tetraclitellinae, by virtue of geological age and comparative morphology. Considering the biogeography of the two extant species from the Indo-West Pacific, the genus is apparently favored by the special requirements related to perpetuation of insular populations. The more highly evolved genus *Tetraclita*, on the other hand, is for the most part prevalent on continental shores where the opportunities for competitive interactions are greater. Recognition of a new species of *Tesseropora* from Bermuda and the Azores corroborates the primarily insular nature of the genus and enhances the concept that oceanic islands can act as refugia for ancient forms.

In consideration of the special adaptations needed by marine organisms to perpetuate their populations on oceanic islands on one hand, and the isolation, ephemerality, short faunal lists and concomitant unbalanced biotas of oceanic islands on the other, one would expect vagile, eurytopic taxa, or the descendents thereof, to be disproportionately prevalent on them. Many such taxa are early members of lineages having advanced members more commonly found in centers of distribution frequently contiguous with continental shores, and this is apparently the basis for the concept that insular situations can act as refugia for ancient forms.

Tesseropora isseli (de Alessandri, 1895: 296), from the Oligocene of Italy, is the oldest known tetraclitid. Pilsbry (1916: 259), when reflecting on the significance of the single row of parietal tubes in the wall of the only extant species of the genus known at the time, remarked " . . . [*T. rosea* (Krauss, 1848)] is to be regarded as an unprogressive form, which retains characters of the ancestral stock of the genus, elsewhere found [in the Tetraclitidae] only in an early stage of development", a fact noted earlier by Darwin (1854:336). Since Pilsbry, *Tesseropora* has maintained a more or less central position in considerations of the evolution of the tetraclitine and tetraclitelline branches of the family (Zullo, 1968:274; Ross, 1969:239; Newman and Ross, 1976:47).

From a biogeographic point of view, *Tesseropora* as previously known would be considered primarily an insular Indo-Pacific genus; *T. rosea* occurring solely in the southern hemisphere from the southern tip of South Africa to southern Australia, the Kermadec Islands and New Caledonia, and *T. wireni* (Nilsson-Cantell, 1921: 366) for the most part in the northern hemisphere, from Dar-es-Salaam east, from Chagos Bank to Wake and perhaps the Hawaiian Islands. The counterpart of *Tesseropora* on continental shores is the more advanced genus *Tetraclita*. Recognition of an Atlantic *Tesseropora*, on Bermuda and the Azores, is therefore of considerable significance not only in extending the modern distribution of the genus, but also in corroborating biogeographical inferences that oceanic islands can act as refugia for ancient forms (see Fig. 4).

SAN DIEGO SOC. NAT. HIST., TRANS. 18(12):207-216, 24 FEBRUARY 1977

Superfamily Coronuloidea Leach, 1825[1]
Family Tetraclitidae Gruvel, 1903
Subfamily Tetraclitinae Gruvel, 1903
Tesseropora Pilsbry, 1916
Tesseropora atlantica n. sp.

Tetraclita porosa: Verrill, 1901:22 (Bermuda).
Tetraclita squamosa stalactifera: Henry, 1958:224 (Bermuda); Ross, 1962:33; Werner, 1967:70; Ross, 1968:8.
Tetraclita squamosa var. *elegans*: Baker, 1967: 46 (Azores).

Diagnosis.—A small (diameter of largest spec. approx. 10mm), white *Tesseropora* with moderately developed radii having eroded and (or) oblique summits concomitant with a somewhat flaring, toothed orifice; scutal adductor ridge in line and nearly continuous with articular ridge; intermediate articles of cirrus VI supporting five pairs of setae; crest of labrum lacking obvious teeth.

Description.—Shell white or with a slight pinkish cast; conical; radii and alae moderately well developed with summits parallel to base; commonly, when eroded, orifice moderately toothed (Fig. 1). Surface of solid radii marked by transverse ridges, and of paries by low longitudinal ribs equal to the number of longitudinal tubes in the wall. Sheath white, adpressed, continuous with interior surface of paries; region below sheath smooth or marked by reminiscences of small basal denticles in the form of numerous fine ribs. Longitudinal septa normal to inner and outer laminae, forming a single row of irregular tubes (Fig. 2d); one or more incomplete septa may be present on inner surface of outer lamina. None of the specimens available is sufficiently eroded to expose the secondary filling of the parietal tubes, but grinding revealed a white filling near the apex. No calcareous spines extend from the inner surface of the outer lamina into the parietal tubes as reported for *wireni* by Henry (1957: 33), and as we have observed in *rosea*, but older and larger specimens might have them. Basis calcareous, solid, thick, adhering strongly to the wall. Opercular valves white. Scutum with well defined adductor muscle pit and ridge, the curvature of the latter being virtually continuous with that of the articular ridge (Fig. 2b); rostral and lateral depressor muscle crests well defined in larger specimens, apparently increasing in number with age; rostral depressors essentially lacking in small specimens. Tergum with material forming beak undifferentiated from rest of valve and readily broken or worn away; spur furrow open, broad and shallow.

Trophi undistinguished except for the lack of conspicuous teeth on the labrum (Fig. 3g). Cirral counts for two specimens from Bermuda follow:

	I	II	III	IV	V	VI
Specimen 1	$\frac{12}{6}$	$\frac{8}{9}$	$\frac{7}{10}$	$\frac{14}{16}$	$\frac{16}{18}$	$\frac{17}{18}$
	$\frac{12}{8}$	$\frac{8}{8}$	$\frac{8}{9}$	$\frac{14}{14}$	$\frac{16}{18}$	$\frac{16}{17}$
Specimen 2	$\frac{11}{6}$	$\frac{6}{7}$	$\frac{7}{7}$	$\frac{12}{16}$	$\frac{16}{17}$	$\frac{16}{\text{xx}}$
	$\frac{12}{6}$	$\frac{6}{7}$	$\frac{7}{9}$	$\frac{12}{14}$	$\frac{15}{17}$	$\frac{18}{19}$

---

[1] Due to an oversight on our part the superfamilial name Balanomorphoidea must be suppressed in favor of Coronuloidea (see Newman and Ross, in press).

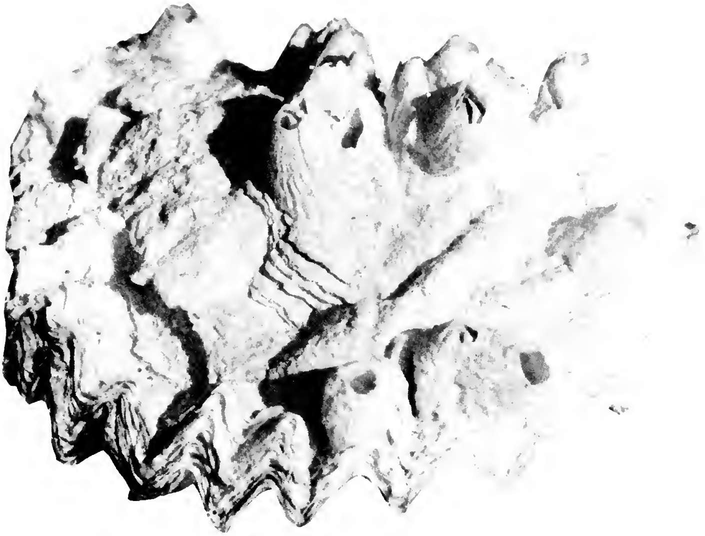


Figure 1. *Tesseropora atlantica* n. sp., on an oyster from Argus Tower, Bermuda.

The third cirrus is normal in form (rami not antenniform); supporting three types of bipectinate setae (Fig. 3c-e), the heaviest (card) being rarely observed; surfaces of the lesser curvature armed with short, curved spines or denticles (Fig. 3f). Intermediate articles of cirrus VI bearing five pairs of setae with occasional pairs or small clusters of short bristles between major pairs (Fig. 3b). The intromittant organ is normal.

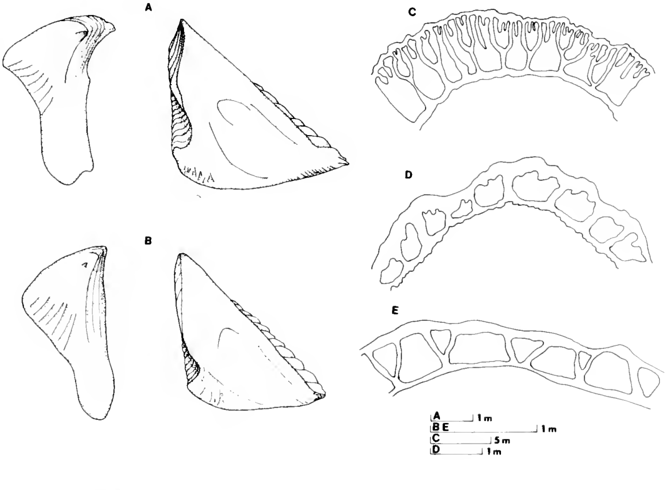


Figure 2. A, Right tergum and scutum of *Tesseropora wireni* (Nilsson-Cantell) from Wake Island (type locality of *T. w. pacifica*, approx. 20mm basal diam.); and B, of *T. atlantica* n. sp. from Bermuda (type, approx. 11mm diam.); C, D, and E, basal margins of parietes of *T. wireni, T. atlantica* and very young *Tetraclita stalactifera* (Lamarck), respectively.

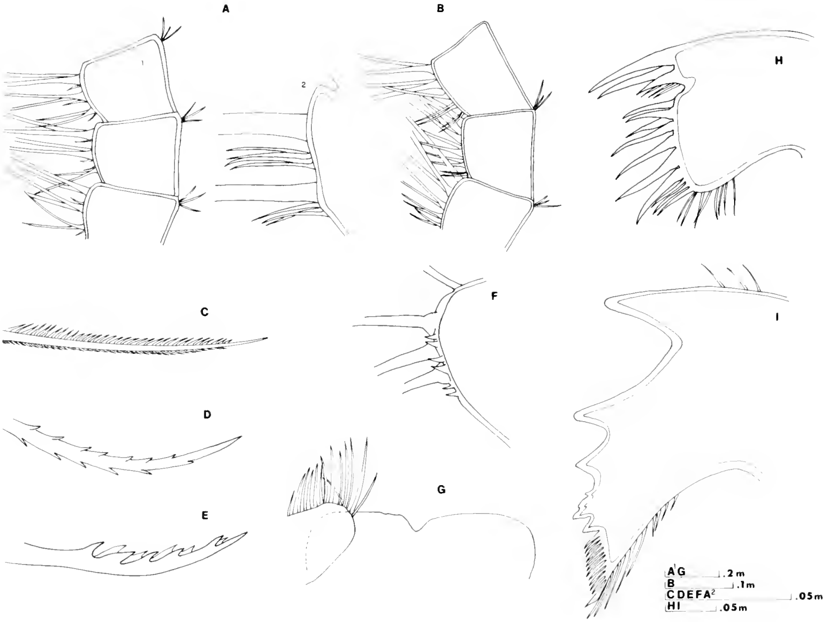


Figure 3. A^1, intermediate articles of sixth cirrus in *Tesseropora wireni* (approx. 20mm diam.) and A^2, portion of an intermediate article of the sixth cirrus in *T. wireni* (approx. 40mm diam.) from Wake I., the latter showing the increase in number of small spines below each of the larger two pairs of setae. B-I *Tesseropora atlantica* n. sp.: B, intermediate articles of sixth cirrus; C, D, and E, specialized setae; F, spines found on the third cirrus; G, labrum (right palp deleted); H, first maxilla, I, mandible.

Type material.—Gurnet Rock, Bermuda (type locality), intertidal with *Chthamalus* and *Catophragmus* (see Henry, 1958); USNM cat. no. 168472 (holotype); BM(NH) 1976.1281 (paratype) [USNM cat. no. 102827 (type lot; USNM acc. no. 195758)]. Argus Tower, southwest of Bermuda, subtidal (2-3m), dried, on an oyster (cf. *Lopha frons*), W. Sterrer coll., April, 1976, BM(NH) 1976.1282, USNM cat. no. 168473. Urzelina, São Jorge, Azores, subtidal, Chelsea College Azores Expedition (see Baker, 1967), A. J. Southward leg., BM(NH) 1976.1283.

Reference material.—One often must rely on published descriptions in making judgements on the distinctiveness of a species. By good fortune *Tesseropora* is a small genus, and we had comparative materials in our collections of the other species upon which to base our analysis.

Tesseropora wireni (Nilsson-Cantell):

Wake Island [type locality of *T. w. pacifica* (Pilsbry)], numerous large specimens with *Euraphia intertexta* (Darwin), 1854, R. McFarlan coll., 27 Dec. 1964.

Ulupau, Hawaii, numerous small specimens from 6″ pipe of seawater system, B. L. Burch leg., 28 Sept. 1976 (not *T. wireni* s. s., see discussion below).

South Field Beach, Moen Island, Truk, Caroline Islands, a single small specimen from the underside of an intertidal coral boulder resting on sand, W. A. Newman coll., June, 1956.

Dublon Channel, Truk, Caroline Islands, numerous small specimens on dead coral from underside of buoy, W. A. Newman coll., June, 1956 (see Newman, 1960, pl. 20, fig. 1).

Table 1. **Distinguishing characteristics of extant species of *Tesseropora*.**

Species	Form and size	Color: 1-wall 2-sheath 3-filling 4-valves	Radii	Parietal tubes	Scutum	Labrum	Cirrus III	Intermediate segments Cirrus VI
atlantica	Steeply conical when young; ? when old; approx. 10 mm in basal diameter	1-white 2-white 3-white 4-white	moderately wide	in single row	adductor ridge in line with articular ridge	apparently without conspicuous teeth	occasionally armed with heavy bipectinate setae (cards)	five pairs of setae per article
rosea	Steeply conical; up to 30mm	1-white 2-dirty white tinted pink 3-usually pink 4-white	ditto	ditto	adductor ridge overlapping articular ridge	with several teeth on each side of shallow notch	armed with numerous cards	three pairs of setae per article, numerous short setae in dense bunches below two major prs.
wireni	Steeply conical when young; low when old; up to 40mm	1-white 2-usually dark red-brown 3-usually pink 4-white	extremely narrow to lacking	divided into secondary and tertiary rows basally	ditto	ditto	armed with bipinnate but not bipectinate setae (cards)	as *rosea* but with a few short setae in groups below two major pairs

Kwajalein Atoll, Marshall Islands, Carmarsel Expedition (CRS-325), intertidal, on iron piling, numerous specimens with *E. intertexta*, W. A. Newman coll., 2 April 1967.

Ulul Island, Namonuito Atoll, Caroline Islands, Carmarsel Expedition (CRS-307), several specimens in *Heliopora*, with *Lithoglyptes wilsoni* Tomlinson, 1969, 10m, W. A. Newman coll., 15 Feb. 1967.

Port of Palau, Arakabesan Passage near Periryu Island, Caroline Islands, in *Heliopora*, Seto Marine Biological Laboratory no. 81, F. Hiro coll., 1934 (see Hiro, 1935: 5; the collection studied consists of some fragments of *Tesseropora*, and several complete specimens of a pyrgomatid imbedded in the coral).

Tesseropora rosea (Krauss):

Gerroa (south of Port Kembla), New South Wales, Australia, on mid-tidal rocks, E. Pope coll., 2 April 1963.

Bouvail-Baie des Tortues, New Caledonia, a single large specimen, dried, from a rock, J. C. Plaziat coll., 5 Nov. 1973.

DISCUSSION

Only one species referrable to *Tesseropora* (*Conia rosea* Krauss) was known when Darwin (1854) published his incomparable monograph on the sessile barnacles. The second, *T. isseli* (de Alessandri, 1895), from the Oligocene of Italy, while morphologically close to *rosea*, is known only by the wall and need not concern us here. A third species, *wireni*, was described by Nilsson-Cantell (1921: 366), followed by *wireni pacifica* (Pilsbry, 1928: 312) and *wireni africana* (Nilsson-Cantell, 1932: 14). Henry (1957: 33) elevated *pacifica* to specific rank. We believe, as Zullo (1968) seemingly did, that there is presently insufficient data to distinguish *pacifica* from *wireni* at the specific or the subspecific level, and believe the same is true of *africana*. Therefore, we tentatively treat living *Tesseropora* as containing but two taxa, *rosea* and *wireni*.

The new species, *T. atlantica*, can be distinguished from both *rosea* and *wireni* by a number of characters (Table 1), the most obvious being the alignment of the scutal adductor ridge with the articular ridge rather than passing well inward of it (compare Figs. 2b and 2a), and the intermediate segments of cirrus VI bearing five rather than three pairs of setae (compare Figs. 3b and 3a). *Tesseropora rosea*, known from New South Wales, South Africa and New Caledonia, differs from mature *wireni* in retaining a single row of parietal tubes throughout life. While secondary riblets develop on the interior of the outer lamina, as noted by

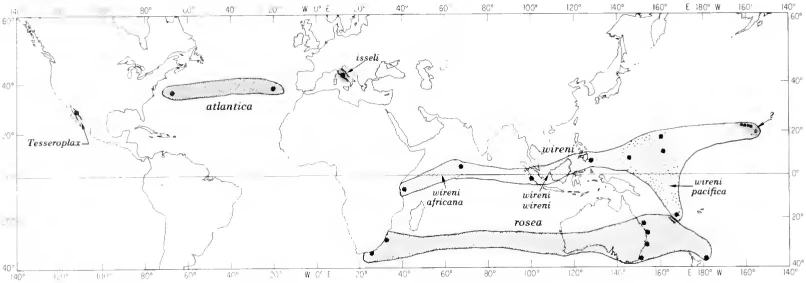


Figure 4. Distribution of *Tesseropora* spp. and the closely related *Tesseroplax unisemita* (Zullo, 1968). The latter is known only from Pliocene sediments in the Gulf of California (cf. Ross, 1969). The other significant fossil record is that for *Tesseropora isseli* from the Oligocene of Italy. The Indo-West Pacific species, *T. rosea* and *T. wireni*, while morphologically distinct, are more closely related to each other than to *T. atlantica* from Bermuda and the Azores. At the present level of our knowledge the taxonomic status of the so-called subspecies of *T. wireni* cannot be sustained. The assignment of the Hawaiian form to *T. wireni* is questioned herein.

Darwin (1854: 336), they are normal to the surface and thereby fail to join the primary septa to form secondary tubes. Young *wireni*, and it is young specimens that are apparently most commonly collected and described, also have a single row of essentially square parietal tubes, but with growth the longitudinal septa join some of the riblets on the interior of the outer lamina, singly or in pairs, leading to the dendritic pattern of the septa separating the secondary tubes formed in the process. (Fig. 2c). Although we have not observed secondary tubes in *atlantica*, Henry (1958: 224) noted a few in the rostrum of the largest specimen she examined. The appearance of large, eroded *atlantica* may appear more like that of *wireni* than that of *rosea*.

Young, uneroded *rosea* were described by Darwin (1854: 323), and apparently the best character that might be used to distinguish them from young *wireni* would be moderate to well developed radii in the former. It follows that young uneroded *rosea* cannot be distinguished from *atlantica*, at the present state of our knowledge, since both have radii. The only characters presently known that will separate them are the interiors of the scuta, the pinkish rather than white filling of the parietal tubes, and the nature of the cirri described above.

The specimens of *Tesseropora* from Hawaii are not typical of *wireni*. All available are small, less than 3 mm in basal diameter, and therefore they had not likely completed their development. Nonetheless, several contained larvae and were therefore at least sexually mature (see discussion of larvae below). This Hawaiian material is similar to the *wireni* studied from elsewhere in having much reduced radii and in having a toothed labrum, but the adductor ridge of the scutum is closer to being in line with the articular ridge (similar to *atlantica*), the sheath is white (Pilsbry, 1928: 313, noted that the sheath of *wireni* ranges from prussian blue to white, but his material included specimens from Necker Island in the Hawaiian Archipelago as well as from Wake Island), the cirral counts are lower, cirrus III has bipectinate (cards) as well as bipinnate setae, and the intermediate segments of cirrus VI bear three, four or five pairs of setae (on the same ramus), but commonly four, a number intermediate between that found in *atlantica*, and *wireni* and *rosea*. The differences noted here make it difficult to assign this material to *wireni* for, if consistent, they would be sufficient to allow one to propose the Hawaiian form as a new species. However, such a decision will have to await further study.

Both *rosea* and *wireni* can attain basal diameters approaching 40 mm, and in most large specimens the outer lamina of the shell is all but completely eroded, exposing the generally pinkish, more resistent material lining the interior of the parietal tubes. In a specimen of *rosea* from New Caledonia most of these run continuously from the apex to the base, but a few can be observed on the exterior, beginning more than halfway down the wall rather than at the apex, and this indicates, although there is predominantly a single row of tubes in the wall, a few supernumerary ones occasionally develop. Zullo (1968: 272) noted comparable development in this species from southeast Australia. In appearance, *wireni* is comparable, but many more of the pillars exposed by erosion, other than the primary ones, begin at varying distances down the shell below the apex. Thus, the general ribbing appears finer because of the more numerous development of secondary parietal tubes. None of the specimens of *atlantica* is sufficiently eroded to expose the pillars.

It is perhaps significant that *wireni*, although ranging from East Africa to Wake Island and perhaps to Hawaii, appears to be a relatively rare species. Also, most of the material described has been of relatively young uneroded specimens, up to but generally smaller than 15 mm or so in diameter. One is led to suspect the same thing may be true for *atlantica* — the specimens on hand are relatively young individuals and the species is likely not confined solely to Bermuda and the Azores.

Verrill (1901: 22) identified a Bermudan form as *Tetraclita porosa (= squamosa)*. Although we cannot prove he had *Tesseropora* rather than *Tetraclita* s. s., it does seem highly likely because he stated, "This is the common, small, sessile barnacle found on the rocks between tides, with the general appearance of some species of *Balanus*". Species of *Tetraclita*, however, are generally relatively large, and it is the erosion of the outer lamina of the shell, exposing the colored infilling of the parietal tubes, that gives them the characteristic tetraclitid appearance. On the other hand, *atlantica* is known as a small species, and in being uneroded it does have a somewhat balanid appearance. In any event, his identification apparently led Henry (1958: 224) to consider the Stephensons' material to be *T. squamosa stalactifera*, the only "subspecies" of the *squamosa* complex known from the Caribbean. The single row of tubes in the wall did not invalidate this conclusion for, as Darwin (1854: 323) noted, in very young specimens of *Tetraclita* there is only a single row of tubes (Fig. 2e). During growth, these are added to by bifurcation of the septa at the outer lamina very early in *Tetraclita* and *Tetraclitella*, quite a little later in *wireni* and possibly *atlantica*, and hardly at all in *rosea*. It is important to note that in *Tetraclita* the septa forming the single row of tubes are at angles other than normal to the inner lamina, but in *Tesseropora* they are normal or essentially normal (compare Figs. 2c and 2d with 2e). This and the presence of a calcareous basis in the latter serves to distinguish the two genera.

The development of radii, a tubiferous wall and a strong calcareous basis would appear to be fundamental to the Tetraclitidae, all three being the principal advances in the shell made over the bathylasmatid (ancestral) level of organization (Newman and Ross, 1976: 20). Radii greatly strengthen the wall, important in the surf zone (Darwin, 1854: 56; Barnes, Read and Topinka, 1970: 82). A tubiferous wall, especially when secondarily filled, places an additional barrier to erosion and boring organisms (Ross, 1970: 9; Newman and Ross, 1971: 159). A calcareous basis conveys an advantage in forming a strong attachment (Newman, Zullo and Wainwright, 1967: 170) and in retarding desiccation in intertidal forms, especially in the tropics where porous reef limestones are common (Southward and Newman, in press). *Tesseropora* has these advanced features. But the most successful tetraclitid today, in terms of being an abundant intertidal dominant, is *Tetraclita*. The genus has carried the filled tubiferous wall to the extreme, and perhaps the great thickness achieved has allowed it to give up radii, but why it has also given up a calcareous basis is an enigma, unless it has gained a degree of limited motility, as was demonstrated for *Semibalanus balanoides* by Crisp (1960: 1208).

Tetraclitella divisa, also primarily an insular species, is known to carry embryonic development through to the cyprid stage, passing the naupliar stages in the egg (Nilsson-Cantell, 1921: 93, 364; Ross, 1961: 211). Cyprid larvae are incapable of feeding and, because they also are not known to remain long in the plankton, they are not likely propagules for long-range disperal (Newman and Tomlinson, 1974: 208). The direct production of the non-feeding stage in *divisa* could be an adaptation to the relatively sterile waters of most oceanic situations, but because most balanomorphans of such regions apparently have nauplii, this could be only part of the reason, another being the selection for mechanisms that favor maintaining populations on isolated oceanic islands too distant to be regularly reached from elsewhere by ordinary means. Species having a tendency to suppress the nauplius would thereby be likely candidates for maintaining populations on isolated insular situations. It is interesting therefore to note that the larvae of *Tesseropora* from Hawaii just mentioned are released as cyprids, and it will be interesting to see if the life histories of other populations or species of the genus are so modified.

Although the suppression of the nauplius may aid in maintaining isolated insular populations, such populations would appear to have removed themselves from the list of potential island colonizers by larval propagules. Furthermore, because islands are ephemeral in terms of geological time relative to continental shores, the time to extinction of such lineages would be substantially shortened. However, this problem can and apparently has been circumvented because some sedentary species with short range larvae have achieved and apparently maintain distributions over great expanses of open water. So far as *divisa* is concerned, and the likewise virtually cosmopolitan *Balanus trigonus*, transport of adult propagules by rafting, but more so by other organisms, seems likely. One of us (W.A.N.) has found adults of the former washed ashore on Majuro Atoll in the Marshall Islands attached to the shell of the pelagic barnacle *Lepas*, and of the latter, attached to the shell of the whale barnacle *Coronula*. These species therefore have the potential of being transported great distances as adults, and this may explain their virtually cosmopolitan distributions in the warm seas of the world.

No tetraclitid is known to form an obligate commensal relationship, although individuals of some species are found on other organisms, the most notable being *wireni*, which occurs embedded in the blue coral *Heliopora*. If the history of the genus continues and it is eventually completely replaced as a free-living form, conceivably *wireni* could persist as an obligate commensal.

ACKNOWLEDGMENTS

We thank Alan J. Southward, Marine Biological Association of the United Kingdom, for bringing this problem to our attention and for providing specimens from Bermuda and the Azores. We would also like to thank T. E. Bowman, National Museum of Natural History, William K. Emerson, American Museum of Natural History, W. D. Hartman, Yale Peabody Musuem and W. E. Sterrer, Bermuda Biological Station for their attempts to locate voucher specimens from Bermuda collected either by Verrill or others near the turn of the century; and G. A. Boxshall, British Museum (Natural History) for attempts to locate material from the Azores. Thanks are also due Huzio Utinomi, who kindly arranged for the loan of specimens from the Seto Marine Biological Laboratory, Beatrice L. Burch for the somewhat enigmatic specimens from Hawaii, and Gayle Kidder for technical assistance and preparation of the figures. Work supported, in part, by the National Science Foundation (DEB-7517149).

REFERENCES

Baker, I. H., 1967. Cirripedia *in*, Chelsea College Azores Expedition, 1965. Final Report: 46-47. University of London.

Barnard, K. H., 1924. Contributions to the crustacean fauna of South Africa. No. 7. Cirripedia. Annals South African Museum 20: 1-103.

Barnes, H., R. Read and J. Topinka, 1970. The behaviour on impaction by solids of some common cirripedes and relation to their normal habitat. Journal of Experimental Marine Biology and Ecology 5(1): 70-87.

Crisp, D. J., 1960. Mobility of barnacles. Nature 188(4757): 1208-1209.

Darwin, C., 1854. A Monograph on the subclass Cirripedia with figures of all the species. The Balanidae, the Verrucidae, etc. Ray Society, London, 684pp.

de Alessandri, G., 1895. Contribuzione allo studio dei Cirripedi fossili d'Italia. Societa Geologica Italiana, Bollettino 13(3): 234-314.

Edmondson, C. H., 1946. Reef and shore fauna of Hawaii. Bernice P. Bishop Museum Special Publication 22. 381pp.

Endean, R., W. Stephenson and R. Kenny, 1956. The ecology and distribution of intertidal organisms on certain islands off the Queensland coast. Australian Journal of Marine and Freshwater Research 7(3): 317-342.

Foster, B. A., 1974. The barnacles of Fiji, with observations on the ecology of barnacles on tropical shores. Pacific Science 28(1): 35-56.

Henry, D. P., 1957. Some littoral barnacles from the Tuamotu, Marshall, and Caroline Islands. Proceedings U.S. National Museum 107(3381): 25-38.

Henry, D. P., 1958. Intertidal barnacles of Bermuda. Journal of Marine Research 17: 215-234.

Hiro, F., 1936. On the commensalism between the cirripeds and other animals. Ecological Review, Sendai 2(1): 58-65.

Hiro, F., 1937. Cirripeds of the Palao Islands. Palao Tropical Biological Station Studies 1: 37-72.

Krauss, F., 1848. Die sudafrikanischen Mollusken. Ein Beitrag zur Kenntniss der Mollusken des Kap-und Natal-landes und zur geographischen Verbreitung derselben, mit Beschreibung und Abbildung der neuen Arten. Stuttgart.

Macnae, W. and M. Kalk (eds.), 1969. A natural history of Inhaca Islands, Mozambique. Witwatersrand University Press, Johannesburg, South Africa. 163pp.

Matsuda, C., 1973. A shoreline survey of free-living intertidal barnacles on the island of Oahu, Hawaii. 60pp. Unpublished master's thesis, Dept. of Zoology, University of Hawaii.

Newman, W. A., 1960. The paucity of intertidal barnacles in the Tropical Western Pacific. Veliger 2(4): 89-94.

Newman, W. A. and A. Ross, 1971. Antarctic Cirripedia. Antarctic Research Series 14. 257 pp. American Geophysical Union.

Newman, W. A. and A. Ross, 1976. Revision of the balanomorph barnacles; including a catalog of the species. San Diego Society of Natural History, Memoir 9. 108pp.

Newman, W. A. and A. Ross, in press. Superfamilies of the Balanomorpha. Crustaceana.

Newman, W. A. and J. T. Tomlinson, 1974. Ontogenetic dimorphism in *Lithoglyptes* (Cirripedia:Acrothoracica). Crustaceana 27(2): 204-208.

Newman, W. A., V. A. Zullo and W. A. Wainwright, 1967. A critique on recent concepts of growth in Balanomorpha (Cirripedia, Thoracica). Crustaceana 12(2): 167-178.

Nilsson-Cantell, C. A., 1921. Cirripeden-Studien. Zur Kenntnis der Biologie, Anatomie und Systematik dieser Gruppe. Zoologiska Bidrag Uppsala 7:75-395.

Nilsson-Cantell, C. A., 1932. Neue Balaniden aus Sud-und Ost-Afrika in dem Berliner Museum. Arkiv fur Zoologi 24A(6):1-18.

Pilsbry, H. A., 1916. The sessile barnacles (Cirripedia) contained in the collections of the U.S. National Museum; including a monograph of the American species. Bulletin of the U.S. National Museum 93:1-366.

Pilsbry, H. A., 1928. Littoral barnacles of the Hawaiian Islands and Japan. Proceedings Academy Natural Sciences Philadelphia 79: 305-317.

Pope, E., 1945. A simplified key to the sessile barnacles found on the rocks, boats, wharf piles and other installations in Port Jackson and adjacent waters. Records of the Australian Museum 21(6): 351-372.

Ross, A., 1961. A new cirriped from the Hawaiian Islands. Crustaceana, 2(3): 209-212.

Ross, A., 1962. Results of the Puritan-American Museum of Natural History Expedition to western Mexico. No. 15. The littoral balanomorph Cirripedia. American Museum Novitates 2084: 1-44.

Ross, A., 1968. Bredin-Archbold-Smithsonian Biological Survey of Dominica. 8. The intertidal balanomorph Cirripedia. Proceedings U.S. National Museum 125 (3663): 1-22.

Ross, A., 1969. Studies on the Tetraclitidae (Cirripedia: Thoracica): Revision of *Tetraclita*. Transactions San Diego Society of Natural History 15(15):

237-251.

Ross, A., 1970. Studies on the Tetraclitidae (Cirripedia: Thoracica): A proposed new genus for the austral species *Tetraclita purpurascens breviscutum*. Transactions San Diego Society of Natural History 16(1): 1-12.

Smith, W. A., 1971. Crustacea: Cirripedes from Diego Garcia. Atoll Research Bulletin 149:103.

Southward, A. J. and W. A. Newman, in press. Aspects of the ecology and biogeography of the intertidal and shallow-water balanomorph Cirripedia of the Caribbean and adjacent sea-areas. CICAR-II Symposium, Caracas, Venezuela, July 12-16, 1976.

Verrill, A. E., 1901. Additions to the fauna of the Bermudas from the Yale Expedition of 1901, with notes on other species. Transactions Connecticut Academy of Arts and Sciences 11(1): 15-62.

Werner, W. E., 1967. The distribution and ecology of the barnacle *Balanus trigonus*. Bulletin of Marine Science 17(1): 64-84.

Zullo, V. A., 1968. *Tesseropora* Pilsbry (Cirripedia, Thoracica) from the Pliocene of the Gulf of California. Crustaceana 15(3): 272-274.

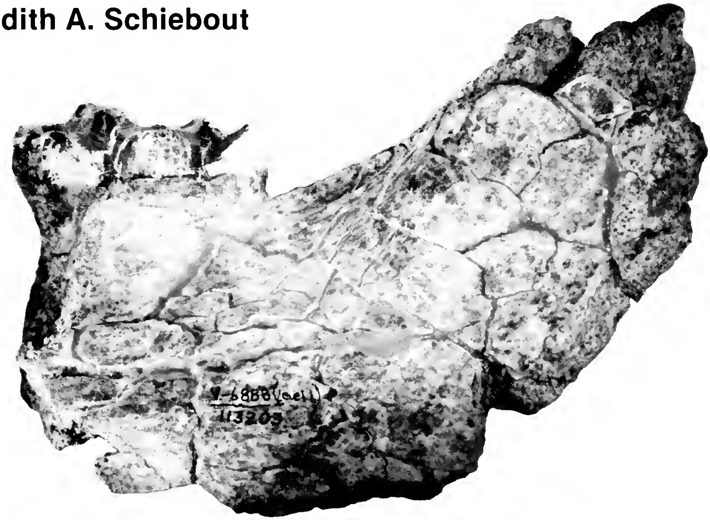
Scripps Institution of Oceanography A-002, La Jolla, California 92093 and Natural History Museum, Box 1390, San Diego, California 92112.

Contribution No. 692 from the Bermuda Biological Station for Research, Inc.

Contribution of the Scripps Institution of Oceanography, new series.

EOCENE PERISSODACTYLA FROM THE LA JOLLA AND POWAY GROUPS, SAN DIEGO COUNTY, CALIFORNIA

Judith A. Schiebout



TRANSACTIONS

OF THE SAN DIEGO
SOCIETY OF
NATURAL HISTORY

VOL. 18, NO. 13 20 APRIL 1977

Eocene Perissodactyla from the La Jolla and Poway Groups, San Diego County, California

Judith A. Schiebout

ABSTRACT.—Fragmentary remains of tapirs *(Dilophodon)*, rhinocerotoids *(Amynodon)* and titanotheres *(Metarhinus?)* occur in Eocene formations of the La Jolla and Poway Groups in San Diego Co., California. *Amynodon* and *Metarhinus?* were reported previously from this area, but tapirs were not, although a single Eocene tapir tooth, questionably referred to *Dilophodon*, is known from the more northern Sespe Fm. of Ventura Co. The need for taxonomic revision of the titanotheres and rhinocerotoids, coupled with the fragmentary nature of the present specimens, prevents them from being biostratigraphically significant. Nonetheless, the presence in the Friars Fm. of a *Dilophodon* intermediate in size between *D. minisculus* and *D. leotanus* suggests that it is early Uintan in age (late Eocene).

The only studies on San Diego Co. Eocene Perissodactyla are those of Stock, who described *Metarhinus? pater* (Stock, 1937) and *Amynodon reedi* (Stock, 1939) from the Poway Fm. (now the Friars Fm. of the Poway Group; see Kennedy and Moore, 1971). Beginning in 1971 San Diego State University and the University of California, Berkeley, began a joint program to increase our knowledge of the San Diego Eocene terrestrial vertebrate fauna with the hopes of collecting as many specimens as practicable from those localities being destroyed or covered over by construction. The present study on the larger perissodactyls is an outgrowth of this project, and is one in a series on this rich and varied fauna (see also Lillegraven, 1976; Lillegraven and Wilson, 1975; Novacek, 1976).

DISCUSSION

All of the perissodactyls described here were recovered from sediments in the Friars Fm. of the La Jolla Group, and the Scripps Fm., Stadium Conglomerate and Mission Valley Fm. of the Poway Group (stratigraphic terminology of Kennedy and Moore, 1971). Conglomerates such as the Stadium Conglomerate were deposited in major river valleys and on fan deltas, which spread westward across the San Diego area. The mudstones and sandstones of the underlying Scripps and Friars Fms. and the overlying Mission Valley Fm. were deposited seaward of the fans or between them (Kennedy and Moore, 1971; Peterson, 1971; Pierce and Peterson, 1975). In addition to the facies changes encountered in traverses perpendicular to the Eocene shoreline, there is considerable lateral facies variation caused by high relief on pre-Eocene rocks.

Both the titanotheres and amynodont rhinocerotoids are taxonomically over-split and in need of revision. Future revisions may result in synonymizing both *Amynodon reedi* and *Metarhinus? pater* with older names applied to specimens from the Rocky Mountain area, but such a revision is not now possible possible. If *Amynodon reedi* and *Metarhinus? pater* are indeed distinct valid species, their presence, combined with the apparent lack of equids in southern California Eocene faunas, would indicate a pronounced West Coast endemism among the large perissodactyls. Black and Dawson (1966: 332) reported that rodents and primates in the faunas of the Southern California Eocene seemed to show a lot of endemism. Lillegraven (1976) concluded from the similarity of San Diego Co. Eocene didelphids (Marsupalia) and *Uintasorex* (?Primates) to those of the Rockies and High Plains that dispersal routes between these areas must have been available some time during the early Eocene. The small reptiles (Schatzinger, MS) do not exhibit the endemism suggested by the perissodactyls.

SAN DIEGO SOC. NAT. HIST., TRANS. 18(13): 217-228, 20 April 1977

Based on several lines of evidence there is agreement (Wolfe and Hopkins, 1967; Lillegraven, 1976) that the general North American late Eocene was more tropical and equable than the present time, but local semiarid conditions may have prevailed in the San Diego area.

Peterson et al. (1975) and Pierce and Peterson (1975) discussed the origin and distribution of caliche in the Friars and Mission Valley Fms. Caliches develop under semiarid climates where there is an annual rainfall of less than 75 cm, and alternating wet and dry seasons. San Diego Co. didelphids and *Uintasorex* discussed by Lillegraven (1976: 100) as likely forest-associated types could have inhabited local wooded areas near streams and thus, perhaps, were less affected by local aridity than larger perissodactyls.

Near-shore terrestrial Eocene vertebrate fossils such as those found in San Diego Co. are rare in North America. The local interfingering of fossiliferous marine and continental beds allows temporal correlation on the basis of both terrestrial and marine faunas. Previous work on San Diego Co. invertebrates and vertebrates suggests that the Bridgerian and Uintan North American "land mammal ages" of Wood et al. (1941), often informally equated with the time intervals "middle Eocene" and "late Eocene" respectively, do not equate with local West Coast divisions of Eocene time based upon marine invertebrates. Controversy exists over whether the Stadium Conglomerate should be considered "late middle Eocene" or "late Eocene" on the basis of studies of foraminifera, whereas the small mammals indicate an early Uintan age. The occurrence of the San Diego *Dilophodon* specimens, recovered slightly below the base of the Stadium Conglomerate, is consistent with an early Uintan age for their locality. Their occurrence strengthens the conclusion that the Poway Group mammal faunas are post-Bridgerian.

Abbreviations.—A-P—anteroposterior length. CIT—California Institute of Technology (fossils from CIT collections are now housed at the Natural History Museum of Los Angeles County). CM—Section of Vertebrate Fossils, Carnegie Museum of Natural History. est.—Estimate. LACM—Natural History Museum of Los Angeles County (Los Angeles County Museum). min.—Measurement given is a minimum figure (a small amount of cracking or chipping has affected the measurement). UCMP—Museum of Paleontology, University of California, Berkeley. USNM—U.S. National Museum. V—Precedes locality numbers of UCMP specimens. W—Transverse width. W-TAL—width of talonid. W-TRI—width of trigonid.

SYSTEMATIC PALEONTOLOGY

Order Perissodactyla Owen, 1884
Superfamily Brontotherioidea Hay, 1902
Family Brontotheriidae Marsh, 1873b
Subfamily Dolichorhininae Osborn, 1929
Genus *Metarhinus* Osborn, 1908
Metarhinus? pater Stock, 1937

Pl. 1, figs. 1-3; Pl. 2, figs. 1-2; Pl. 3, fig. 1

Type.—LACM (CIT) 2037, right half of the muzzle of a skull from the anterior edge of the orbit to the anterior of the maxilla with C-M^3 inclusive.

Distribution of species.—San Diego Co., Calif.

Material.—UCMP 113200, right P^4; UCMP 95774, right maxilla fragment with M^1-M^3; USNM 214887, left maxilla fragment with M^2-M^3; LACM 56125, right M^1; UCMP 113198, left M^1; UCMP 113199, crushed left M^2; UCMP 96430, heavily worn right M^3; UCMP 113195, labial half of left M^2; UCMP 113189, right ?P_2; UCMP 113201, right mandible lacking ascending ramus with P_2 talonid and P_3-M_1; UCMP 95780, left mandible fragment with M_1-M_3 and ascending ramus; UCMP 113203, left mandible fragment with M_3; UCMP 113184, right mandible fragment with sockets of canine, P_1, and P_2; UCMP 11397, left P_4; UCMP 95775, left lower premolar trigonid; LACM 55550, right M_1; UCMP 106011, right P_3, P_4, M_2; UCMP 113200, badly worn and chipped left P_3 in small mandible fragment; LACM 55975, right lower molar fragment including metaconid; UCMP 113182, shattered mandible with right P_3-M_3, left P_4-M_3 and fragments of left P_1, P_2, and P_3; UCMP 113194, right mandible fragment with worn M_2.

Localities.—Scripps Fm.: approximately 150 m north of the pier of Scripps Institution of Oceanography (USNM 214887); Friars Fm.: V-6840, V-6888, V-6889, V-68156, V-71056, V-7120 (All specimens referred to *M.? pater* except those listed as from the Scripps and Mission Valley Fms.); Mission Valley Fm.: V-72158, V-72176 (UCMP 106011, UCMP 113182, UCMP 113199).

Description.—The available upper premolar lacks a hypocone. Upper molars are similar in form to one another. They lack protoconules and metaconules. M^3 of UCMP 95774 has a prominent hypocone and $M^{\underline{3}}$ of USNM 214887 has a small one. The broken base of the zygomatic arch on specimens UCMP 95774 and USNM 214887 indicates that the arch was strong and thick.

Damage to UCMP 113201, the only specimen on which the anterior mandible can be studied, makes it impossible to determine the number of incisors or the shape of incisors or canine. The canine must have been small, because its root is little larger than that of P_1. A small diastema separates the canine and P_1, and a smaller one separates P_1 from P_2. Lower premolars have shallower trigonid and talonid basins than the molars but are otherwise similar. The lack of crowding of lower premolars indicates a dolichocephalic or long-headed form.

Discussion. This specimen is conspecific with LACM (CIT) 2037, the type and only previously-referred specimen of *Metarhinus? pater.* Specimen UCMP 113201 would articulate well with the upper dentition of LACM 2037 although the specimens do not belong to the same individual. Diagnostic features of *M.? pater* according to Stock (1937: 49) are a deep naso-maxillary recess, large antorbital foramen, small $P^{\underline{1}}$ and $P^{\underline{2}}$, and a $P^{\underline{4}}$ long in proportion to its width. The protocone of UCMP 113200 is slightly shorter anteroposteriorly in proportion to transverse tooth width than the protocone of P^4 of the type, but otherwise the teeth are similar. Nothing can be determined about the nasomaxillary recess of UCMP 95774. M^3 of the type and of UCMP 95774 have similar large hypocones. UCMP 95774 (an M^3) has a posterolingual cingulum, which is lacking in the type and USNM 214887.

The mandible is deeper beneath the M_3 position in UCMP 95780 than in UCMP 113201 (Plate 2). The less robust mandible and small canines of UCMP 113201 are probably characteristics of a female.

A great many of the characters used by previous workers to subdivide the titanotheres cannot be observed in any of the Eocene titanothere material from

TABLE 1. Measurements in millimeters for teeth of *Metarhinus? pater* from San Diego Co., California.

No.	Tooth	A-P	W	W-TRI	W-TAL
UCMP 95774	RM^1	30.0 min.	30.0 min.		
	RM^2	37.4 min.	36.8		
	RM^3	38.4	40.7		
USNM 214887	LM^2	36.1	35.2		
	LM^3	37.6	37.0		
LACM 56125	RM^1	30.0	28.8		
UCMP 113198	LM^1	34.0 est.	30.6		
UCMP 113200	RP^4	21.5	26.2		
UCMP 113189	R?P$_2$	18.4		9.5	10.1
UCMP 113201	RM$_1$	28.3		15.6	17.2
UCMP 95780	LM$_1$	25.7 min.		—	17.8
	LM$_2$	33.8 min.		20.0	20.9
	LM$_3$	47.7 min.		—	—
UCMP 113203	LM$_3$	48.3		21.3	19.8
UCMP 106011	RP$_3$	19.4		11.4	12.8
	RM$_2$	33.4		18.8	—
UCMP 113182	RP$_4$	19.7 min.			
	RM$_3$	40.1 min.			

San Diego Co. Also, the evolutionary importance of some characters used in making major subdivisions in the past, as in Osborn's (1929) monumental work, is questionable. The phyletic reality of assignment of many titanothere species to genera is presently questionable. Until the titanotheres are revised, the validity of *M.? pater*, and many other species and genera based on fragmentary material, cannot be evaluated properly.

Suborder Ceratomorpha Wood, 1937
Superfamily Tapiroidea Gill, 1972
Family Helaletidae Osborn, 1892
Genus *Dilophodon* Scott, 1883
Dilophodon sp. indet.
Pl. 4, figs. 1-5

Material.—LACM 55976, left M^1 or M^2 with hypocone broken off; LACM 55977, left M^1 or M^2 with paracone broken off; LACM 55978, anterolabial corner of right upper molar; UCMP 113196, left mandible fragment with DP$_3$, DP$_4$, M$_1$, partially erupted M$_2$ with posterior edge broken off; LACM 55980, left ?M$_1$ with anterointernal corner missing; LACM 55979, right M$_3$; UCMP 113181, right M$_3$ trigonid.

Locality.—All material is from the San Diego Mission locality (V-6840). Specimens occur in the Friars Fm. just below the base of the Stadium Conglomerate.

Description.—Molars have well developed cross lophs. Upper molar metacones are slightly convex labially and have a cingulum on their labial faces. M$_3$ lacks a hypoconulid. DP$_3$ is similar to DP$_4$ and M$_1$ but is smaller and relatively longer in proportion to its width. DP$_4$ has a metalophid but M$_1$ and M$_2$ do not.

Discussion.—Lack of a metalophid on molars places this tapir in the helaletids. Small size suggests *Dilophodon*, the smallest known helatetid. Absence of a hypoconulid on M$_3$ is also a diagnostic *Dilophodon* feature (Radinsky, 1963: 52).

TABLE 2. Measurements in millimeters for teeth of *Dilophodon* sp. indet. from the Eocene of California.

No.	Tooth	A-P	W	W-TRI	W-TAL
UCMP 113196	$\mathrm{LDP}_{\bar{3}}$	6.5 min.		3.4	3.8
	$\mathrm{DP}_{\bar{4}}$	6.7		4.3	4.5
	$\mathrm{LM}_{\bar{1}}$	7.7		5.3	5.4
LACM 55979	$\mathrm{RM}_{\bar{3}}$	10.0		6.3	5.8
LACM (CIT) 1949/180	$\mathrm{RM}^{\underline{3}}$	8.7	9.1 min.		

Size and degree of molarization of the premolars are the criteria for distinguishing the two species of *Dilophodon*, *D. minusculus* and *D. leotanus*, according to Radinsky (1963: 54-56). *D. minusculus* from the late Bridgerian is larger and has less molariform premolars than the late Uintan *D. leotanus*. No permanent premolars are available for the San Diego *Dilophodon*, but the deciduous premolars of UCMP 113196 are similar in degree of molarization to those of CM 11849, type specimen of *D. leotanus*. Upper molars of the San Diego *Dilophodon* are too badly broken for accurate measurement, but I estimate that they would have fallen within the *D. minusculus* range as given by Radinsky (1963, Table 8). $M_{\bar{1}}$ of UCMP 113196 is only 1 mm. less in length than the smallest previously known $M_{\bar{1}}$ of *D. minusculus* and LACM 55979, an $M_{\bar{3}}$, falls within the *D. leotanus* size range (Table 2; Radinsky, 1963, Table 8). Lillegraven (pers. comm.) working with small mammals, and Golz (pers. comm.), working with artiodactyls both consider mammal faunas from the Friars and Mission Valley Fms. to be early Uintan. Features of the San Diego *Dilophodon* are consistent with their being intermediate in age between *D. minusculus* and *D. leotanus*, i.e., early Uintan. If permanent premolars of the San Diego *Dilophodon* are discovered the specimens may be placed in one of the two species, or the species may be redefined or synonymized.

The only other tapir reported from the California Eocene is an isolated upper molar, LACM (CIT) 1949, from the Sespe Fm., Tapo Canyon local fauna, Ventura Co. The Tapo Canyon fauna was considered late Uintan by Gazin (1956: 7). I believe that the Tapo Canyon specimen is possibly conspecific with the tapiroid here described from San Diego, but more complete upper dentitions of California *Dilophodon* would be needed for confirmation. Its size is similar, and differences between it and the San Diego upper molars are explained if it is considered to be $M^{\underline{3}}$. Stock (1936: 260) called LACM (CIT) 1949, *Dilophodon* sp., and Radinsky (1963: 56, 57) reexamined the specimen and called it "*Dilophodon* species indeterminate." Both Stock and Radinsky considered it to be an M^1 or M^2. Its metacone is lingually displaced in comparison with the San Diego specimens and it lacks the facet on the posterolingual side of the metacone, which the two San Diego *Dilophodon* upper molars show. This facet, which is lacking on third upper molars, results from contact with the protoconid of the lower molar posterior to the faceted upper molar.

Superfamily Rhinocerotoidea Gill, 1872
Family Amynodontidae Scott & Osborn, 1883
Amynodon Marsh, 1877
Amynodon reedi Stock, 1939
Pl. 3, fig. 2

Type.—LACM (CIT) 2529, left P^4-M^3 in a skull fragment.

Distribution.—San Diego Co., Calif.

Material.—UCMP 95851, left maxilla fragment with M^3 having the hypocone broken off and the anterior edge of the parastyle chipped; UCMP 95812, right upper canine lacking the right half of the crown.

Localities.—Friars Fm.: V-68161 (UCMP 95851), V-68156 (UCMP 95812).

Description.—M^3 is roughly square in outline except for its labially projecting parastyle. Its ectoloph and metaloph are nearly perpendicular to one another. The broken specimen is 30.5 mm in anteroposterior length. The upper canine had a small oval wear facet on the posterior side of its base.

Discussion.—The square outline and metacone position definitely place this animal among the amynodont rhinocerotoids. Comparison with the type and only previously assigned specimen of *Amynodon reedi* (Stock, 1939: 270-272) from what is now the Friars Fm., revealed no significant differences in M^3 size and shape. Stock defined *Amynodon reedi* principally on the animal's small size.

Canines of *Amynodon reedi* are not known. UCMP 95812 is placed with *A. reedi* because of its occurrence in the Friars Fm. and its similarity to canines of *Amynodontopsis bodei* in the Natural History Museum of Los Angeles County. *Amynodontopsis bodei* was described by Stock (1933) on the basis of material collected from the Sespe Fm. in Ventura Co., California.

ACKNOWLEDGMENTS

I thank Jason A. Lillegraven, who suggested this study, provided use of most of the fossils, and allowed me access to the facilities of the laboratory under his supervision at San Diego State University. I appreciate having been allowed to study specimens from the collections of the Natural History Museum of Los Angeles County, University of California at Riverside, the University of California Museum of Paleontology at Berkeley and the U.S. National Museum. Discussions with Lillegraven, David J. Golz, and Michael O. Woodburne were helpful. I appreciate Leonard B. Radinsky's reviewing the manuscript and providing suggestions for improvement.

LITERATURE CITED

Black, C. C. and M. R. Dawson, 1966. A review of the late Eocene mammalian faunas from North America. American Journal of Science 264: 321-349.

Gazin, C. L., 1956. The geology and vertebrate paleontology of upper Eocene strata in the northeastern part of the Wind River Basin, Wyoming, Part 2. The mammalian fauna of the Badwater Area. Smithsonian Miscellaneous Collections 131 (8): 1-35.

Kennedy, M. P. and G. W. Moore, 1971. Stratigraphic relations of Upper Cretaceous and Eocene formations, San Diego coastal area, California. Bulletin American Association of Petroleum Geologists 55: 709-722.

Lillegraven, J. A., 1976. Didelphids (Marsupalia) and *Uintasorex* (? Primates) from later Eocene sediments of San Diego County, California. Transactions San Diego Society of Natural History 18 (5): 85-112.

Lillegraven, J. A. and R. W. Wilson, 1975. Analysis of *Simimys simplex*, an Eocene rodent (? Zapodidae). Journal of Paleontology 49 (5): 856-874.

Novacek, M. J., 1976. Insectivora and Proteutheria of the later Eocene (Uintan) of San Diego County, California. Contributions in Science 283: 1-52.

Osborn, H. F., 1929. The titanotheres of ancient Wyoming, Dakota, and Nebraska. U.S. Geological Survey Monographs 55, 2 vols., 953 pp.

Peterson, G. L., 1971. Stratigraphy of the Poway area, southwestern California. Transactions San Diego Society of Natural History 16 (9): 225-236.

Peterson, G. L., S. E. Pierce and P. L. Abbott, 1975. Paleogene paleosols and paleoclimates, southwestern California, *in,* Weaver, D. W., Hornaday, G. R., and Tipton, A. *(eds.),* Paleogene Symposium and Selected Technical Papers: American Association of Petroleum Geologists, Society of Economic Paleontologists and Mineralogists, and Society of Exploration Geophysicists (Pacific Sections): 401-408.

Pierce, S. E. and G. L. Peterson, 1975. Paleoclimatic implications of caliche in the nonmarine Friars and Mission Valley formations, southwestern California, pp. 71-76. *in,* Ross, A. and R. J. Dowlen *(eds.),* Studies on the geology of Camp Pendleton and western San Diego County, California. San Diego Association of Geologists.

Radinsky, L., 1963. Origin and early evolution of North American Tapiroidea. Peabody Museum of Natural History Bulletin 17: 1-106.

Schatzinger, R. A., MS. Later Eocene (Uintan) lizards from the greater San Diego area, California. M.A. Thesis, San Diego State University (San Diego). [1975.]

Stock, C., 1933. An Amynodont skull from the Sespe deposits, California. Proceedings National Academy of Sciences 19: 762-767.

Stock, C., 1936. Perissodactyla of the Sespe Eocene, California. Proceedings National Academy of Sciences 22: 260-265.

Stock, C., 1937. An Eocene titanothere from San Diego County, California, with remarks on the age of the Poway Conglomerate. Proceedings National Academy of Sciences 23: 48-53.

Stock, C., 1938. A titanothere from the type Sespe of California. Proceedings National Academy of Sciences 24: 507-512.

Stock, C., 1939. Eocene amynodonts from southern California. Proceedings National Academy of Sciences 25: 270-275.

Wolfe, J. A. and D. M. Hopkins, 1967. Climatic changes recorded by Tertiary land floras in northwestern North America, pp. 67-76. *in,* Tertiary correlations and climatic changes in the Pacific (K. Hatai, *ed.*), Symposium 11th Pacific Science Congress, August—September, 1966.

Wolfe, J. A., 1975. Some aspects of plant geography of the northern hemisphere during the Late Cretaceous and Tertiary. Annals of the Missouri Botanical Garden 62: 264-279.

Wood, H. E., R. W. Chaney, J. Clark, E. H. Colbert, G. L. Jepsen, J. B. Reedside, and C. Stock, 1941. Nomenclature and correlation of the North American continental Tertiary. Geological Society of America Bulletin 52: 1-48.

Department of Geology, Louisiana State University, Baton Rouge, Louisiana 70803

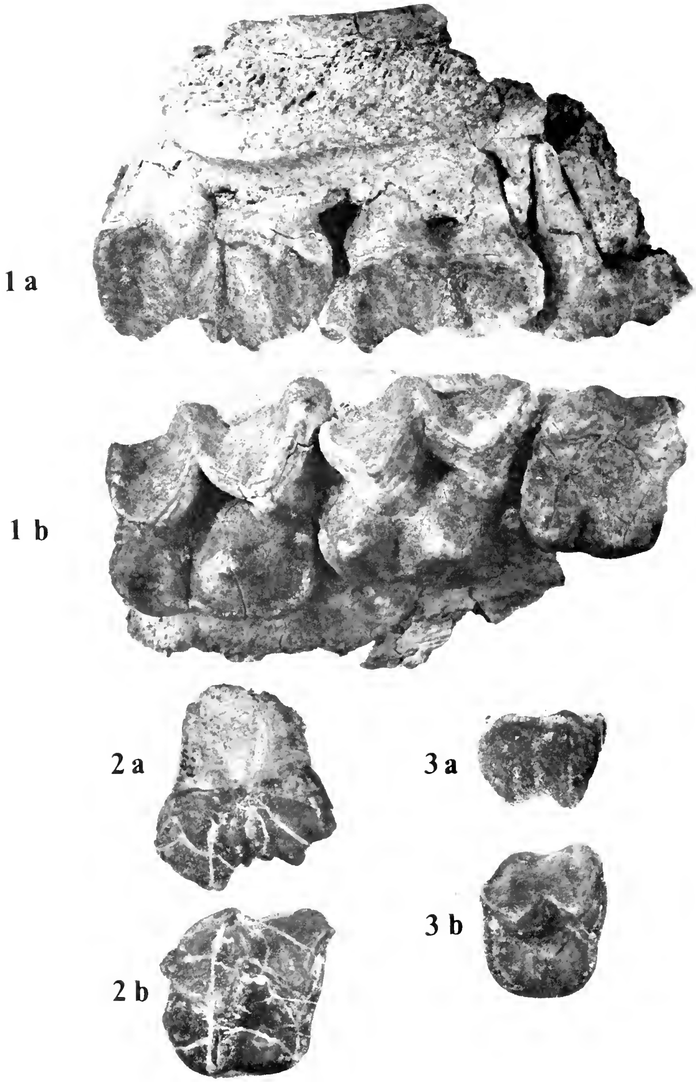


Plate 1. *Metarhinus? pater* from San Diego Co., California. All 1X. 1. UCMP 95774, right maxilla fragment with $\mathrm{M}^{\underline{1}}$ - $\mathrm{M}^{\underline{3}}$; 2. UCMP 56125, right $\mathrm{M}^{\underline{1}}$; 3. UCMP 113220, right $\mathrm{P}^{\underline{4}}$. a and b are labial and occlusal views, respectively.

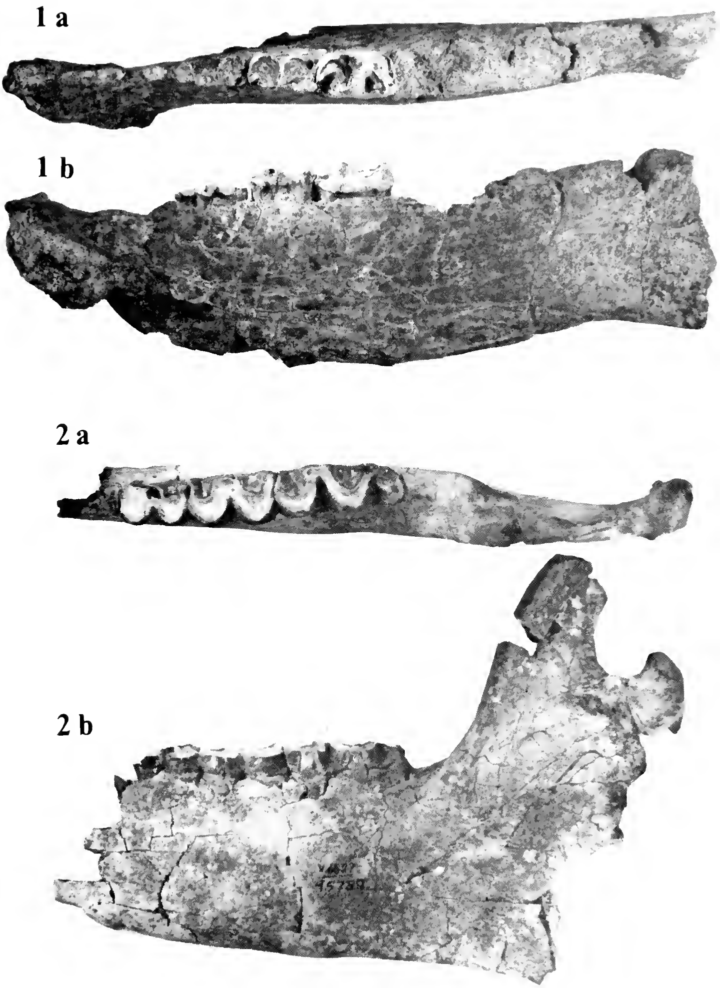


Plate 2. *Metarhinus? pater* from San Diego Co., California. All 1/2X. 1. UCMP 113201, partial right mandible with $P_{\overline{2}}$ talonid and $P_{\overline{3}}$ - $M_{\overline{1}}$, a. occlusal view, b. lingual view; 2. UCMP 95780, left mandible fragment with $M_{\overline{1}}$ - $M_{\overline{3}}$, a. occlusal view, b. labial view.

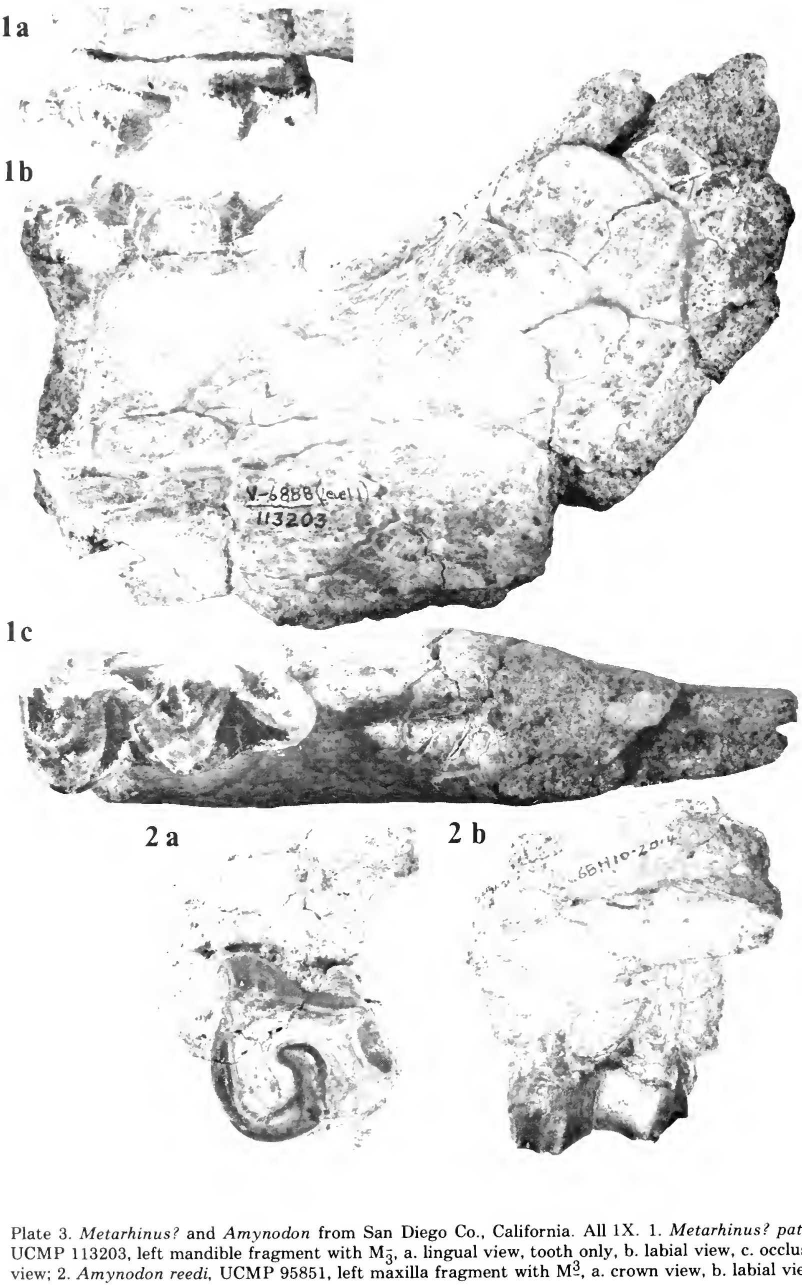


Plate 3. *Metarhinus?* and *Amynodon* from San Diego Co., California. All 1X. 1. *Metarhinus? pater*, UCMP 113203, left mandible fragment with $M_{\bar{3}}$, a. lingual view, tooth only, b. labial view, c. occlusal view; 2. *Amynodon reedi*, UCMP 95851, left maxilla fragment with $M^{\underline{3}}$, a. crown view, b. labial view.

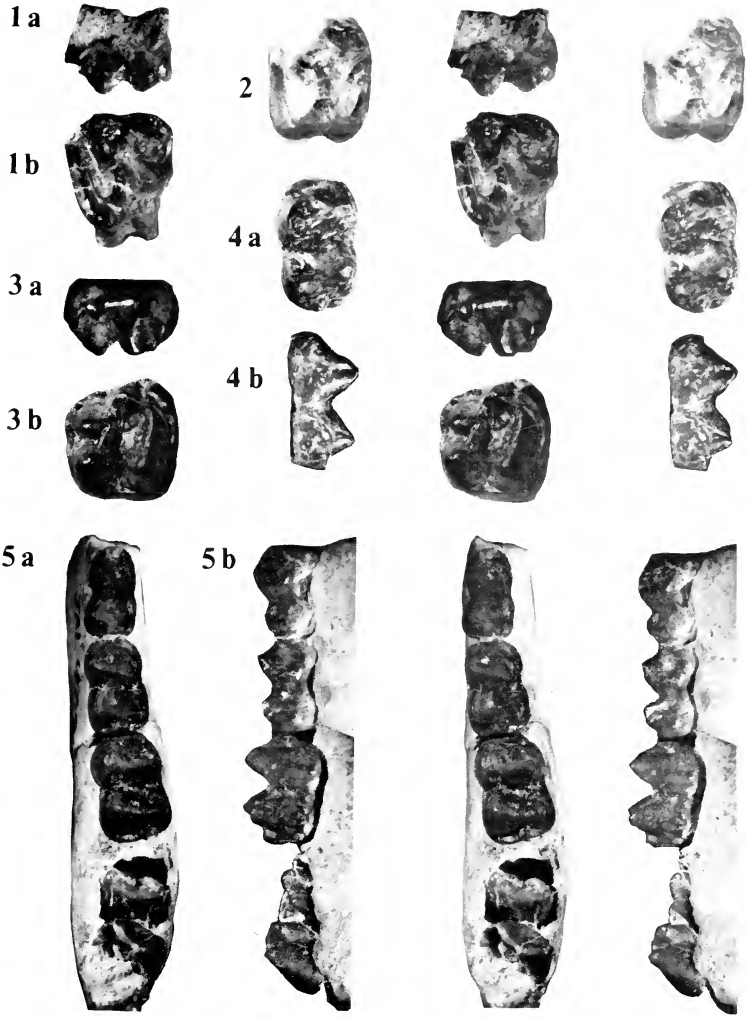
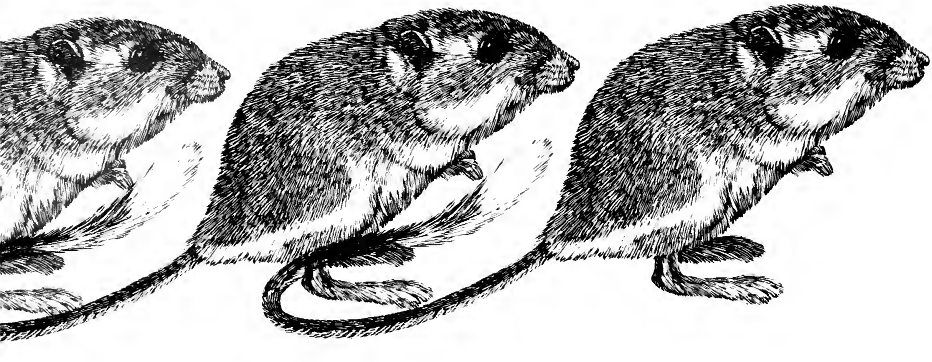


Plate 4. Stereophotographs of *Dilophodon* from California. All 2X. 1. UCMP 55976, left $M^{\underline{1}}$ or $M^{\underline{2}}$, a. labial view, b. occlusal view; 2. LACM 55977, left $M^{\underline{1}}$ or $M^{\underline{2}}$, occlusal view; 3. LACM (CIT) 1949, right $M^{\underline{3}}$, a. labial view, b. occlusal view; 4. LACM 55979, right $M_{\overline{3}}$, a. occlusal view, b. lingual view; 5. UCMP 113196, left mandible fragment with $DP_{\overline{3}}$, $DP_{\overline{4}}$, $M_{\overline{1}}$ - $M_{\overline{2}}$. a. occlusal view, b. lingual view, teeth only.

AN ANNOTATED LIST OF THE MAMMALS OF SAN DIEGO COUNTY, CALIFORNIA

Suzanne I. Bond



TRANSACTIONS

OF THE SAN DIEGO
SOCIETY OF
NATURAL HISTORY

VOL. 18, NO. 14 29 APRIL 1977

An annotated list of the mammals of San Diego County, California

Suzanne I. Bond

In 1921, Frank M. Stephens, veteran San Diego naturalist and Curator at the Natural History Museum, published the first list of the mammals of San Diego County. He cited 65 species of land mammals (plus additional subspecies), and gave brief descriptions of their range and habitat. In the intervening five decades, much new information has become available as local scientists, including L. M. Huey and R. C. Banks, former Curators at the Natural History Museum, continued detailed studies of the local fauna. Unfortunately, there is no recent compilation of this information, and Stephen's paper has long since been out of print, so that local students have had little to guide them.

In this paper I have attempted to summarize current knowledge of the status and habitat preferences of each species, and to give details on scientific reference material in the San Diego Natural History Museum and other major western collections. I recognize 80 species (plus many more subspecies) as occurring in the county. The increase is due to the introduction of several species, the occurrence of natural vagrants (mainly migratory bats), and taxonomic changes. There is no up-to-date compilation of marine mammals that occur along the county coastline. For general information in California see Daugherty, 1972, Marine Mammals of California.

Scientific and common names in this paper are those used by Jones, Carter and Genoway's (1973) *Checklist of North American Mammals North of Mexico*, except where noted. Species are included here on the basis of specimens examined or from literature references. Localities are arranged alphabetically. "San Diego area" includes the area north to La Jolla, east to Santee-Lakeside-El Cajon, and south to and including Chula Vista. Locality names are those used on current maps and the spelling may differ slightly from that on the collected specimens. For example, Mountain Springs was formerly known as Mountain Spring.

Life-zones listed are after J. Grinnell (1933). Life-zones, theoretically, are areas characterized by distinct assemblages of plants and animals (across North America from south to north, or from low to high). Three zones occur in San Diego County, as shown in Figure 1. One of the easiest ways to recognize life-zones is to learn the plants that typify them. In the Lower Sonoran Zone one finds desert plants such as cacti, agave, mesquite, creosote bush, yucca, arrowweed, and so forth. In the Upper Sonoran Zone, chamise, scrub oak, flat-top buckwheat, and chaparral plants predominate. The Transition Zone, at higher elevations, includes pines, firs, and cedars. Some species of mammals are restricted to certain zones and habitat types, whereas others are widespread.

I wish to thank the following for allowing me to examine catalogs and (or) specimens in their care: L. C. Binford, California Academy of Sciences (CAS); D. R. Patton, Los Angeles County Museum of Natural History (LACM); M. Getty, Anza Borrego Desert State Park (ABDSP); and W. Z. Lidicker, Jr., Museum of Vertebrate Zoology (MVZ). Gail Culver prepared the map. Ross Dingman added comments and several site records. For permission to reproduce the cover and text illustrations of Sheridan Oman, I thank Richard C. and Sharon Nelson, Tecolote Press, Inc. of Glenwood, New Mexico.

SAN DIEGO SOC. NAT. HIST., TRANS. 18(14):229-248, 29 APRIL 1977

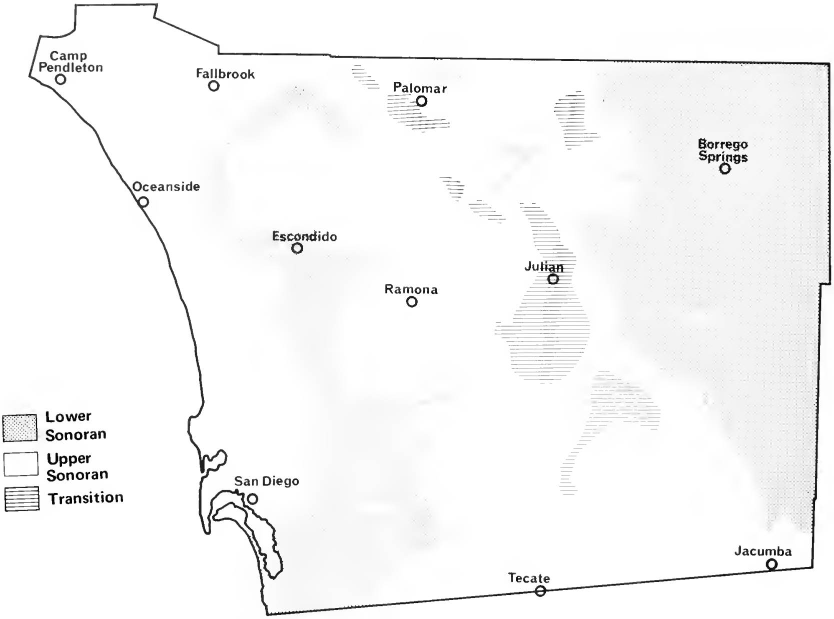


Figure 1. Life-zones of San Diego County (from Higgins, 1949, San Diego Soc. Nat. Hist., Occ. Paper 8).

SPECIES ACCOUNTS

Order Marsupialia

Family Didelphidae (Opossums)

• *Didelphis virginiana* • Opossum

An introduced species first captured wild in California in 1914 near Agnew, Santa Clara Co. (J. Grinnell, 1915: 114), and first taken in the county in La Puerta Valley in 1926 (Bryant, 1927: 146). Opossums are omnivorous and are most often found in coastal drainage areas near human habitation where they often act as scavengers. Now rather common. SDNHM specimens: La Puerta Valley, San Diego area.

Order Insectivora

Family Soricidae (Shrews)

• *Sorex ornatus ornatus* • Ornate Shrew

Most abundant in the Upper Sonoran life-zone but found from the coast to the mountains. Usually in damp earth on slopes and sometimes in dry areas beneath chaparral. Uncommon. SDNHM specimens: Kearny Mesa, Julian, San Diego area. Stephens (1906: 252) reported finding two dead near Santa Ysabel. Other specimens (MVZ): Dulzura.

- *Notisorex crawfordi crawfordi* • Desert Gray Shrew

Found mainly in the Lower Sonoran life-zone although not restricted to any particular habitat. Uncommon. SDNHM specimens: Borrego Palm Canyon, Encinitas, Escondido, San Diego area. Other specimens (MVZ): Bernardo, Santa Ysabel, Vallecito. New trapping techniques with better results indicate that shrews may not be as rare as previously thought.

Family Talpidae (Moles)

- *Scapanus latimanus occultus* • Broad-footed Mole

Found mainly in the Upper Sonoran life-zone. The main limitation to its range seems to be sufficient soil moisture (Palmer, 1937: 281). Most common in the mountains. SDNHM specimens: Alpine, Ballena, Escondido, Jamacha, Julian, Ramona, Tecate. Other specimens (MVZ): Warner Pass, Witch Creek.

Order Chiroptera

Family Phyllostomatidae (Leaf-nosed Bats)

- *Macrotus waterhousii californicus* • California Leaf-nosed Bat

Found in the Lower Sonoran life-zone. This colonial species lives in caves or other protected areas and is seen only on the wing after twilight (Banks, 1965: 13). It probably hibernates during the colder months. SDNHM specimens: Anza Borrego Desert State Park area, Dulzura, Pauma Valley, Vallecito. H. Grinnell (1918: 255) reported them at De Luz and the Santa Margarita Ranch and River.

- *Choeronycteris mexicana* • Long-tongued Bat

Found usually in the Sonoran life-zone (Ingles, 1965: 117). This nectar-feeding bat is apparently a fall vagrant from Central Mexico. It was first recorded from the county in September 1946 (Olson, 1947: 183). Many subsequent records were obtained in October 1947 and 1963 and December 1947. SDNHM specimens: (39) all San Diego area.

Family Vespertilionidae (Evening Bats)

- *Myotis lucifugus* • Little Brown Myotis

Never before recorded from southern California, this vagrant is listed here on the basis of a single specimen taken at Lake Hodges Dam in 1943 (LACM #8081). Found generally in forested areas, its southern limit is the San Bernardino Mountains (Miller and Allen, 1928: 51).

- *Myotis yumanensis sociabilis* • Yuma Myotis

Found chiefly in the Upper Sonoran life-zone west of the desert but east of the humid coastal belt in areas of oaks and pines or broken chaparral. SDNHM specimens: Barret Dam, El Monte Park, Lake Hodges. Other specimens (MVZ): Doane Valley, 4 mi. E Laguna Junction, San Diego area, Warner Springs. Miller and Allen (1928: 69) also reported it from San Luis Rey.

- *Myotis evotis evotis* • Long-eared Myotis

A solitary bat found chiefly in the Transition and Upper Sonoran life-zones. Stephens (1921: 52) reported, "found throughout the county. Not common." There are no specimens in the collection, although they have been reported from Witch Creek (H. Grinnell, 1918: 294) and Dulzura and Twin Oaks (Miller and Allen, 1928: 117). Other specimens: Palomar Mountain (CAS); Doane Valley, Cuyamaca State Park (MVZ). Our catalog lists specimens from: Laguna Mountain (1059), Ballena (81), Witch Creek (82); all are missing.

- *Myotis thysanodes thysanodes* • Fringed Myotis

Said to be found in the Upper Sonoran life-zone in areas of heavy chaparral or mixed forest and chaparral (J. Grinnell, 1933: 88). SDNHM specimens: Pine Valley (one). Other specimens (MVZ): Doane Valley, Laguna Junction. Miller (1897: 80) reported them at Dulzura.

• *Myotis volans interior* • Long-legged Myotis
Found from the Upper Sonoran to Transitional life-zones, Stephens (1921: 52) stated, "Generally distributed but not common in the coast region." SDNHM specimens: Julian (two). Other specimens (MVZ): Cuyamaca Mountains. Also reported from Dulzura (Miller and Allen, 1928: 143).

• *Myotis californicus californicus* • California Myotis
Found in the Transition and Upper Sonoran life-zones in wooded canyons or chaparral slopes along the Pacific coast region west of the mountains. SDNHM specimens: Ballena, Lake Henshaw, La Puerta Valley, Palomar Mountains, San Diego, Witch Creek. Other specimens (MVZ): Cuyamaca, Descanso, Julian area, Hubbard's Grove, Pala, Warner Springs. Another race, *M. c. stephensi*, is found in the Lower Sonoran life-zone in the desert region east of the mountains. SDNHM specimens: Anza Borrego Desert State Park area.

• *Myotis leibii melanorhinus* • Small-footed Myotis
A non-colonial species found in the Upper Sonoran and Transition life-zones among trees in semiarid areas. Fairly common. SDNHM specimens: Grapevine Canyon, Oriflamme Canyon, Pine Valley, San Diego, Santa Ysabel, and surprisingly Borrego Springs. Other specimens (MVZ): Boulder Oaks, Cuyamaca Rancho State Park, Julian, Laguna Junction, Manzanita, McCain Valley, near Vallecito (see Banks, 1965: 16), Wynola. Other localities: Dulzura, Jacumba, Santa Ysabel (H. Grinnell, 1918: 292); Twin Oaks, Witch Creek (Miller and Allen, 1928: 170).

• *Lasionycteris noctivagans* • Silver-haired Bat
Never recorded in southern California prior to 1973, when one was collected in a mist net at Agua Caliente Springs in February 1973 (specimen SDNHM). Subsequently, two others have been banded in the winter (T. McDonnell, pers. com.). Normally confined to the Transition life-zone, its former southern limit was Pacific Grove, Monterey Co. (H. Grinnell, 1918: 302).

• *Pipistrellus hesperus* • Western Pipistrelle
This is the smallest and most common of our bats. It is solitary and usually first seen at early dusk. The desert race, *P. h. hesperus*, is found mainly in the Lower Sonoran life-zone east of the Pacific divide. SDNHM specimens: Borrego Desert area. Also reported from: Dulzura and Santa Ysabel (H. Grinnell, 1918: 310). The coastal race, *P. h. merriami*, is found in the Upper Sonoran life-zone west of the Pacific divide. SDNHM specimens: De Luz, San Diego, San Marcos, Suncrest. Other localities (H. Grinnell, 1918: 312): Escondido, Twin Oaks, Witch Creek. H. Grinnell (p. 310) stated, "Specimens from Witch Creek (or Santa Ysabel), San Diego County, are allocated with difficulty, some appearing to be nearest *hesperus* and others nearest *merriami.*"

• *Eptesicus fuscus pallidus* • Big Brown Bat
This bat is said to occur chiefly in the Upper Sonoran and Transition life-zones, although Krutzsch (1946: 240) reports them, "taken from all life-zones in San Diego County." There are no winter specimens, and Krutzsch considered them migratory. SDNHM specimens: Alpine, Ballena, Barrett Junction, Dehesa, Escondido, Julian, Potrero, Witch Creek; MVZ specimens: Campo, Cuyamaca Mountains, Deluz, Descanso, Doane Valley, El Monte Oaks, Fallbrook, Foster, Jamacha, Lakeside,

San Onofre, Santee; ABDSP specimens: Pinyon Mountain Valley. Other localities: San Felipe Canyon, Agua Caliente Hot Springs and Vallecito Stage Station (Banks, 1965: 20).

• *Lasiurus borealis teliotus* • Red Bat
A solitary, tree-dwelling bat found west of the desert divide in the winter and spring. The sexes seem to separate during the summer with the females in the Lower Sonoran life-zone and the males in the Upper Sonoran (H. Grinnell, 1918: 326). SDNHM specimens: San Diego area, San Onofre, San Ysidro, Witch Creek. Other specimens: Escondido (MVZ); Santa Ysabel (H. Grinnell, 1918: 329).

• *Lasiurus cinereus cinereus* • Hoary Bat
Also a solitary, tree-dwelling, migratory bat found in the valleys during the winter. SDNHM specimens: Del Mar, Jamacha, Jamul, Rancho Santa Fe, San Diego area. Other specimens (MVZ): Bonsall, San Marcos, San Pasqual. Also reported from Santa Ysabel (H. Grinnell, 1918: 329).

• *Lasiurus ega xanthinus* • Southern Yellow Bat
A vagrant from southern Mexico that was first recorded from the county in June 1967 (Bond, 1970: 115). The six specimens in the collection are from Borrego Springs.

• *Euderma maculatum* • Spotted Bat
Vagrant. This bat is reported from the county on the basis of one specimen taken at the University of San Diego and now in their collection (August and Dingman, 1973: 166). Miller and Stebbins (1964: 283) report, "The natural history of this rare bat is almost unknown. The occurrences of it are chiefly in the arid or semiarid sections of the western United States."

• *Plecotus townsendii pallescens* • Townsend's Big-eared Bat
Found mainly in the Lower and Upper Sonoran life-zones either in colonies or singly. This bat is a cave-dweller, but is sometimes found in attics and barns. SDNHM specimens: Barrett Dam, Escondido, Julian, Ramona, San Diego, Vallecito. Other specimens (MVZ): Agua Caliente, Banner, Blair Valley, Borrego Palm Canyon, El Monte Oaks. Krutzsch is said to have reported them at Otay Mountain (Hall and Kelson, 1959: 200).

• *Antrozous pallidus* • Pallid Bat
Primarily a species of the Lower and Upper Sonoran life-zones. These bats are found in colonies during the spring, summer, and early fall months. Little is known of their winter behavior. They occur in various habitats (see Orr, 1954). Two races are found in the county. *A. p. pacificus* occurs along the Pacific slope side of the mountains. SDNHM specimens: Jamacha, Ramona, San Diego area, Santa Ysabel. Other specimens (MVZ): Ballena, Campo, Descanso, Fallbrook, Las Flores, Julian. *A. p. pallidus* is found in our desert region. SDNHM specimens: Jacumba. Other specimens: Agua Caliente Hot Springs (ABDSP); Vallecito (H. Grinnell, 1918: 351).

Family Molossidae (Free-tailed Bats)

• *Tadarida brasiliensis mexicana* • Brazilian (Mexican) Free-tailed Bat
A colonial bat found in the Lower and Upper Sonoran life-zones. In the county they are most abundant on the western slopes of the mountains. Krutzsch (1955: 236) reported them from 4 mi. E Fallbrook to 2 mi. E San Pasqual, Green Valley Falls, Santee and El Monte Oaks Park. SDNHM specimens: Borrego Springs, Carrizo Creek, Dulzura, Escondido, Jacumba, Ramona, San Diego area, Sweetwater Dam. Other specimens: Descanso, Fallbrook (MVZ); San Luis Rey (USNM, Shamel,

1931: 6). Banks (1965: 23) reported a specimen from Agua Caliente in our collection that cannot be found.

• *Tadarida femorosacca* • Pocketed Free-tailed Bat
Another colonial bat evidently found in the Lower Sonoran life-zone and into the Upper Sonoran (Krutzsch, 1944: 414). There are no specimens in the collection, but Krutzsch (1944: 201) observed them in Palm Canyon, Borrego Valley and at Suncrest (1944: 410, 414). There are two specimens in the MVZ from Palm Canyon.

• *Tadarida macrotis* • Big Free-tailed Bat
A rare bat found in the Lower Sonoran life-zone. It is a vagrant known from three specimens collected in San Diego (SDNHM, Huey, 1932: 160; 1954: 435; and Natural History Museum of the University of San Diego, August and Dingman, 1973: 165).

• *Eumops perotis californicus* • Western Mastiff Bat
Found in the Lower and Upper Sonoran life-zones. A permanent resident in southern California where chaparral and live oaks are found, and in more arid, rocky areas. SDNHM specimens: Bow Willow Ranger Station (Borrego Desert), Dulzura, San Diego, and Yaqui Wells. Other specimens (MVZ): Barrett Junction, Lake Hodges. H. Grinnell (1918: 372) reported them from Dos Cabezas (Borrego Desert) and Otay.

Order Lagomorphia

Family Leporidae (Rabbits and Hares)

• *Sylvilagus bachmani cinerascens* • Brush Rabbit
A common cottontail rabbit found in the Upper Sonoran life-zone from sea level to the mountains, and in dense chaparral along the Pacific coast region. They do not appear to make use of burrows as does the Desert Cottontail (Orr, 1940: 173). SDNHM specimens: Ballena, Encinitas, Escondido, Lyon's Peak, San Diego area, San Felipe Valley, San Marcos. Other specimens (MVZ): Alpine, Cuyamaca Mountains, Dulzura, Grapevine Springs. Other reported localities (Nelson, 1909: 253): Laguna, Jacumba, Santa Ysabel.

• *Sylvilagus audubonii* • Desert (Audubon) Cottontail
A common cottontail of the lowlands that might be mistaken for a Brush Rabbit except for its larger size. It never penetrates far into the chaparral (Orr, 1940: 126). The desert race, *S. a. arizonae*, is found in the Lower Sonoran life-zone. SDNHM specimens: La Puerta Valley, Palm Spring-Mesquite Oasis. Other specimens (MVZ): Vallecito. *S. a. sanctidiegi* is found in the Lower and Upper Sonoran life-zones along the coast from sea level to above 4000 feet in chaparral or open grassland. SDNHM specimens: Carlsbad, Grapevine Canyon, Ramona, San Diego area, Santa Ysabel, Tia Juana River Valley. Other specimens (MVZ): Cuyamaca Mountains, Dulzura, Escondido, Julian, Oak Grove, Otay Valley, San Felipe Canyon, Warner Pass, Witch Creek. Other reported localities: Jacumba, Twin Oaks, Mountain Springs, Warner Valley (Nelson, 1909: 220); San Marcos (Orr, 1940: 122).

• *Lepus californicus* • Black-tailed Jack Rabbit (Hare)
Our largest "rabbit," generally found only in open or semi-open country. Thick chaparral or forested regions are unsuitable (Orr, 1940: 80). *L. c. bennettii* is found in the Upper Sonoran life-zone along the coast to the western base of the coastal mountains from sea level to 6000 feet on Cuyamaca Mountain (J. Grinnell, 1933: 201). SDNHM specimens: Live Oak Springs, San Diego, Santa Ysabel. Other specimens: San Marcos (MVZ); Escondido, Tijuana River (Orr, 1940: 74); Dulzura, Jacumba, Jamul Creek, Laguna Mountains, Mountain Springs, Twin Oaks (Nelson, 1909: 137). The type specimen for this animal was collected in the early 1840s at

San Diego during the voyage of H.M.S. Sulphur, under the command of Captain Sir Edward Belcher. The desert race, *L. c. deserticola*, is found east of the coastal mountains in the Lower Sonoran life-zone along the foothills in clear chaparral areas and on the desert floor. This is the common desert "rabbit." SDNHM specimens: La Puerta Valley, San Felipe Canyon, Vallecito. Specimens from the last two localities have been allocated to both races (Orr, 1940: 73; Nelson, 1909: 140).

Order Rodentia
Family Sciuridae (Squirrels)

• *Eutamias merriami merriami* • Merriam's Chipmunk
Found in the Upper Sonoran to lower Transition life-zones in mixed forest. This is the only chipmunk found in the county. SDNHM specimens: Cuyamaca Mountains, Laguna Mountains, Palomar Mountain, Warners Ranch, Witch Creek. Other specimens: Julian (MVZ); Jacumba, Mountain Springs, Santa Ysabel, Volcan Mountain, Warner Pass (Howell, 1929: 126).

• *Ammospermophilus leucurus leucurus* • White-tailed Antelope (Ground) Squirrel
A common desert ground squirrel, found mainly in the Lower Sonoran and occasionally Upper Sonoran life-zones where the general environment is desert-like with thick vegetation. SDNHM specimens (many) are all from the desert region east of the mountains. Also reported from Jacumba and Mountain Springs (Howell, 1938: 172).

• *Spermophilus beecheyi nudipes* • California Ground Squirrel
Found from the Lower Sonoran to the Transition life-zones, but most abundant in the Upper Sonoran zone. This is the common ground squirrel from the mountains and west to the sea. SDNHM specimens: Ballena, Camp Pendleton area, Cuyamaca Mountains, Jamacha, Laguna Mountain, Pine Hills, San Diego area, Santa Ysabel, Valley Center, Witch Creek. Other specimens (MVZ): Campo, Dulzura, Grapevine Springs, Jacumba, Julian, Mountain Springs, Oak Grove, Warner Pass, Wynola. Banks (1964: 15-16) observed them at Culp Valley, Pena Spring, Pinyon Mountain Valley, and Sentenac Canyon. Also reported at McCain Valley and Borrego Palm Canyon (R. Dingman, pers. obs.).

• *Spermophilus tereticaudus tereticaudus* • Round-tailed Ground Squirrel
Another common desert ground squirrel, found in the Lower Sonoran life-zone where the vegetation is low and sparse. Told from the White-tailed Antelope Squirrel by the lack of body stripes. Seldom seen in the winter months. Specimens in the collection are from the desert area.

• *Sciurus carolinensis* • Gray Squirrel
This species of tree squirrel was introduced from the eastern part of the United States into many city parks and private estates. A note found in the mammal catalog from 1924 states it was introduced into Balboa Park by the San Diego Zoo. Its present status is not known. There is one specimen in the collection from Balboa Park.

• *Sciurus griseus anthonyi* • Western Gray Squirrel
Found generally in the Transition life-zone, this is the common tree squirrel in mixed oak and pine forest of the mountains. SDNHM specimens: Banner Grade, Barona Indian Reservation, Cuyamaca Mountains, Escondido, Julian, Laguna Mountains, Palomar Mountains, Pine Mountain. Other specimens (MVZ): Warner Pass.

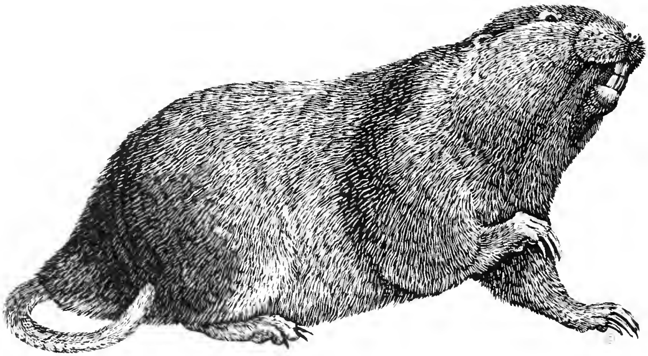
- *Sciurus niger* • Fox Squirrel

Another species introduced from the eastern United States (date unknown). This squirrel can be commonly seen in Balboa Park. SDNHM specimens: three from Balboa Park. The earliest specimen is dated 1929.

Family Geomyidae (Pocket Gophers)

- *Thomomys bottae*[1] • Southern Pocket Gopher

This is one of the most common and widespread mammals in the county. It occurs wherever vegetation grows and the soil is loose enough for them to burrow through. A fossorial gopher rarely seen above ground. There are five recognized races: *T. b. affinis*, from the Jacumba area; *T. b. boregoensis*, from Borrego Desert region; *T. b. nigricans*, found largely in the mountains; *T. b. puertae*, restricted to the La Puerta, San Felipe valleys; *T. b. sanctidiegi*, found along the coastal region.



Pocket Gopher

Family Heteromyidae (Pocket Mice)

- *Perognathus longimembris* • Little Pocket Mouse

This is the smallest species of pocket mouse and the smallest rodent in the county. Like all pocket mice, it is nocturnal and seldom seen. Generally found in areas of fine sandy ground. There are four recognized races. *P. l. bangi*, found in the Lower Sonoran life-zone in our eastern desert region. SDNHM specimens: Borrego Desert area. *P. l. brevinasus*, found in the high Lower to low Upper Sonoran life-zones. SDNHM specimens: near Oak Grove, Ranchita, Warner Pass. *P. l. internationalis*, found in the immediate area of Jacumba, although Huey (1939: 48) stated that specimens from La Puerta, San Felipe Valley, and Warner's Pass were not typical. SDNHM specimens: Jacumba area, La Puerta Valley, San Felipe Valley, W side Blair Valley. There appears to be some intergradation of subspecies in the La Puerta Valley area (Banks, 1964: 21). *P. l. pacificus*, found in the Upper Sonoran life-zone along a narrow coastal strip running from the Tia Juana River Valley north to Los Angeles Co. SDNHM specimens: Oceanside, San Onofre, Tia Juana Valley. Also reported from mouth of Santa Margarita River (von Bloeker, 1932: 129).

---

[1] *bottae* after Patton and Dingman, 1968: 1-13.

- *Perognathus formosus mesembrinus* • Long-tailed Pocket Mouse

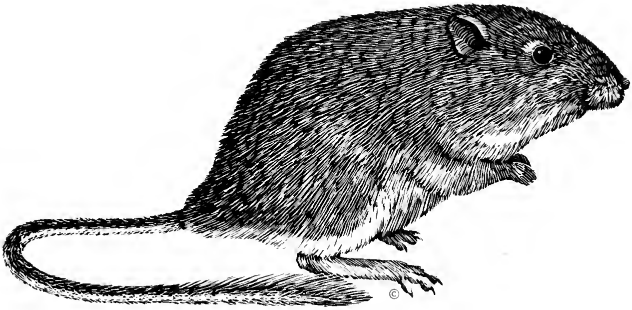
Found in the Lower Sonoran life-zone in gravelly, rocky areas in our desert. SDNHM specimens: Fish Creek Wash, Ocotillo Wells, San Felipe Canyon, Vallecito area. Other localities: La Puerta Valley (von Bloeker, 1932: 279); Borrego Palm Canyon (R. Dingman, pers. obs.).

- *Perognathus baileyi hueyi* • Bailey's Pocket Mouse

This rare pocket mouse is found in the Upper Sonoran life-zone on rocky steep slopes in our desert region. SDNHM specimens: San Felipe Narrows (only two). Other specimens: Mountain Springs, Yaqui Wells (MVZ); Borrego (CAS). Also reported from Banner and La Puerta Valley (von Bloeker, 1932: 279).

- *Perognathus penicillatus angustirostris* • Desert Pocket Mouse

Found in the Lower Sonoran life-zone in open sandy desert areas. SDNHM specimens: Borrego Desert area, La Puerta Valley, San Felipe Narrows, Vallecito.



Pocket Mouse

- *Perognathus fallax* • San Diego Pocket Mouse

Found from the Lower to Upper Sonoran life-zones usually in somewhat open, sandy land with weeds. The coastal race, *P. f. fallax*, is found on the Pacific drainage side of the mountains. SDNHM specimens: Ballena, Del Mar, Dulzura, Jacumba area, Lake Hodges, Pala, San Diego area, San Marcos, Tia Juana River Valley. *P. f. pallidus* is found mainly in the Lower Sonoran life-zone on the eastern side of the mountain divide. SDNHM specimens: Earthquake Valley, Grapevine Canyon, La Puerta Valley, Ranchita, San Felipe Valley. Other records: 4 mi. W Yaqui Wells and San Felipe Narrows (Banks, 1964: 27).

- *Perognathus californicus fermoralis* • California Pocket Mouse

This pocket mouse is found chiefly in the Upper Sonoran life-zone in the coastal and montane regions on chaparral slopes. SDNHM specimens: Banner, Campo, Dehesa, Dulzura, Escondido, Pala, Rainbow, Ramona, Palomar Mountain, San Marcos, Santee, Santa Ysabel, Witch Creek. Other localities: San Felipe Valley (MVZ); La Puerta Valley (von Bloeker, 1932: 279).

• *Perognathus spinatus rufescens* • Spiny Pocket Mouse
Found in the Lower Sonoran life-zone in rocky rough terrain on the desert and east slopes of the coastal mountains. SDNHM specimens: Borrego Desert area, La Puerta Valley, Ranchita, San Felipe Canyon, San Felipe Narrows, Vallecito. Also reported from Mountain Springs (J. Grinnell, 1933: 156).

• *Dipodomys stephensi* • Stephens' Kangaroo Rat
A rare kangaroo rat found in the Lower Sonoran life-zone in areas of sparse vegetation. It is known in the county only from an isolated area near Bonsall (Lackey, 1967). SDNHM specimens: Bonsall, 7 mi. E Oceanside, 2 mi E San Luis Rey Mission.

• *Dipodomys agilis* • Agile Kangaroo Rat
This is the common kangaroo rat of the Pacific Coast of southern California. *D. a. cabezonae* is found in the Lower Sonoran life-zone on the slopes of the coastal mountains in loose soil with sparse vegetation. SDNHM specimens: Banner, Jacumba area, Oakgrove, Sunrise Highway, Warner Springs. Other specimens: Borrego Desert area, Julian, McCain Valley, Mountain Springs (MVZ); Culp Valley (ABDSP). Other localities: Grapevine Spring, La Puerta Valley, San Felipe Valley (J. Grinnell, 1922: 96). *D. a. simulans* occurs chiefly in the Upper Sonoran life-zone on the Pacific slopes of the mountains in areas of chaparral and sandy ground. SDNHM specimens: Bonsall, Cuyamaca Mountains, De Luz, Dulzura, Escondido, Jack Creek, Lake Hodges, Pala, Palomar Mountain, Pine Valley, Proctor Valley, Poway, Rincon Springs, San Diego area, San Marcos, San Pasqual Valley, Santa Ysabel, Tia Juana River Valley, Witch Creek.

• *Dipodomys merriami* • Merriam's Kangaroo Rat
This small kangaroo rat is found generally in the Lower Sonoran life-zone in loose, sandy, gravelly ground with sparse vegetation. This is the common desert kangaroo rat. There are three recognized races in the county based on Lidicker's (1960) studies. *D. m. arenivagus* is a desert race. SDNHM specimens: Borrego Valley area, Bow Willow, Carrizo Creek, Mortero Canyon, Ocotillo Wells, Vallecito area. *D. m. collinus* is another desert dweller found in the western part of the desert. SDNHM specimens: Blair Valley, Earthquake Valley, La Puerta Valley, Oak Grove, San Felipe Valley. *D. m. trinidadensis* occurs in the Jacumba area (only one SDNHM specimen). Lidicker (1960: 196-198) lists specimens from Mountain Springs and Jacumba and states that this race intergrades with *D. m. arenivagus* in the Mountain Springs region. *D. m. arenivagus* and *D. m. collinus* also appear to intergrade in the San Felipe Narrows and Vallecito area. For details on intergradation see study by Lidicker (1960: 190-196).

• *Dipodomys deserti deserti* • Desert Kangaroo Rat
This is our largest kangaroo rat found in the Lower Sonoran life-zone in areas of deep wind-driven sand and sparse vegetation. SDNHM specimens: Borrego Valley, Carrizo Creek, La Puerta Valley, Scissors Crossings. Other specimen (ABDSP): Vallecito.

Family Castoridae (Beavers)

• *Castor canadensis* • Beaver
The beaver, the largest native rodent in North America, was introduced into the county in 1944. It is now found in the Upper Sweetwater River in the Cuyamaca Mountains (Cal. Fish and Game, pers. comm.) and in the San Luis Rey River below the Lake Henshaw dam (pers. obs.). There are no specimens in the collection from the county.

Family Cricetidae (Native Rats and Mice)

• *Reithrodontomys megalotis longicaudus* • Western Harvest Mouse
Found mainly in the Upper Sonoran life-zone and locally in the Lower Sonoran in moist grassy areas. SDNHM specimens: from the Tia Juana River Valley north along the coast to Oceanside-Vista area to Los Flores, Ballena, Cuyamaca Mountain, Descanso, El Monte, Escondido, Grapevine Canyon, Laguna Mountain, Lake Hodges, La Puerta Valley, Pinyon Mountain Valley, Proctor Valley, Sentenac Canyon, Warner, Vallecito. Other specimens (ABDSP): Earthquake Valley, Palm Springs, Mesquite Oasis. J. Grinnell (1933: 170) considered specimens from Vallecito and Mountain Springs to be intergrades toward *R. m. megalotis.*

• *Peromyscus crinitus stephensi* • Canyon Mouse
This member of the White-footed mouse group is found in the Lower Sonoran life-zone in rough rocky areas in our desert region. SDNHM specimens: Borrego Valley, Bow Willow Campground, Fish Creek Wash, Mortero Canyon, Ocotillo Wells area, Pinyon Mountain, Seventeen Palms Oasis. Also reported from San Felipe Valley (Osgood, 1909: 234). This mouse is similar to the Cactus Mouse *(P. eremicus)* and is sometimes difficult even for experienced persons to identify.

• *Peromyscus californicus insignis* • California Mouse
This is the largest of the White-footed mice in the county. It is commonly found in the Upper Sonoran life-zone in chaparral covered slopes. SDNHM specimens: from the San Diego area north along the coast to Los Flores Mission, Dehesa, Dulzura, Escondido, Poway, Rainbow, Santa Ysabel, Scissors Crossing, Witch Creek. Other localities: Campo, Jacumba, Jamul Creek, Mountain Springs, Santa Ysabel, Twin Oaks (Osgood, 1909: 238); 6 mi. N Foster, Julian, La Puerta Valley, San Felipe Valley, Warner Pass (Grinnell and Orr, 1934: 220).

• *Peromyscus eremicus* • Cactus Mouse
This is the second commonest White-footed mouse in the county. The desert race, *P. e. eremicus,* is found in the Lower Sonoran life-zone in arid lowlands on sandy desert floors. It is the most abundant rodent in our desert and SDNHM specimens are from various areas in the Borrego Desert (see Banks, 1964: 43-46). *P. e. fraterculus* is the coastal race found in the Upper Sonoran life-zone west of the coastal mountains in areas of sparse, shrubby vegetation. SDNHM specimens: Dehesa, Dulzura, Escondido, Pala, Poway, San Diego area, San Marcos, San Pasqual, Tia Juana River Valley. Other localities: Chihuahua Mountains, Jamul Creek, Jacumba, Mountain Springs, Santa Ysabel, Twin Oaks (Osgood, 1909: 244); Campo (J. Grinnell, 1933: 173). The races seem to intergrade in the Mountain Springs and Jacumba areas (Grinnell, op. cit.).

Cactus Mouse

• *Peromyscus maniculatus* • Deer Mouse
This is the most abundant, widespread mammal in California. In the county it is found in nearly all the habitats from the Lower Sonoran to the Transition zones. Two subspecies occur. *P. m. gambelii*, with over 250 specimens in our collection, ranges from the extreme western edge of the desert to the coastal area. *P. m. sonoriensis*, the desert race, is found in the Lower Sonoran life-zone. SDNHM specimens: Borrego Valley, Jacumba, La Puerta Valley, San Felipe Valley, Warner's Ranch, Vallecito. The two races intergrade in the mountains and western desert area (see Banks, 1964: 46, and J. Grinnell, 1933: 174).

• *Peromyscus boylii rowleyi* • Brush Mouse
Common locally in the Upper Sonoran life-zone, on wooded or brushy slopes in arid or semi-arid regions. SDNHM specimens: Ballena, Cuyamaca Mountains, Dehesa, Doane Valley, El Monte, Escondido, Jamul Rancho, Laguna Mountains, Margarita Peak, Pinyon Mountain Valley, Rainbow, Santa Ysabel, Sentenac Canyon, Witch Creek. Other localities (Osgood, 1909: 146-147): Chihuahua Mountains, Jacumba, Julian, Mountain Springs, Oak Grove, Smith (= Palomar) Mountain.

• *Peromyscus truei martirensis* • Piñon Mouse
This mouse of the high country is found in the Upper Sonoran to the Transition life-zones on dry slopes covered with scrub oak type vegetation. Not common. SDNHM specimens: Culp Valley, Mountain Springs, Monument Peak in the Laguna Mountains.

• *Onychomys torridus* • Southern Grasshopper Mouse
This mouse resembles a short-tailed *Peromyscus* and does not seem to be restricted to any one habitat. It is not as common as the white-footed group. Two races are found in the county. *O. t. pulcher* is found in the Lower Sonoran life-zone in desert areas of shrubby vegetation. SDNHM specimens: Blair Valley, Grapevine Canyon, Mason Valley, Mountain Springs. Other specimens: Earthquake Valley (ABDSP); Scissors Crossing (MVZ). *O. t. ramona* is found in the Lower and Upper Sonoran life-zones on the Pacific slopes. SDNHM specimens: Carlsbad, Culp Valley, Dulzura, San Diego, San Pasqual Valley, Tia Juana River Valley. Other localities (Hollister, 1919: 469): Jacumba, La Puerta Valley, Warner Pass. Banks (1964: 50) states that the two races intergrade and that identification is difficult.

• *Neotoma albigula venusta* • White-throated Woodrat
This native rat is found in the Lower Sonoran life-zone and reaches its western range limits in our eastern county. Not common. SDNHM specimens: Borrego Springs, Carrizo Creek. Banks (1964: 54) collected one near Ocotillo Wells.

• *Neotoma lepida* • (White-footed) Desert Woodrat
The common name for this mammal is somewhat misleading since it is found in the mountains and along the coast as well as in the desert. There are three recognized races in the county. *N. l. gilva* is found in the Lower and Upper Sonoran life-zones usually in rocky or shrubby vegetative arid plains. There is only one specimen in the collection from Mountain Springs. Other specimens (MVZ): Jacumba, Manzanita. Goldman (1932: 64) states that *gilva* is an intergrading form connecting *lepida* and *intermedia*. A common coastal wood rat, *intermedia*, occurs mainly in the Upper Sonoran life-zone on the western slopes of the mountains in chaparral areas. SDNHM specimens: Bonsall, Mission San Luis Rey north along the coast to San Onofre Mountain, Fortuna Mountain, Mission Gorge, Murphy Canyon, Murray Dam, Proctor Valley, San Diego area, Santa Ysabel, mouth of the Tia Juana River, Witch Creek. Other specimens (MVZ): Dulzura, Jacumba, Julian. Also reported from Jamul and Poway (Goldman, 1910: 44). *N. l. lepida* is a desert race

restricted to rocky and (or) agave covered areas in the Lower Sonoran life-zone. SDNHM specimens: various localities within Anza Borrego Desert State Park (see Banks, 1964: 56), Borrego Springs, near Ocotillo Wells.

• *Neotoma fuscipes macrotis* • Dusky-footed Woodrat
This large woodrat is found chiefly in the Upper Sonoran life-zone in heavy chaparral areas usually near water. It occurs from the mountains to the coast. SDNHM specimens: Tia Juana River Valley, San Diego area north along the coast to San Clemente, Grapevine Canyon, Poway, near Ranchita, San Marcos, Santa Ysabel, Witch Creek. Other specimens (MVZ): Campo, Canebrake Canyon, Oakgrove, Warner Pass. Hooper (1938: 232) examined specimens from Escondido and Julian.

• *Microtus californicus sanctidiegi* • California Vole
This medium size mouse with coarse brown fur, short ears, and a short tail is found in the Lower Sonoran to Transition life-zones. It is common near water in grassy or marshy areas. SDNHM specimens: San Diego area north along the coast to Oceanside, inland from Ballena, Palomar Mountain, Escondido, Julian, Ramona, Santa Ysabel, Witch Creek. Specimens from Sentenac Canyon may prove to be an undescribed race (Banks, 1964: 58). Other specimens (MVZ): Dulzura, Jacumba, La Puerta Valley, Mountain Springs, Vallecito. Also reported from the Cuyamaca Mountains and Warner Pass (Kellogg, 1918: 31).

Family Muridae (Old World Rats and Mice)

• *Rattus rattus* • Black (Roof) Rat
This Old World rat was introduced in the New World as early as 1544 and has been found in San Diego since 1856 (Baird, 1857: 440). It was not considered numerous in 1921 (Stephens, 1921: 46) but is now commonly found around areas of human habitation. SDNHM specimens: San Diego area.

• *Rattus norvegicus* • Norway (Brown) Rat
Another introduced Old World rat that first appeared in 1775. Before 1851 it was not found on the Pacific coast, but was abundant in 1856, when specimens were taken in San Diego (Baird, 1857: 439). This rat is also found around human habitation and Stephens (1921: 45) reported them as "thoroughly established. Abundant in towns and becoming common in the country." There are no specimens in the collection from the county. The Black Rat seems to have replaced it (San Diego County Department of Public Health, pers. comm.).

• *Mus musculus* • House Mouse
This Old World animal probably came to the New World with the earliest explorers. Found in both cultivated and uncultivated areas, it was reported from San Diego as early as 1856 (Baird, 1857: 444). Now very common. SDNHM specimens: El Cajon, Fortuna Mountain, Oceanside, San Diego area.

Family Capromyidae (Coypus)

• *Myocaster coypus* • Nutria or Coypu
This South American rodent, first introduced in California in 1942, near Oakdale, Stanislaus Co. (Howard, 1953: 513), has since become feral. It inhabits areas around water much like the muskrat *(Ondatra)* and has been reported wild in San Diego Co. since 1948 (Ingles, 1965: 309). There is a partial skull in the collection which was found in Mission Valley. According to the California State Fish and Game Department (pers. comm.) there are none in the area at this time.

Order Carnivora
Family Canidae (Dogs and Allies)

- *Canis latrans clepticus* • Coyote

This native dog is commonly found in the Upper and Lower Sonoran life-zones up into the Transition zone inhabiting open valley floors and forested areas with clearings. This race is said to be a connecting form between *ochropus* on the north and *peninsulae* on the south (Jackson, 1951: 295). It also intergrades with *mearnsi* on the east and it is difficult to properly ascribe specimens to race. SDNHM specimens: Borrego Springs, La Puerta Valley, Los Flores Mission, Los Penasquitos Canyon, Poway, San Diego area, Warner Springs, Vallecito. Other reported localities: Jacumba, Julian, San Marcos (Jackson, 1951: 295); San Felipe Valley, San Onofre, Tia Juana River (as *C. l. ochropus*, Grinnell, et al., 1937: 501).

- *Vulpes macrotis arsipus* • Kit Fox

This uncommon small fox is found in level desert areas of the Lower Sonoran life-zone where the substrate is sandy. There is only one specimen in the collection, from La Puerta Valley. Stephens (1921: 50) reported trapping them at Borrego Springs. The Anza Borrego Desert State Park Rangers report seeing them throughout the park (M. Getty, pers. comm.).

- *Vulpes macrotis macrotis* • Long-eared Kit Fox — EXTINCT

This race of the kit fox occurred along the coast in the Lower Sonoran life-zone and is "rather certainly now extinct" (Allen, 1942: 197). One specimen (skin only) in the collection was taken one mile north of Rancho Santa Fe in 1931. Its identity was confirmed by R. S. Hoffman (1976, Visiting Fellow, National Museum of Natural History).

- *Urocyon cinereoargenteus californicus* • Gray Fox

A common fox found chiefly in the Upper Sonoran life-zone and down into the Lower Sonoran in chaparral areas. It feeds primarily on ground squirrels and other small mammals. SDNHM specimens: Anza Borrego Desert State Park, Ballena, Escondido, Los Flores Mission, Potrero Grade, Ramona, San Diego area, San Marcos, Santa Ysabel, Witch Creek. Other specimens (MVZ): Campo, Cranebrake Canyon, La Puerta Valley, Pine Mountain.

Family Ursidae (Bears)

- *Ursus americanus* • Black Bear

This species, which normally occurs from Ventura Co. north, was introduced to the Campo area and the Cuyamaca Mountains between 1917-1919 by a group of servicemen (Abbott, 1935: 150). Apparently they soon died out. The collection contains a single skull of a female taken in 1934 at Potrero, probably the last of this group of animals. In recent years the black bear has been sighted in Camp Pendleton (1975) and Lake Henshaw and the Palomar Mountain area (1976), and an adult male was shot in June 1976 near Buckman Springs, 5 miles south of Pine Valley. These bears are thought to be coming in from the San Bernardino Mountains to the north.

- *Ursus magister* • Southern California Grizzly — EXTINCT

This, the largest grizzly bear known outside of Alaska, was "rather common in the mountains" nearly one hundred years ago (Stephens, 1921: 51). There are no specimens in the collection from the county, but two taken at San Onofre and Trabuco canyons are in the USNM (nos. 156594, 160155). The last individual was shot in 1908 (Storer and Tevis, 1955: 28). Other recorded sites: Palomar Mountain (Bell, 1930: 108); Pine Valley (Abbott, 1935: 151); Santa Rosa Mountains (J. Grinnell, 1933: 98).

Family Procyonidae (Raccoons and Allies)

• *Bassariscus astutus octavus* • Ringtail (Ring-tailed Cat)
Found on the Pacific slope in the Upper Sonoran life-zone in brush and chaparral, along with *Peromyscus* and *Neotoma*, its main food. A nocturnal animal not commonly seen. SDNHM specimens: Borrego area on the Montezuma Grade, Live Oak Springs, San Diego, San Luis Rey River near Escondido, Sentenac Canyon. Other localities: foot of Palomar Mountain (Stephens, 1921: 51); Jacumba (J. Grinnell, 1933: 100).

• *Procyon lotor psora* • Raccoon
Found generally in the Upper Sonoran life-zone along streams, in marshes and near lakes. Seldom seen due to its nocturnal habits. It is probably the most omnivorous native carnivore in the county (Ingles, 1965: 357). SDNHM specimens: Los Flores Mission, San Diego area, Santa Ysabel. Other specimens (MVZ): Cuyamaca Mountains, Julian. Also reported from Palomar Mountain (R. Dingman, pers. obs.).

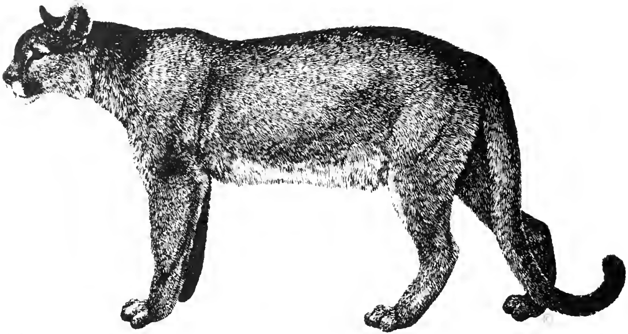
Family Mustelidae (Weasels and Allies)

• *Mustela frenata latirostris* • Long-tailed Weasel
Found in all habitats near water, from the Lower Sonoran through the Upper Sonoran life-zones. Frequently found in area of old gopher *(Thomomys)* and ground squirrel *(Spermophilus)* burrows, which it uses for its nest area. Active both day and night, feeding mostly on small rodents. SDNHM specimens: Cardiff, Escondido, Lakeside, Jamacha, Mount Woodson, San Diego area, San Marcos, Santee, Tia Juana River bottom. Other reported localities (Hall, 1951: 327): Ballena, El Cajon, Julian, Twin Oaks, Witch Creek.

• *Taxidea taxus* • Badger
Not commonly seen, the badger is most active during the late afternoon hours. There are two races in the county. *T. t. berlandieri* is found on the eastern side of the coastal mountains. SDNHM specimens: La Puerta Valley. *T. t. neglecta* is found west of the mountains and appears to have no zonal restrictions (J. Grinnell, 1933: 108). It is found in levelish, open, unforested areas. SDNHM specimens: Lakeside, Escondido, Ramona, San Marcos, Sweetwater Reservoir, Witch Creek. Other reported sites are near El Cajon (Grinnell, et. al., 1937: 361).

• *Spilogale gracilis microrhina* • Western Spotted Skunk
This uncommon small skunk is found in the Lower and Upper Sonoran life-zones usually in dry rocky or brushy hillsides. SDNHM specimens: Jamul, Ramona, San Diego area, Santa Ysabel, Witch Creek. Other localities: Julian, Escondido, Cuyamaca Mountains (Hall, 1926: 53); La Puerta, Dulzura (Hall and Kelson, 1952: 355).

• *Mephitis mephitis holzneri* • Striped Skunk
The common skunk of the county is found chiefly in the Upper Sonoran life-zone and into the Lower Sonoran. Usually it occurs in brushy woodland and chaparral hillsides, but it has become adapted to city living where it acts as a scavenger. SDNHM specimens: Lake Hodges, Otay, San Diego area, San Onofre, Santa Ysabel. Other reported localities (Grinnell, et. al., 1937: 317): Campo, Cuyamaca Mountain, Warner Pass, Witch Creek, Vallecito.

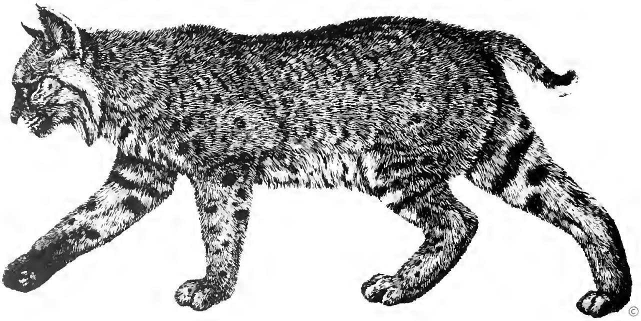


Mountain Lion

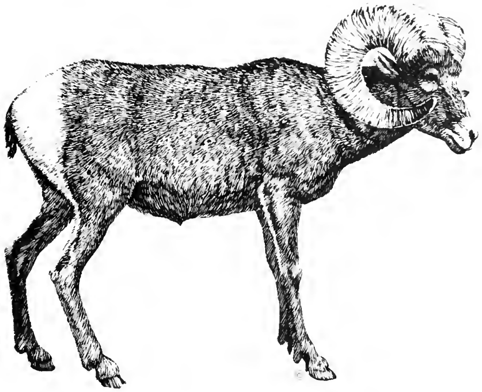
Family Felidae (Cats)

• *Felis concolor californicus* • Mountain Lion (Cougar, Puma)
Found in the Upper Sonoran and Transition life-zones mainly in forested or chaparral-covered mountains where deer *(Odocoileus)*, its chief food, are present. SDNHM specimens: Buckman Springs, Campo, Mesa Grande, Pine Valley, Smith (= Palomar) Mountain. Other specimens (MVZ): south base Los Pinos Mountain, Laguna Indian Reservation, Wynola. Also reported from the Cuyamaca Mountains (J. Grinnell, 1933: 114). According to Stephens (1921: 49), "Still occasionally found in San Diego County. I have never seen one alive out of a cage." At the present time, the California State Fish and Game Department estimates a county population of approximately 25.

• *Lynx rufus* • Bobcat (Wildcat)
The bobcat is found throughout the county from the desert to the coast. *L. r. baileyi* is found in the Lower Sonoran life-zone east of our mountains in brushy and rocky areas usually near springs. Specimens: Sentenac Canyon (SDNHM), Vallecito (MVZ). Paul Johnson, ranger at Anza Borrego Desert State Park, reported seeing them along the western region of the park. *L. r. californicus* is found west of the desert region most abundantly in the foothill chaparral. SDNHM specimens: Alpine, Cuyamaca State Park, Del Mar, Flynn Springs, Los Flores Mission, Otay, Paradise Valley, Pine Valley, Ramona, San Diego area, San Marcos, Santa Ysabel, Volcan Mountain, Witch Creek. Other specimens (MVZ): Campo, Foster (near Lakeside), Pine Mountain.



Bobcat



Bighorn

Order Artiodactyla

Family Cervidae (Deer and Allies)

• *Cervus elaphus* • Wapiti or American Elk
Introduced. Twelve elk of mixed Tule-Rocky Mountain stock were liberated in the Laguna Mountain area in 1919 (Dasmann, 1958: 21). They are no longer found in the county, the last report listed seven adults and one young in 1922 (Reddington, 1922: 191).

• *Odocoileus hemionus fuliginata* • Southern Mule Deer
Found in the Lower Sonoran to Transition life-zones, in chaparral to open forest areas. SDNHM specimens: Alpine, Descanso, Cuyamaca Mountains, Grapevine Spring, Laguna Mountains, and Smith (= Palomar) Mountain. Other specimens (MVZ): Barona Ranch, De Luz, San Mateo Valley: Colb Valley (Cowan, 1933: 327). According to George McCleary, Camp Pendleton Game Warden, there are approximately 3000 to 4000 mule deer on the base. Also reported at Torrey Pines State Reserve and Miramar NAS (R. Dingman, pers. obs.).

Family Antilocapridae (Pronghorns)

• *Antilocapra americana* • Pronghorn (American Antelope) — EXTINCT
This animal, unique to North America, was the first species of mammal to be recorded in California at San Diego Bay (Ferrel, 1879: 304). Stephens considered them practically extinct in 1921, although he saw four at Carrizo Creek "many years ago" (1921: 44). The last report was of a band of five near Campo in 1922 (Nelson, 1925: 27). There are no specimens from the county.

Family Bovidae (Cattle, Sheep and Allies)

• *Ovis canadensis* • Mountain Sheep (Bighorn)
This native sheep, also known as the Desert Bighorn, is found in the Lower and Upper Sonoran life-zones on open, rough, barren slopes of our desert region. According to Paul Johnson, Park Ranger at Anza Borrego Desert State Park, the present population numbers 300-400 and has remained constant for the past few years. SDNHM specimens: Borrego area, Carrizo Gorge, Split Mountain, Vallecito, and southeast county. These animals are probably referable to *O. c. cremnobates.* Specimens at MVZ from Julian have been referred to as *nelsoni,* although Cowan (1940: 567) considers them intermediate between the two.

LITERATURE CITED

ABBOTT, C. G., 1935. Bears in San Diego County, California. Journal of Mammalogy 16: 149-151.

ALLEN, G. M., 1942. Extinct and vanishing mammals of the Western Hemisphere with the marine species of all the oceans. American Committee for International Wild Life Protection, Special Publication 11. 620 p.

AUGUST, P.V. and R. E. DINGMAN, 1973. Two additional records of *Tadarida macrotis* and *Euderma maculatum* from San Diego, California. Southern California Academy of Sciences Bulletin 72: 165-166.

BAIRD, S. F., 1857. Reports of explorations and surveys to ascertain the most practicable and economical route for a railroad from the Mississippi River to the Pacific coast. Volume 8. Washington, D.C.

BANKS, R. C., 1964. The rodents of Anza-Borrego Desert State Park, San Diego County, California. A report to the California Division of Beaches and Parks. 61 p. (mimeograph).

BANKS, R. C., 1965. The bats of Anza-Borrego Desert State Park, San Diego County, California. A report to the California Division of Beaches and Parks. 30 p. (mimeograph).

BELL, H., 1930. On the old west coast. Being further reminiscences of a ranger. Grosset & Dunlap, New York. 336 p.

BOND, S. I., 1970. The status of the southern yellow bat in California. Southern California Academy of Sciences Bulletin 69: 115-117.

BRYANT, H. C., 1927. The opossum reaches San Diego County. California Fish and Game 13: 146.

COWAN, I. M., 1933. The mule deer of southern California and northern Lower California as a recognizable race. Journal of Mammalogy 14: 326-327.

COWAN, I. M., 1940. Distribution and variation in the native sheep of North America. American Midland Naturalist 24: 505-580.

DASMANN, W. P., 1958. Big game of California. State of California, Department of Fish and Game, Sacramento, California. 56 p.

DAUGHERTY, A. E., 1972. Marine mammals of California, State of California, Department of Fish and Game, Sacramento. 91 p.

DIXON, J., 1924. Notes on the life history of the gray shrew. Journal of Mammalogy 5: 1-6.

FERREL, B., 1879. Voyage of Cabrillo, p. 293-314. *In*, U.S. Geographical Surveys West of the hundredth meridian. Volume 7, Archaelogy.

GOLDMAN, E. A., 1910. Revision of the wood rats of the genus *Neotoma*. North American Fauna 31: 1-124.

GOLDMAN, E. A., 1932. Review of woodrats of *Neotoma lepida* group. Journal of Mammalogy 13: 59-67.

GRINNELL, H.W., 1918. A synopsis of the bats of California. University of California Publications in Zoology 17: 223-404.

GRINNELL, J., 1915. The Tennessee possum has arrived in California. California Fish and Game 1: 114-116.

GRINNELL, J., 1922. A geographical study of the kangaroo rats of California. University of California Publications in Zoology 24: 1-124.

GRINNELL, J., 1933. Review of the recent mammal fauna of California. University of California Publications in Zoology 40: 71-234.

GRINNELL, J., J. S. DIXON and J. M. LINSDALE, 1937. Fur-bearing mammals of California. University of California Press, Berkeley, 2 volumes.

GRINNELL, J. and R. T. ORR, 1934. Systematic review of the californicus group of the rodent genus *Peromyscus*. Journal of Mammalogy 15: 210-220.

HALL, E. R., 1926. A new subspecies of the California spotted skunk *(Spilogale phenax merriami)*. Journal of Mammalogy 7: 53-56.

HALL, E. R., 1951. American weasels. University of Kansas Publications, Museum of Natural History 4: 1-466.

HALL, E. R. and K. R. KELSON, 1952. Comments on the taxonomy and geographic distribution of some North American marsupials, insectivores and carnivores. University of Kansas Publications, Museum of Natural History 5: 319-341.

HALL, E. R. and K. R. KELSON, 1959. The mammals of North America. Ronald Press Company, New York. 2 Volumes.

HOLLISTER, N., 1914. A systematic account of the grasshopper mice. Proceedings of the United States National Museum 47: 427-490.

HOOPER, E. T., 1938. Geographical variation in woodrats of the species *Neotoma fuscipes*. University of California Publications in Zoology 42: 213-246.

HOWARD, W. E., 1953. Nutria *(Myocaster coypus)* in California. Journal of Mammalogy 34: 512-513.

HOWELL, A. H., 1929. Revision of the American chipmunks (genera *Tamias* and *Eutamias)*. North American Fauna 52: 1-157.

HOWELL, A. H., 1938. Revision of the North American ground squirrels, with a classification of the North American Sciuridae. North American Fauna 56: 1-256.

HUEY, L. M., 1932. The large-eared free-tailed bat in San Diego. Journal of Mammalogy 13: 160.

HUEY, L. M., 1939. The silky pocket mice of southern California and northern Lower California, Mexico, with the description of a new race. San Diego Society of Natural History Transactions 9: 47-54.

HUEY, L. M., 1954. Second record of *Tadarida molossa* from San Diego, California. Journal of Mammalogy 35: 435-436.

INGLES, L. G., 1965. Mammals of the Pacific states. Stanford University Press, Stanford. 506 p.

JACKSON, H.H.T., 1951. Classification of the races of the coyote, p. 227-341. *In* Young, S. P. and H.H.T. Jackson, The clever coyote. Stackpole Company, Harrisburg, Pennsylvania, and Wildlife Management Institute, Washington, D.C. 411 p.

JONES, J. K., Jr., D. C. CARTER and H. H. GENOWAYS, 1973. Checklist of North American mammals north of Mexico. Museum Texas Tech University Occasional Papers No. 12.

KELLOGG, R., 1918. A revision of the *Microtus californicus* group of meadow mice. University of California Publications in Zoology. 21: 1-42.

KRUTZSCH, P. H., 1944. Notes on the little-known pocketed bat. Journal of Mammalogy 25: 201.

KRUTZSCH, P. H., 1944. California lyre snake feeding on the pocketed bat. Journal of Mammalogy 25: 410.

KRUTZSCH, P. H., 1944. Fourth record of the pocketed bat in California. Journal of Mammalogy 25: 413-414.

KRUTZSCH, P. H., 1946. Some observations on the big brown bat in San Diego County, California. Journal of Mammalogy 27: 240-242.

KRUTZSCH, P. H., 1955. Observations on the Mexican free-tailed bat, *Tadarida mexicana.* Journal of Mammalogy 36: 236-242.

LACKEY, J. A., 1967. Biosystematics of *Heermanni* group kangaroo rats in southern California. San Diego Society of Natural History Transactions 14: 313-344.

LIDICKER, W. Z., Jr., 1960. An analysis of intrespecific variation in the kangaroo rat *Dipodomys merriami.* University of California Publication in Zoology 67: 125-218.

MILLER, A. H. and R. C. STEBBINS, 1964. The lives of desert animals in Joshua Tree National Monument. University of California Press, Berkeley and Los Angeles 452 p.

MILLER, G. S., Jr., 1897. Revision of the North American bats of the family Vespertilionidae. North American Fauna 13: 1-140.

MILLER, G. S., Jr. and G. M. ALLEN, 1928. The American bats of the genera *Myotis* and *Pizonyx.* United States National Museum Bulletin 144.

NELSON, E. W., 1909. The rabbits of North America. North American Fauna 29: 1-314.

NELSON, E. W., 1925. Status of the pronghorn antelope, 1922-1924. United States Department of Agriculture, Department Bulletin 1346.

OLSON, A. C., Jr., 1947. First record of *Cyoeronycteria mexicana* in California. Journal of Mammalogy 28: 183-184.

ORR, R. T., 1940. The rabbits of California. California Academy of Sciences Occasional Papers 19: 1-227.

ORR, R. T., 1954. Natural history of the pallid bat, *Antrozous pallidus.* California Academy of Sciences Proceedings 4th series, 28: 165-246.

OSGOOD, W. H., 1909. Revision of the mice of the American genus *Peromyscus.* North American Fauna 28: 1-285.

PALMER, F. G., 1937. Geographic variation in the mole *Scapanus latimanus.* Journal of Mammalogy 18: 280-314.

PATTON, J. L. and R. E. DINGMAN, 1968. Chromosome studies of pocket gophers, genus *Thomomys.* I. The specific status of *Thomomys umbrinus* (Richardson) in Arizona. Journal of Mammalogy 49: 1-13.

REDDINGTON, P. G., 1922. Elk increase on Cleveland National Forest. California Fish and Game 8: 191.

SHAMEL, H. H., 1931. Notes on the American bats of the genus *Tadarida.* United States National Museum Bulletin 78: 1-27.

STEPHENS, F., 1906. California mammals. West Coast Publication Company, San Diego 351 p.

STEPHENS, F., 1921. An annotated list of the mammals of San Diego County, California. San Diego Society of Natural History Transactions 3: 41-56.

STORER, T. I. and L. P. TEVIS, Jr., 1955. California grizzly. University of California Press, Berkeley and Los Angeles 335 p.

VON BLOEKER, J. C., Jr., 1932. New locality records for *Perognathus baileyi* from California, Journal of Mammalogy 13: 279-280.

VON BLOEKER, J. C., Jr., 1932. A new race of *Perognathus longimembris* from southern California. Biological Society of Washington Proceedings 45: 127-129.

Department of Birds and Mammals, Natural History Museum, Box 1390, San Diego, CA 92112

SANDSTONES CEMENTED BY A RELICT PHYLLOSILICATE, SAN DIEGO, CALIFORNIA

Brian M. Smith, Richard G. Berggreen and
Patrick L. Abbott

TRANSACTIONS
OF THE SAN DIEGO
SOCIETY OF
NATURAL HISTORY

VOL. 18, NO. 15 3 JUNE 1977

Sandstones cemented by a relict phyllosilicate, San Diego, California

Brian M. Smith, Richard G. Berggreen and Patrick L. Abbott

ABSTRACT.—Eocene and Pleistocene paralic sandstones in the northern San Diego area are colored reddish and yellowish brown by a cement that has been assumed to be iron oxide. However, microscopic examination of the cement suggests it may be an iron-rich phyllosilicate similar to glauconite or nontronite. Although the optical properties are good, the cement appears amorphous to x-rays. This seeming paradox may be due to the changed diagenetic conditions to which the rocks have been exposed. The cement apparently grew as a ferrous iron-rich phyllosilicate mineral under reducing conditions. Later diagenesis under oxidizing conditions changed the iron to the ferric state which destroyed the crystallinity of the cement. Advanced diagenesis has created some blebs of iron oxide.

In the Del Mar and northern part of the La Jolla 7.5′ quadrangles the most common sedimentary units are of Eocene age overlain by strata of Pleistocene age (Kennedy, 1975). The Eocene sandstones are weakly bound by a dull reddish to yellowish-brown cement that generally has been assumed to be iron oxides and has been described as such (e.g. Kennedy, 1975; Kennedy and Peterson, 1975). This cement is abundant enough in the Torrey Sandstone to form large cannonball concretions that are prominently exposed in Torrey Pines State Park (Fig. 1). Petrographically the presumed iron-oxide cement is a pore-filling, translucent material of micaceous habit that occurs both perpendicular and parallel to the framework grains. The many questions that arose as to the mineralogy of the cement and the conditions under which it formed prompted this study.

LOCATION OF DETAILED STUDY AREA

Three areas were selected where samples for detailed analyses were collected (Fig. 2). One area is the roadcut along old U.S. 101 near Torrey Pines State Beach (Fig. 3); samples were taken from the barrier bar and associated sands of the Middle Eocene Torrey Sandstone, a concretion within the Torrey SS., and the sediment fill of a canyon incised through the Torrey SS. In the second sample area, friable beach and nearshore marine sands of the Pleistocene Lindavista Fm. were collected from the southern roadcut at the crest of Ardath Road where it crosses the northern end of Mt. Soledad. Deep red, older Pleistocene sands of the Lindavista Fm. were taken from the third area, an elevated beach ridge exposed in the northern roadcut along Clairemont Mesa Boulevard just west of Murphy Canyon Road.

PETROGRAPHY AND PROVENANCE OF SANDSTONES

All sand grains apparently were derived from the Peninsular Ranges province to the east. The short distance of transport and the high relief in the source area combined to produce mineralogically-immature sands. Depositional environments contained enough energy to winnow away fine sediment and leave sands that generally were moderately sorted. The chemical and mineralogical composition of the cement is probably closely related to the types of grains deposited to form the sandstones. Thus, an understanding of the origin of the cement is dependent on a fairly detailed knowledge of the original framework mineralogy of each stratigraphic unit.

SAN DIEGO SOC. NAT. HIST., TRANS. 18(15): 249-258, 3 JUNE 1977

Figure 1. Dark, spherical concretion in Middle Eocene Torrey SS., Torrey Pines State Park.

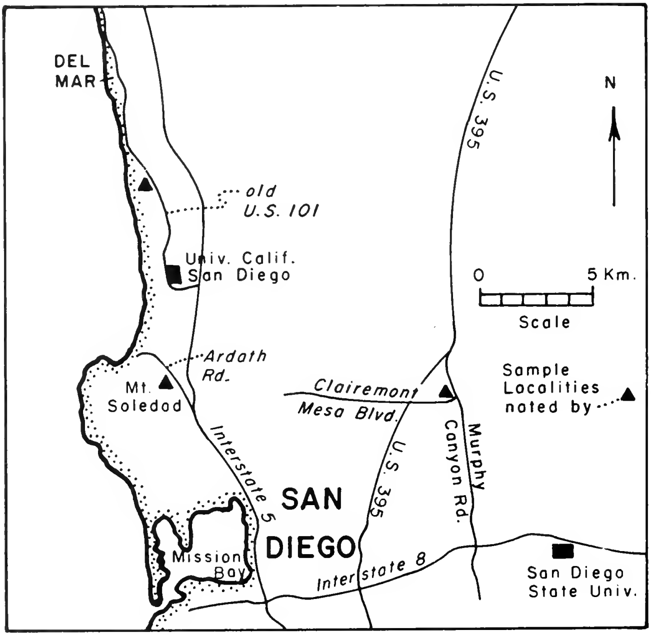


Figure 2. Index map.

Any sandstone is comprised architecturally of framework grains (F), matrix (M), cement (C) and porosity (P); FMCP must total 100%. The framework mineralogy is dominated by quartz (Q), plagioclase (P), potassium feldspar (K) and rock fragments (R); QPKR is arbitrarily made to total 100% for clan description purposes. The mineralogic clan names are derived from the classification of Folk, Andrews, and Lewis (1970).

TORREY SANDSTONE

Two samples from the same bed were described in detail during point counts. One specimen was taken from the concretion shown in Figure 1 (also recognizable in Fig. 3) and the other was taken from the same sedimentation unit about 5m to the south.

The architecture of the non-concretionary sample is $F_{75}M_0C_8P_{17}$ and the dominant framework components are $Q_{31}P_{21}K_{20}R_{28}$. The specimen from the concretion is comprised of $F_{66}M_0C_7P_{27}$ and the main framework constituents are $Q_{33}P_{11}K_{26}R_{30}$. Because the microcrystalline to medium crystalline platy cement is easily crumbled, it is probable that some was plucked from each specimen during thin-section preparation. Thus, the porosity is overestimated and the percentage of cement underestimated, particularly in the sample from the concretion.

Both specimens are described as plutonic lithic felsarenite: moderately sorted, angular, slightly granular coarse sandstone. The provenance of the quartz grains appears to have been the Peninsular Ranges; the dominant types are common (plutonic) quartz with some metamorphic and vein quartz but no volcanic quartz was recognized. Plagioclase ranges from An_{17} to An_{35} and is commonly zoned. Feldspar grains are mostly fresh, plagioclase less so than potassium feldspar, but some are moderately to heavily sericitized. Rock fragments all appear to have

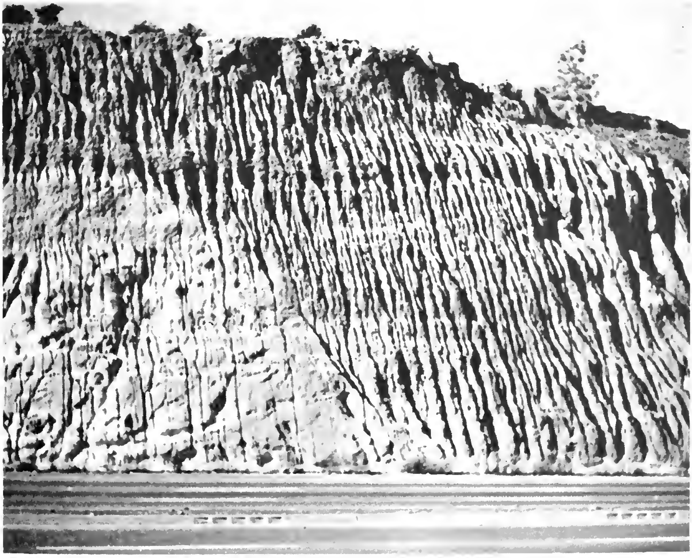


Figure 3. Torrey SS. (towards left) is cut by a large, filled channel (upper portion of left valley wall is shown). Valley fill has been distinctly rilled by runoff water. Concretion pictured in Figure 1 is visible in lower left corner.

been derived from Peninsular Ranges source rocks; they are 70% plutonic, 15% metamorphic and 15% basic volcanic rock fragments. The absence of matrix and the degree of sorting of framework grains are consistent with a postulated barrier bar-associated depositional environment. The unimodal angularity of framework grains, regardless of composition, along with the unimodal plot of grain elongation, indicate that no sedimentary rocks existed in the source area. Coarse grains appear to be as angular as fine grains, suggesting that deposition occurred near the source terrane.

Minor framework constituents include biotite, brown and green hornblende, muscovite, magnetite, sphene and pistacite. Biotite is the most abundant and forms up to 3% of the framework. Biotite commonly exhibits moderate to strong alteration, local expansion, and, in some instances, appears to have been molded around framework grains during diagenesis. Some biotite grains have drusy coats of iron oxide, bleached color, or textures transitional to the cement.

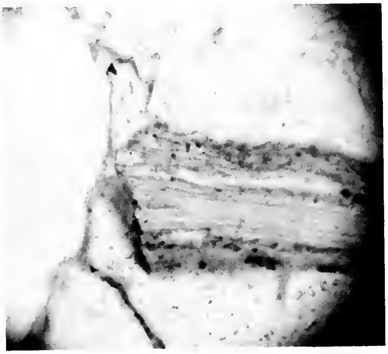
Hornblende is unaltered to moderately altered in the concretion but is conspicuously absent in the non-concretionary sample. This may be due to diagenetic dissolution of hornblende in the sandstone and transport of the constituent ions into the area of concretion growth.

TROUGH FILL

Two samples from the trough fill shown in Figure 3 were examined. The average architecture of the sandstones is $F_{62}M_0C_{16}P_{22}$ and the main framework components are $Q_{26}P_{19}K_9R_{46}$. Both samples are feldspathic plutonic litharenite: moderately sorted, subangular to angular, bimodal fine and coarse sandstone. The architecture and major framework-grain types are very similar to the Torrey SS. Main differences are the higher proportion of rock fragments and the addition of a fine sand mode to a dominantly coarse sandstone.

Biotite forms 1 to 2% of the framework. It varies from slightly to severely altered, may be expanded, and shows textures transitional to the cement. Authigenic magnetite occurs as euhedral cubes in biotite cleavages.

4



5

Figure 4. Photomicrograph of Pleistocene Lindavista Fm. sample from Ardath Road locality (magnification 10x). Specimen is a moderately sorted, subangular, medium sandstone with dark cement partially filling the pores.

Figure 5. Photomicrograph of Eocene Torrey SS. concretion sample from old U.S. 101 locality (magnification 120x). Notice the biotite grain is fresh toward the center, expanded toward its upper contact, and severely altered near its lower contact.

Hornblende comprises almost 1% of the framework and varies from virtually unaltered grains to grains with severely altered rims and only slightly altered cores. Pistacite is severely altered and coated with iron oxides.

LINDAVISTA FORMATION

An older Lindavista sandstone sample from the Clairemont Mesa Boulevard roadcut and a younger specimen from the Ardath Road locality were examined. The Clairemont Mesa Blvd. sample is constructed as $F_{61}M_0C_{28}P_{11}$ and the major framework components are $Q_{53}P_{31}K_7R_9$. The rock is a plagioclase felsarenite: well sorted, angular, medium sandstone. The Ardath Road specimen is constituted as $F_{68}M_0C_{20}P_{12}$ and the most abundant framework grains are $Q_{48}P_{18}K_7R_{27}$. It is a feldspathic plutonic litharenite: moderately sorted, subangular, medium sandstone (Fig. 4). The samples are comprised of Peninsular Ranges detritus and are similar despite their differences in plagioclase and rock fragment content which place them in different mineralogic clans.

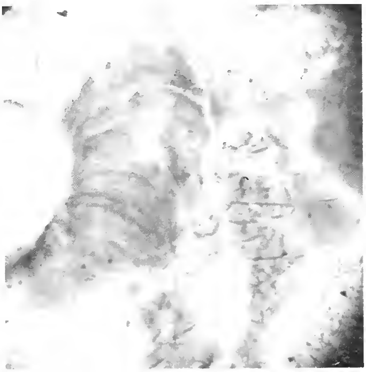
The same suite of minor framework grains is present in the Lindavista Fm. Biotite comprises about 1% of the framework; it is moderately to strongly altered and expanded in both localities (Fig. 5). Hornblende forms 7% of the framework in the Ardath Road specimen; grains are moderately to completely altered. Trace amounts of pistacite, sphene, zircon and garnet are present.

DESCRIPTION OF CEMENT

In our analyses of the cement we employed petrographic microscopy, scanning electron microscopy, x-ray diffraction and x-ray fluorescence.

DATA FROM MICROSCOPE ANALYSES

Examination of the cement in thin section reveals that an orangish material of micaceous habit has grown both perpendicular and parallel to framework grains (Figs. 6, 7). The cement is commonly translucent and homogeneous and has a biaxial negative interference figure, weak pleochroism, a variable 2V angle $\leq 20°$,


6


7

Figure 6. Photomicrograph of Pleistocene Lindavista Fm. sample from Ardath Road locality (magnification 120x). Phyllosilicate cement has grown in pore perpendicular to framework grains.

Figure 7. Photomicrograph of Pleistocene Lindavista Fm. sample from Clairemont Mesa Boulevard locality (magnification 50x). Phyllosilicate cement fills pores with growth habit both parallel and perpendicular to framework grains.

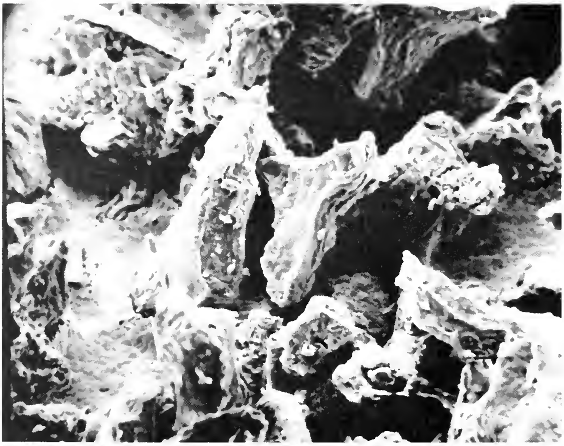


Figure 8. Scanning electron photomicrograph of concentrated cement material from Pleistocene Lindavista Fm., Ardath Road locality (magnification 170x). Cement is platy with apparent cleavages.

and birefringence less than 0.05. Medial sutures exist where the cement has grown with its cleavage perpendicular to framework grains and has met near the middle of former pores. The micaceous nature of the cement is clearly indicated during rotation under crossed nicols by the sweeping extinction pattern of bundles of subparallel plates. Locally, the cement is zoned due to variable amounts of iron incorporated within the structure. The iron can be abundant enough to form iron oxide blebs within the cement.

The optical properties of individual patches of cement also were studied under the petrographic microscope. Sandstone samples were disaggregated, sieved to remove coarser framework grains, and concentrated to 95-98% cement particles with the Frantz magnetic separator. The cement material is somewhat platy and there appears to be a cleavage or parting between these plates. A scanning electron photomicrograph (Fig. 8) shows the parting within the cement. The extinction angle with this parting varies from parallel to about 10°.

The cement plates show patchy first order interference colors but they are masked by the strong orange color of the cement. Indices of refraction were measured with immersion oils by using both white light and D sodium monochromatic light. Resultant values are $x = 1.544$, $y = 1.562$ and $z = 1.564$; all values are $\pm$ 0.002. These indices and the interference figure indicate that the material is biaxial negative; the curve of the isogyres suggests a 2V angle of about 20°. The y-z plane of the indicatrix is generally parallel to the cleavage or parting and x is normal to it; thus the cleavage is length slow.

Much of the cement appears to have very small, high relief, dark blebs on the surface. When treated to remove iron oxide coatings with the dithionite citrate bicarbonate (DCB) method of Mehra and Jackson (1960), these dark blebs disappeared. The remaining cement had a grayish-green color as the treatment appeared to reduce the iron in the cement. Indices of refraction for the reduced material were somewhat lower than those for the untreated orangish cement. Indices for the treated material are $x < 1.540$ and y and z both ≤ 1.556. Birefringence was not affected by the treatment.

DATA FROM X-RAY ANALYSES

Analyses of cement samples on the x-ray diffractometer yielded no distinct or consistent peaks for scans from 2° to 40+° two theta. The lack of a diffraction pattern is surprising because of the distinct and consistent optical properties of the cement. In attempts to get an x-ray diffraction pattern, analyses were run on unground and fine-ground (-200 mesh) powders, on fine-ground smears dried onto glass slides, on flocculated and deflocculated samples, on samples glycolated with ethylene glycol and heated to 350°C. and 500°C. and on samples with iron oxide coatings removed by the aforementioned DCB treatment. Yet no consistent diffraction peaks were noted. Laue photographs of coarse particles of cement also failed to show any consistent internal structure.

X-ray fluorescence analyses were performed on the Ardath Road (Ard) and Clairemont Mesa Boulevard (Claire) samples of the Lindavista Fm. using both untreated and iron oxide-removed material. Analyses were run for silicon, aluminum, iron, potassium, sodium and calcium. One sample from the Ardath Road locality showed a distinct chlorine peak which suggest some sea salt accumulation. No other significant peaks from any element were noted. Machine counts for each element, and their ratio to silicon abundance, are listed in Table 1. Ratio averages

TABLE 1. X-ray fluorescence data from Lindavista Formation cement (Machine Counts x 1000/$\frac{\text{Silicon}}{x}$ Ratio)

Sample	Ard (particle)	Ard (particle)	Ard (large area)	Ard (treated)	Ard (treated)
Si	214 / 1.0	669 / 1.0	19 / 1.0	523 / 1.0	392 / 1.0
Al	108 / 2.0	324 / 2.1	17 / 1.1	261 / 2.0	195 / 2.0
Fe	95 / 2.2	103 / 6.5	2.9 / 6.7	101 / 5.1	96 / 4.1
K	9.3 / 23	16 / 41	0 / —	13 / 39	10 / 39
Na	0.9 / 231	18 / 38	0.4 / 52	9 / 56	6 / 59
Ca	2.4 / 89	2.4 / 279	1.7 / 11	7 / 67	9 / 43
	Claire (particle)	**Claire (large area)**	**Claire (large area)**	**Claire (treated)**	**Claire (treated)**
Si	775 / 1.0	210 / 1.0	147 / 1.0	512 / 1.0	198 / 1.0
Al	224 / 3.2	66 / 3.1	40 / 3.6	153 / 3.3	66 / 3.0
Fe	109 / 7.0	53 / 3.9	26 / 5.5	102 / 5.0	48 / 4.1
K	12 / 63	2 / 86	2.4 / 60	8 / 67	3.9 / 69
Na	0 / —	0 / —	0.4 / 343	5 / 105	0.5 / 355
Ca	5 / 150	3 / 71	2.6 / 55	0 / —	0.3 / 730

for each sample (silicon/other element) are given in Table 2. The lack of comparable standards precluded conversion of the machine-count data into quantitative percentages.

TABLE 2. Element ratio averages from Lindavista Formation cement (Counts of Silicon/Counts of other Element)

	Ard*	Ard (treated)	Claire	Claire (treated)
Si	1.0	1.0	1.0	1.0
Al	2.0	2.0	3.3	3.1
Fe	4.4	4.6	5.5	4.5
K	32	39	66	68
Na	134	73	343	230
Ca	184	50	138	730

*Average excludes Ard (large area) analysis.

The iron content did not appear to decrease significantly in the samples treated to remove iron-oxide coatings. In fact, the Si/Fe ratio decreased in one of the treated samples. Variation between different runs on the same sample ranged as much as the variation between different samples. Additionally, the zoning within the cement observed under the microscope was produced by differing iron concentrations. These observed variations in iron content also could be responsible for the variations in count data.

MINERALOGY OF CEMENT

Why does an x-ray amorphous material have good optical properties? It cannot just be biotite which has been so badly altered as to lose its crystallinity because some textures indicate pore-filling cement has grown outward from unaltered framework grains (Figs. 6, 7). The cement, or at least some of it, must have had good crystallinity in order to have a biaxial negative interference figure, small 2V, micaceous habit, birefringence and x, y, z directions.

The cement mineral has apparently de-crystallized. The loss of crystallinity may have accompanied the formation of the iron oxide and could be due to oxidation of a phyllosilicate mineral containing some ferrous iron. Oxidation of ferrous iron to ferric would leave a charge imbalance that could be rectified by ejection of some iron from the structure or ejection of water made from hydroxyl. Either process would modify the mineral structure and the former mechanism would also provide iron for the iron-oxide coatings and blebs. The phyllosilicate was evidently magnesium poor and iron rich; it was probably an illite or smectite with affinities toward glauconite or nontronite.

ORIGIN OF CEMENT

The phyllosilicate cement grew in matrix-free, moderately sorted, paralic sandstones comprised dominantly of mineralogically-immature detritus from the southern California batholith with lesser contributions from the pre-batholithic Santiago Peak Volcanics and Julian Schist. Petrographic evidence suggests that the alteration of iron-rich, alumino-silicate framework minerals provided the ions for the growth of the phyllosilicate cement. Particularly abundant source minerals in the batholith are biotite and amphibole (Larsen, 1948). For example, the Bonsall tonalite covers 38% of Larsen's batholith study area and averages 18% biotite and 13% amphibole. The Green Valley tonalite covers 8% of the area and averages about 8% biotite and 8% amphibole. The Woodson Mountain granodiorite covers 25% of the area and averages 5% biotite and 1% amphibole.

In the Eocene and Pleistocene sandstones, biotite and amphibole are the most common framework grains after quartz; feldspar and rock fragments. Biotite in thin sections ranges from virtually unaltered grains to relict textures visible in the phyllosilicate cement. Amphiboles are commonly altered and extensively etched although fresh grains are present. This continuum of alteration suggests that indeterminable amounts of biotite and amphibole may have been totally cannibalized to create the cement.

The presence of iron-oxide blebs in the cement and as coatings on the relict phyllosilicate suggests that the iron oxide is formed after prolonged diagenesis has acted upon the cement. This diagenetic sequence is similar to one reported by Walker, Ribbe and Honea (1967). They found that hornblende in Pliocene red beds had altered to iron-rich montmorillonite, which was the source of iron for the later production of hematite.

Apparently, the cement formed as a ferrous iron-rich phyllosilicate mineral under reducing conditions during early diagenesis. During later diagenesis the cement was altered by oxidizing conditions that may have destroyed the crystallinity during transformation of the iron to the ferric state. The amount and kind of cement growth in the Eocene and Pleistocene sandstones of San Diego are quite similar, which suggests a recency to the diagenesis. The Lindavista Fm. formed as beach ridges and associated beds on a platform undergoing tectonic upwarp. Thus its diagenetic environment must have been primarily under the influence of surface processes. The most advanced diagenesis is indicated by the greatest development of later-stage, iron-oxide coatings. This does not occur in the Eocene beds but in the near-surface exposures of the older deposits of the Pleistocene Lindavista Fm. (Clairemont Mesa Boulevard locality).

ACKNOWLEDGEMENTS

We thank Richard W. Berry for his help during the study and his review of the manuscript, Ellis E. Roberts and Thomas E. Moore for their advice, and Enos J. Strawn for drafting the figure.

LITERATURE CITED

Folk, R. L., P. B. Andrews, and D. W. Lewis, 1970. Detrital sedimentary rock classification and nomenclature for use in New Zealand. New Zealand Journal Geology Geophysics 13: 937-968

Kennedy, M. P., 1975. Geology of the San Diego metropolitan area, section A — western San Diego. California Division Mines and Geology Bulletin 200: 9-39.

Kennedy, M. P. and G. L. Peterson, 1975. Geology of the San Diego metropolitan area, section B — eastern San Diego. California Division Mines and Geology Bulletin 200: 43-56.

Larsen, E. S., Jr., 1948. Batholith and associated rocks of Corona, Elsinore, and San Luis Rey quadrangles, southern California. Geological Society America Memoir 29: 1-182.

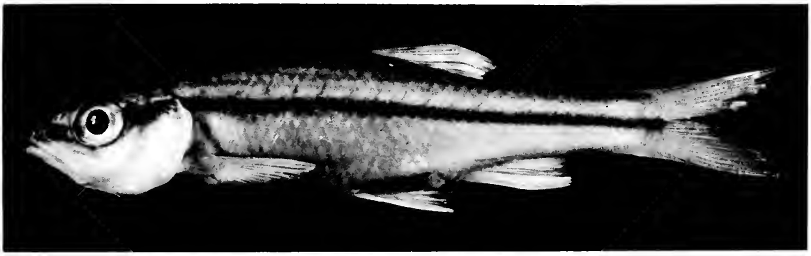
Mehra, O. P. and M. L. Jackson, 1960. Iron oxide removal from soils and clays by a dithionite-citrate system buffered with sodium bicarbonate. *In*, Swineford, A. (ed.), Clays and Clay Minerals, Proc. 7th National Conference on Clays and Clay Minerals. Pergamon Press.

Walker, T. R., P. H. Ribbe and R. M. Honea, 1967. Geochemistry of hornblende alteration in Pliocene red beds, Baja California, Mexico. Geological Society America Bulletin 78: 1055-1060.

Department of Geological Sciences, Brown University, Providence, RI 02912; Woodward-Clyde Consultants, Orange, CA 92668; and Department of Geological Sciences, San Diego State University, San Diego, CA 92182

DIONDA MANDIBULARIS, A NEW CYPRINID FISH ENDEMIC TO THE UPPER RIO VERDE, SAN LUIS POTOSI, MEXICO, WITH COMMENTS ON RELATED SPECIES

Salvador Contreras-Balderas and
Jorge Verduzco-Martínez



TRANSACTIONS

OF THE SAN DIEGO
SOCIETY OF
NATURAL HISTORY

VOL. 18, NO. 16 27 JULY 1977

Dionda mandibularis, a new cyprinid fish endemic to the Upper Río Verde, San Luis Potosí, México, with comments on related species

Salvador Contreras-Balderas and
Jorge Verduzco-Martínez

ABSTRACT.—*Dionda mandibularis,* n. sp., is described from localities in the Upper Rıo Verde, State of San Luis Potosí, México, on the basis of its double S-shaped intestine, longer than the standard length; pharyngeal teeth 4—4; 37—44 lateral-line scales, and 18—23 predorsal scales; 8 or 9 dorsal and usually 8 (7—10) anal rays. Particularly diagnostic is the shape of the mandible, with its lower surface flat and strongly angular in respect to its rami; the lower lip surpasses the upper by a distance nearly equal to its own thickness. This species adds a new element of Nearctic affinities to the interesting endemic fauna of the Río Verde, and to the Panuco-Tamesí system.

RESUMEN.—*Dionda mandibularis,* n. sp., se describe como nueva de localidades del Alto Río Verde, Estado de San Luis Potosí, México, sobre la base de presentar un intestino en doble S, mayor que la longitud patrón; dientes faríngeos 4—4; 37—44 escamas en la línea lateral y 18—23 predorsales; 8 a 9 radios dorsales y generalmente 8 (7—10) anales; particularmente diagnóstica es la configuración de la mandíbula, cuya superficie inferior es plana, y fuertemente angulosa respecto a las rami mandibulares; el labio inferior sobresale del labio superior por una distancia aproximadamente igual a su propio grosor. Esta especie agrega un nuevo elemento endémico de afinidades néarticas, que se agrega a la peculiar fauna de peces de la región del Río Verde Alto, y al systema Pánuco-Tamesí.

The region of La Media Luna, 7 km south of the town of Ríoverde, in the State of San Luis Potosí, México, was explored by the authors and a group of students of the Universidad Autónoma de Nuevo León, in July, 1968. They obtained samples of the interesting endemic fishes of the basin, which is part of the Río Pánuco drainage. Study of these specimens revealed some novelties of Nearctic affinities, one of which, the subject of the present paper, represents a new species referred to the cyprinid genus *Dionda.*

Dionda mandibularis, n. sp.

Material.—HOLOTYPE: Universidad Nacional Autonoma de México (Instituto de Biología) Fish Collection No. P 436; male; 43.7 mm in standard length; from a creek 7 km SSE of town of Ríoverde, San Luis Potosí, México; 14 July 1968; Salvador Contreras *et al.* coll. PARATYPES: Universidad Autónoma de Nuevo León Fish Collection No. 1032 (13; 30.8-47.5 mm); same data as holotype (2 now at Instituto Politécnico Nacional No. P 3679; 2 at Tulane University No. 94115). UANL 1320 (11; 32. 0-48.2); same locality; 15 July 1968, same coll. University of Michigan Museum of Zoology 193474 (11; 31.9-52.1 mm); from a spring-fed marsh on east side of road to Pedro Montoya, 9.7 km S of Ríoverde; 9 December 1972; R. R. and F. H. Miller and N. A. Neff coll. NON-TYPE MATERIAL: UMMZ 196339 (33; 42-58 mm); Puerto del Río, near Cerritos, San Luis Potosí; 5 February 1974; R. R., G. H., and F. H. Miller coll. UMMZ 196703 (6; 38-49 mm); same locality as UMMZ 193474; 21 March 1974, R. R. and F. H. Miller coll.

Diagnosis.—A species of *Dionda* with a double-S intestine longer than the standard length. The lower jaw is prognathous, with a flat mental-gular area that is strongly and abruptly angular to the lower margin of the head farther back, yielding a characteristic profile. Lateral-line scales 37-44; predorsal scales 18-23; dorsal rays 8-9, anal rays 8 (extremes 7-10).

Description.—The general physiognomy of the new species is that of an emaciated fish, like the "consumption" familiar to aquarists. However, after much consideration, we have concluded that it is the normal appearance of the species, and a distinctive trait (Fig. 1).

SAN DIEGO SOC. NAT. HIST., TRANS. 18(16):259-266, 27 JULY 1977

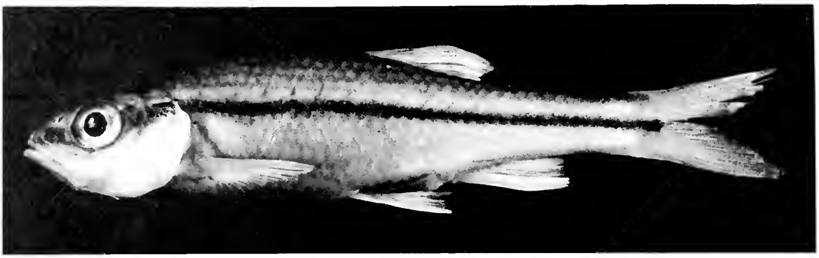


Figure 1. *Dionda mandibularis*, n. sp.: holotype, a male 43.7 mm SL, Universidad Nacional Autonóma de México (Instituto de Biología) Fish Collection No. P 436, collected in a creek 7 km SSE of Ríoverde, San Luis Potosí, México, on 14 July, 1968, by Salvador Contreras *et al.*

The body is moderately robust and slightly compressed. The caudal peduncle is slender. The dorsal profile is markedly convex, whereas the ventral profile is rather flattened. The conical head is subequal in width and height. The snout is convex. The mouth is terminal; the upper lip overhangs the lower by a distance about equal to its transverse width. The lower jaw is flat on the chin-gular surface, a condition easily observed in lateral view. The mandibular rami form a strong angle with the subhorizontal lower margin of the median portion of the head. The lateral line is complete on the anterior half of the body; it is slightly decurved, but on the posterior half it is almost straight, along the lateral band. The dorsal fin originates nearer the caudal base than the snout, over or slightly behind the insertion of the pelvics. The anal fin originates slightly behind the vertical from the end of the dorsal-fin base. In comparison with other species of the genus, all fins are relatively short.

The gut forms a double-S (Fig. 2 C), that derives from an entire twist of the original single loop typical of *Notropis*, in a counterclockwise direction. Peritoneum is black. The slightly oval scales have few apical radii; their exposed fields are usually 1.5 times higher than long, except on the anterolateral parts of the body, where they may be only slightly higher.

The head length measures 3.2–3.7 and the body depth 3.5–4.8 in the standard length. The caudal-peduncle length is 2.0–2.3 times its depth. The depressed dorsal-fin length measures 2.3–2.7 in the predorsal length. The depressed anal-fin length equals the pectoral-fin height. The eye diameter is somewhat less than either the snout length or the interorbital width (which are almost equal, and slightly less than the caudal-peduncle depth). The pectoral-fin tip fails to reach the pelvic-fin origin by a distance slightly less than the eye diameter in males, but longer than the eye in females. The pelvic fin in males reaches the anal origin and in females does not extend back of the anus. The anterior rays are notably longer than the posterior ones in the depressed dorsal fin, but scarcely so in the depressed anal.

Morphometrics and Meristics.—Measurements (Table 1) and counts (Table 2) were taken according to the methods standardized by Hubbs and Lagler (1958, 1964), on the holotype (values underlined in Table 2) and on 30 paratypes.

Nuptial Tubercles.—The tubercles of adult males are small and numerous, although the available material may not present their highest development. These tubercles are distributed in a V-shaped band over the top of the head, with the vertex anteriad, and the rami above the eyes. The band may be continuous over the snout, and between the nostril and the lip, with the lateral bands that occur below the eyes, from the nasal area to the interopercle, with some tubercles on the extreme lower part of the opercle and subopercle. On the body are some

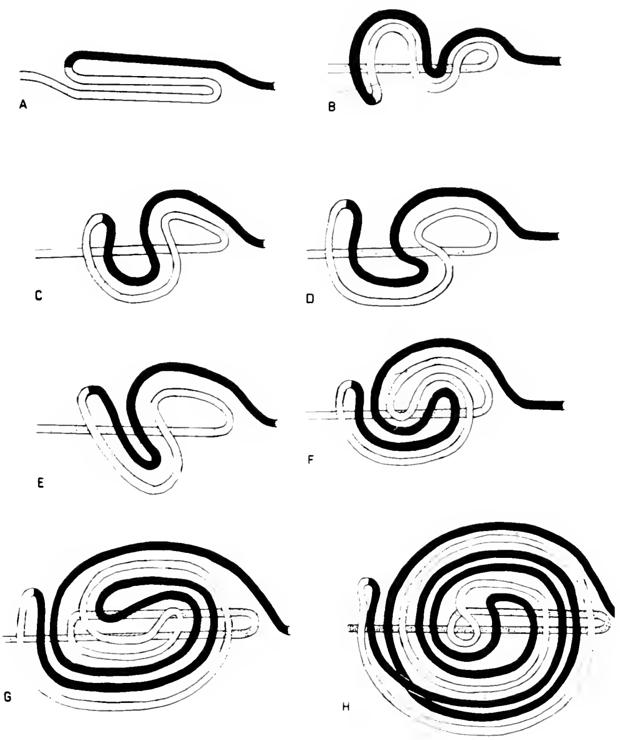


Figure 2. Intestines of several cyprinid fishes: (A) *Notropis* spp., standard type; (B) *Notropis mekistocholas*, modified from Snelson, 1971; (C) *Dionda mandibularis* n. sp., paratype, 35.5 mm SL; (D) *Dionda* sp., 40.7 mm SL, from near Ríoverde, San Luis Potosí; (E) *Dionda erimyzonops*, 28.9 mm SL, from the Río Tamesí, Tamaulipas; (F) *Dionda ipni*, 26.8 mm SL, from Río Pánuco, San Luis Potosí; (G) *Dionda diaboli*, 38.8 mm SL, from Río Salado, Coahuila; (H) *Dionda episcopa*, 30.7 mm SL, from Río San Juan, Nuevo León. All from México. The circulation of the gut contents is from left to right.

tubercles, smaller on the anterodorsal region, and little developed on the lower sides of the caudal peduncle.

Sexual Dimorphism.—As is common in cyprinids, the fins of *Dionda mandibularis* are usually longer in males than in females; the pelvics commonly reach the anal origin and the anus, respectively.

Coloration.—In life, the body is cream-colored, with a black lateral band that becomes wider and more diffuse toward the head. It is much the more strongly marked posteriorly, and terminally forms a basicaudal spot, which is slightly or not at all separated from the band, and does not invade the caudal fin. The dorsal half of the body is marked by two other longitudinal areas: the uppermost is dark green, with the centers of each exposed field on the scales lighter; the lower and lighter area intervenes between the dorsal and lateral bands, and is transgressed by small dark streaks that extend posterodorsad from the lateral band. The venter is light cream, with the black peritoneum noticeable. The head is dark green above, and is silvery below a line that extends from the middle of the upper lip, along the lower part of the orbit, and to the insertion of the opercle; it joins

TABLE 1. Morphometry of *Dionda mandibularis,* from the Upper Río Verde, San Luis Potosí, México, in thousandths of the standard length.

	Holotype	Paratypes	
	UNAM P 436	UANL 1032 & 1320 (19)	UMMZ 193474 (8)
Standard length (mm)	43.7	30.8 . . . 48.2	31.9 . . . 52.1
Predorsal length	568	532 (560.2) 576	551 (562.3) 570
Prepelvic length	529	511 (521.0) 540	515 (525.6) 539
Body depth	266	239 (260.3) 292	227 (253.9) 286
Head length	273	279 (291.3) 310	288 (293.8) 301
Snout length	88	87 (96.8) 114	83 (91.6) 100
Eye diameter	81	79 (87.2) 93	84 (92.4) 99
Interorbital width	92	88 (99.0) 112	89 (92.9) 100
Postorbital length of head	113	114 (120.5) 127	114 (122.4) 132
Caudal-peduncle length	219	198 (216.9) 231	208 (221.8) 233
Caudal-peduncle depth	99	99 (106.8) 116	87 (101.9) 112
Depressed dorsal fin	231	203 (233.4) 259	205 (232.6) 246
Depressed anal fin	194	184 (201.6) 219	182 (201.4) 224
Pectoral fin length	203	185 (201.3) 217	177 (204.4) 223
Pelvic fin length	173	166 (177.0) 197	163 (176.3) 195

the light venter. The basal two-thirds of the fins are yellowish; the dorsal is darkish on its distal third, with a whitish border; the other fins are more or less milky on the distal third, except the caudal, which has little dark pigment.

In alcohol, the scale pockets are finely marked, except along the venter. The lateral band starts on the snout, where its width almost equals that of the pupil; it almost disappears on the eye, to reappear behind, extending through the opercular region. On the body it is almost straight, and is about, or slightly more than, half as wide as the pupil. The dorsal and ventral parts are as described in life. The small streaks of the light dorsolateral band are fine, branched, and formed by deep melanophores. The opercle is silvery. The fins, particularly in the creek population, have relatively few melanophores. Melanophores line the dorsal rays, and occur on the lower half of the interradial membranes, increasing toward the last rays and the point of branching. The anal fin has some pigment along the rays. The first pectoral ray and sometimes the second are also so lined, as are the pelvic rays, but the pectorals are darker near the middle of the length of the rays. The caudal rays, especially the marginals and the 2 to 4 central rays, are also lined.

Etymology.—The name *mandibularis,* derived from *mandibula* (mandible) and the adjectival ending *-aris,* is uniquely applicable to this species; it was suggested by Dr. Carl L. Hubbs.

Ecology.—The water at the type locality at the time of collecting was clear and colorless, and the current was moderate to strong. The sides and bottom were hard, with almost vertical walls, and there was little sand and gravel on the bottom, except in frequent side bays that were shallow and had a deep cover of fine silt. The main channel was so regular, almost straight, 1.2 m wide and 0.9 m deep, as to suggest a rectification of a natural channel. Vegetation was reduced to sparse algae. The water temperature varied from 27° to 29° C. The adults were collected in the main current and the young in the small embayments.

Species associated with *Dionda mandibularis* were a form of *Astyanax mexicanus, Dionda* sp. (Hubbs and Miller, 1977), *Cualac tessellatus* Miller, *Ataeniobius toweri* (Meek), *Cichlasoma bartoni* (Bean), and *C. labridens* Pellegrin. If the *Astyanax* proves to be new, all these species would appear to be endemic either to the Laguna de la Media Luna system, or to this system and the Upper Rio Verde.

TABLE 2. Frequency distributions of meristic characters of *Dionda mandibularis* from the Upper Río Verde, San Luis Potosí, México. Values of the holotype are underlined.

	Lateral-line scales									
	37	38	39	40	41	42	43	44	N	$\bar{X}$
Creek	. .	1	1	7	3	6	. .	2	20	41.15
Springs	1	. .	1	1	1	1	1	1	7	40.86

	Predorsal scales							
	18	19	20	21	22	23	N	$\bar{X}$
Creek	2	6	5	4	1	1	19	19.95
Springs	1	1	2	3	2	. .	9	20.44

	Dorsal rays				Anal rays					
	8	9	N	$\bar{X}$	7	8	9	10	N	$\bar{X}$
Creek	11	9	20	8.45	1	15	3	1	20	8.20
Springs	11	. .	11	8.00	. .	11	. .	. .	11	8.00

	Pectoral rays							Pelvic rays				
	11	12	13	14	15	N	$\bar{X}$	7	8	9	N	$\bar{X}$
Creek	. .	. .	15	21	4	40	13.73	. .	15	25	40	8.63
Springs	1	2	16	3	. .	22	12.95	1	20	1	22	8.00

This interesting fauna has been discussed by Miller (1956) and by Hubbs and Miller (1977).

The body shape and the position and size of the mouth of *Dionda mandibularis* seem to indicate that it is a midwater predator, possibly of recently acquired habits, as the black peritoneum suggests an herbivorous diet, which is common in the genus *Dionda.* Furthermore, the circumstance that the gut is one of the shortest in the genus *Dionda* supports the first interpretation.

Distribution.—Dionda mandibularis is known to the writers from three isolated or semi-isolated populations: one, a distributary channel of the Laguna de la Media Luna; two, a marsh and associated spring 2 km S of this marsh; three, the headwaters of the Rio Verde at Puerto del Río, near Cerritos, ca 80 km NNW of Ríoverde; all in San Luís Potosi (Fig. 3).

Relationships.—In describing *Dionda erimyzonops,* Hubbs and Miller (1974) commented on its inclusion in a group of cyprinid species characteristic of the Pánuco-Tamesí system, now being revised (Hubbs and Miller, 1977). This group is characterized by a short intestine, little circumvoluted, that forms a double-S shape that may have an extra twist (Figs. 2 C–E). *Dionda mandibularis, D. erimyzonops,* and *Dionda* sp. belong to the first type, and *D. ipni* (sensu Hubbs and Miller, 1974) to the second (Fig. 2F). The forms with the strongly coiled intestines present 3 to 4 twists over the original S shape, as in the extralimital species *D. diaboli* (Fig. 2 G) and *D. episcopa* (Fig. 2 H). As an example, *D. episcopa* follows the approximate sequence shown in Fig. 2 A, C, D, F, H, G. These findings are in agreement with the observations of Kafuku (1958) on the developmental sequence in several Eurasian cyprinids and in catostomids.

Double S-shaped intestines have been described in *Luxilus,* a subgenus of *Notropis,* and in *N. mekistocholas* Snelson (1971), but the type of circumvolution in that species (Fig. 2 B) is not the same. This evidence seems to indicate that such forms and the short-intestined species of *Dionda* do not appear to be closely related. As a phyletic line, the forms of *Dionda* from the Río Pánuco-Tamesí

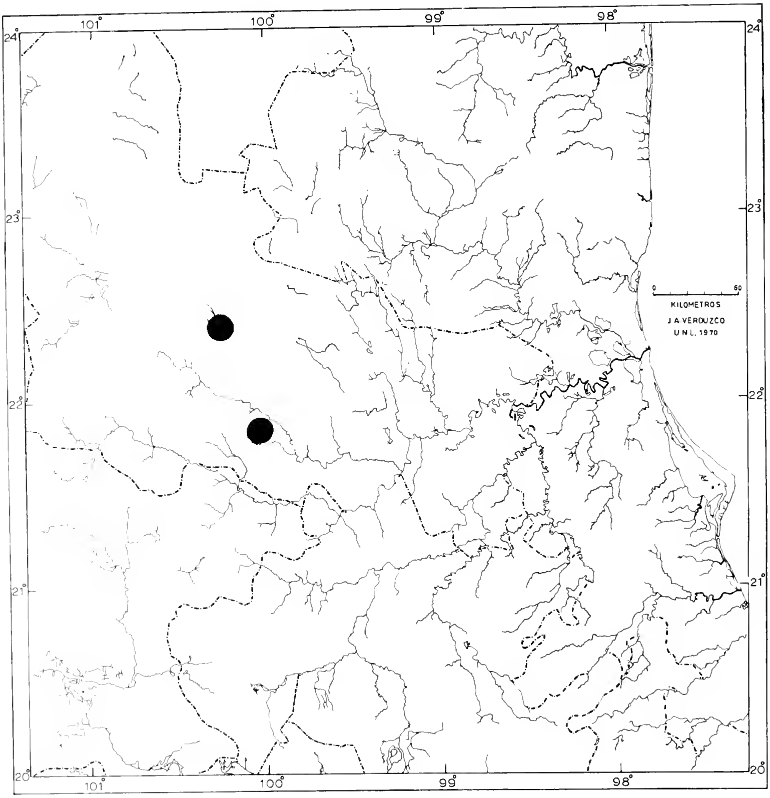


Figure 3. Distribution of *Dionda mandibularis* n. sp.; the upper locality is Puerto del Río, near Cerritos, San Luis Potosí; the lower is the type locality, 7 km SSE of Ríoverde, same state. The third locality, a spring-fed marsh 9.7 km from Ríoverde is not separable on the map.

system seem to comprise a compact and natural grouping, an opinion that we share with Hubbs and Miller (1977). If, perchance, as Hubbs and Miller (1974) suggested, the genus *Dionda* were to be synonymized with *Notropis*, the validity of *Dionda mandibularis* and the other species here mentioned would not be jeopardized. The developmental sequence of these and various other forms is under study and will be described in the near future, in the hope that it will help to understand this interesting complex.

ACKNOWLEDGMENTS

Dr. José Alvarez del Villar (Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, México) loaned specimens for comparison. He, Dr. Carl L. Hubbs (Scripps Institution of Oceanography), and Dr. Robert Rush Miller (University of Michigan Museum of Zoology) have read and criticized the manuscript and have corrected the English version. Also, Drs. Hubbs and Miller made the arrangements for the publication of this paper jointly with their more extended revision of the Mexican species referred to *Dionda.*

Field work was supported by a cooperative program from the Comisión Nacional Consultiva de Pesca (México) granted to the senior author, held in the Universidad Autónoma de Nuevo León from 1967-1968. This program and the permits for collecting were arranged by Biól. Juan Luis Cifuentes-Lemus as Subdirector de Asuntos Pesqueros, Secretaría de Industria y Comercio, México. Assistants in collecting were Biól. Arturo Jiménez Guzmán and former students Julián Javier Alvarado-Ortiz, José Luis Puente-Fragoso, Robert Banda-Silva, and José María Torres-Ayala.

Photographic and drawing services were rendered by Eliézer Alanís (Facultad de Medicina), Arcadio Valdéz, and Gerardo Guajardo (Facultad de Ciencias Biólogicas), all from Universidad Autónoma de Nuevo León. To all colleagues and students mentioned, the authors are grateful.

LITERATURE CITED

HUBBS, C. L. and K. F. LAGLER, 1958, 1964, etc. Fishes of the Great Lakes region. Cranbrook Institute of Science (Bull. 26) and, currently, University of Michigan Press: xv + 213 pp.

HUBBS, C. L. and R. R. MILLER, 1974. *Dionda erimyzonops,* a new, dwarf cyprinid fish inhabiting the Gulf Coastal Plain of Mexico. Occasional Papers of the Museum of Zoology University of Michigan, no. 671: 1-17.

HUBBS, C. L. and R. R. MILLER, 1977. Six distinctive cyprinid fish species referred to *Dionda* inhabiting segments of the Tampico Embayment of Mexico. Transactions San Diego Society of Natural History, 18 (17): in press.

KAFUKU, TAKEICHIRO, 1958. Speciation in cyprinid fishes on the basis of intestinal differentiation, with some references to that among catostomids. Bulletin Freshwater Fisheries Laboratory, 8 (1): 45-78.

MILLER, R. R., 1956. A new genus and species of cyprinodont fish from San Luis Potosi, Mexico, with remarks on the subfamily Cyprinodontinae. Occasional Papers Museum of Zoology University of Michigan, no. 581: 1-17.

SNELSON, F. R., Jr., 1971. *Notropis mekistocholas,* a new herbivorous cyprinid fish endemic to the Cape Fear River Basin, North Carolina. Copeia, 1971 (3): 449-462.

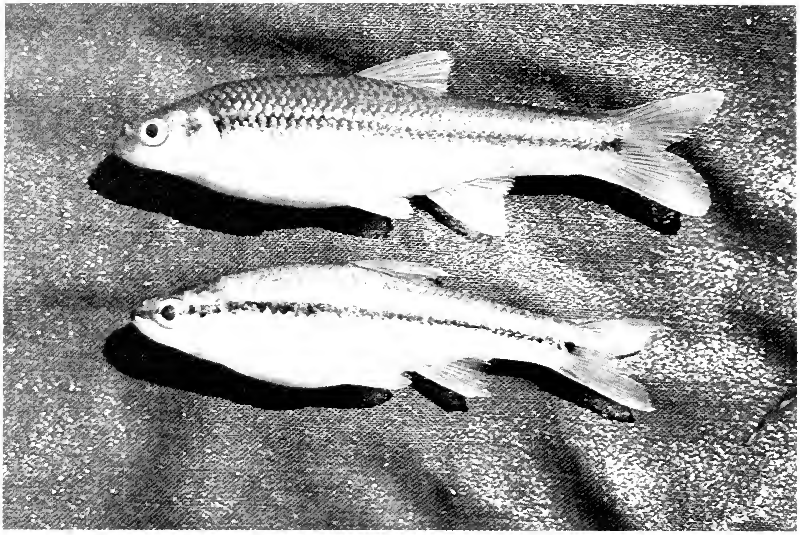
División de Vertebrados (Contribution 15), Facultad de Ciencias Biológicas, Universidad Autónoma de Nuevo León, Ciudad Universiteria, Monterrey, N. L., México.

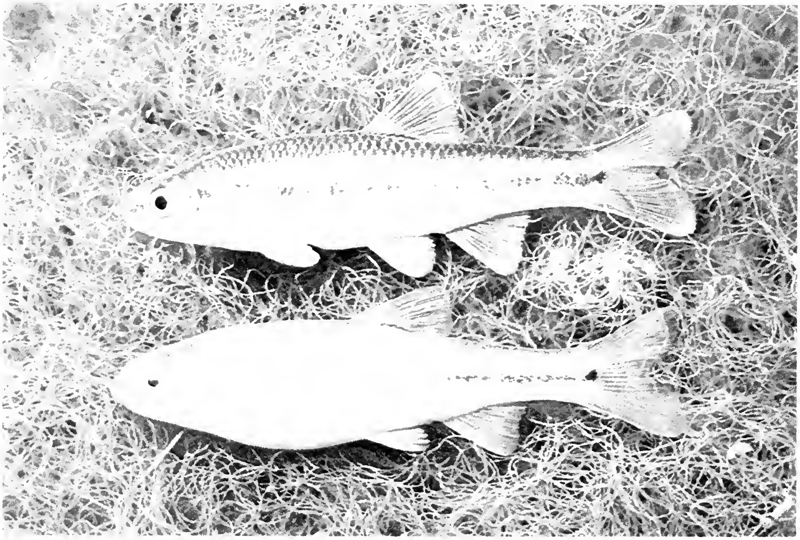
SIX DISTINCTIVE CYPRINID FISH SPECIES REFERRED TO *DIONDA* INHABITING SEGMENTS OF THE TAMPICO EMBAYMENT DRAINAGE OF MEXICO

Carl L. Hubbs and Robert Rush Miller

TRANSACTIONS
OF THE SAN DIEGO
SOCIETY OF
NATURAL HISTORY

VOL. 18, NO. 17 2 SEPTEMBER 1977





Life colors of freshly caught adults of three Mexican species of *Dionda*, photographed under water by Robert Rush Miller.

Upper pair, *D. catostomops* (above) and *D. rasconis*, from Río Tamasopo near Tamasopo, 7 February 1974.

Lower pair, *D. dichroma:* male (above) and female, from Río Verde near Ríoverde, 13 February 1970.

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

Carl L. Hubbs and Robert Rush Miller

SAN DIEGO SOC. NAT. HIST. TRANS. 18(17):267-336, 2 SEPTEMBER 1977

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.

CONTENTS

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, Cazones, 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 Ríoverde (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 Cazones. 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

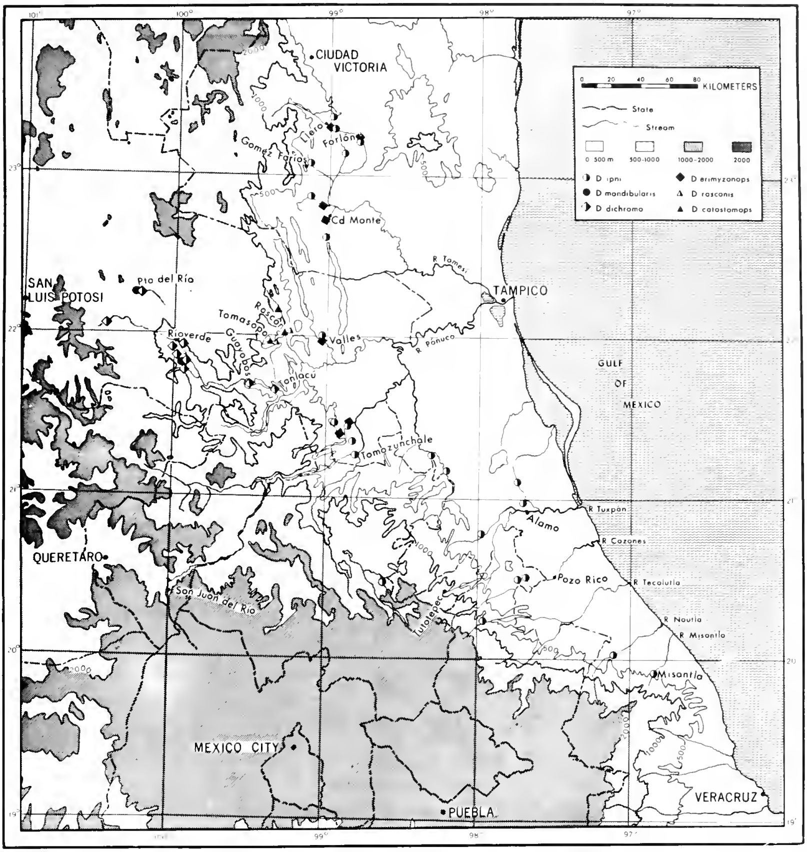


Figure 1. Distribution of the six species referred to *Dionda* in the Tampico Embayment drainage of northeastern México.

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 María, and (or) Río Moctezuma (Fig. 1). This subfauna includes: two cyprinids, *Algansea tincella* (Valenciennes) and *Aztecula* (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 *Xenoophorus 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 *Aztecula 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 circumstance, 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.

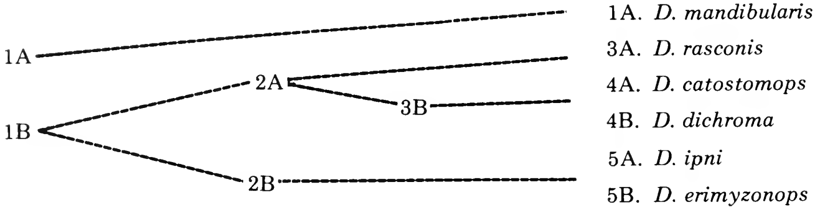
The problem of the generic placement of the six species herein referred to *Dionda* is greatly complicated by the circumstance that the brightly colored species long treated as *Dionda nubila* (Forbes) has recently been referred by Camm C. Swift (in thesis), to *Notropis*, despite its herbivorous habit 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

---

[1] Excluding 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-intermonatane 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 ordinarly 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 southeastward 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 Ríoverde, San Luis Potosí; also from a spring-fed marsh 9.7 km S of Ríoverde 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 Ríoverde, San Luis Potosí (this series was also examined by the describers of the species and was designated by them as paratypic); 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.

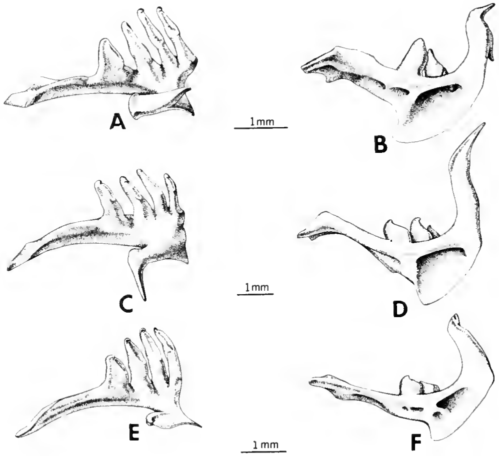


Figure 2. Dorsal and lateral aspects of left pharyngeal arches of three species of *Dionda*. **A–B**, paratype (52 mm SL) of *D. mandibularis* (UMMZ 193474) from marsh 10 km S of Ríoverde, San Luis Potosí. **C–D**, adult (49.5 mm) of *D. rasconis* (UMMZ 193509) from Río Tamasopo, Tamasopo, San Luis Potosí.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

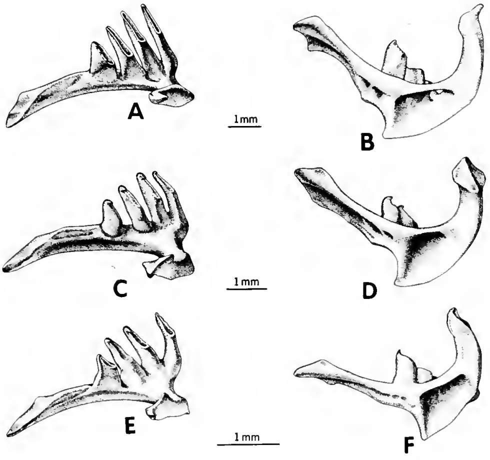


Figure 3. Dorsal and lateral aspects of left pharyngeal arches of three species of *Dionda*. A–B, paratype (55 mm SL) of *D. dichroma* (UMMZ 196338) from Puerta del Río 20 km SE of Cerritos, San Luis Potosí. C–D, adult (48 mm) of *D. ipni* (UMMZ 193492) from tributary of Rio San Marcos at Highway 130, 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-Martinez, 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 puncticulated in males. Above this stripe the conspicuous light streak is somewhat subdued by fine puncticulation 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 puncticulate 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 puncticulation 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 predorsal 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

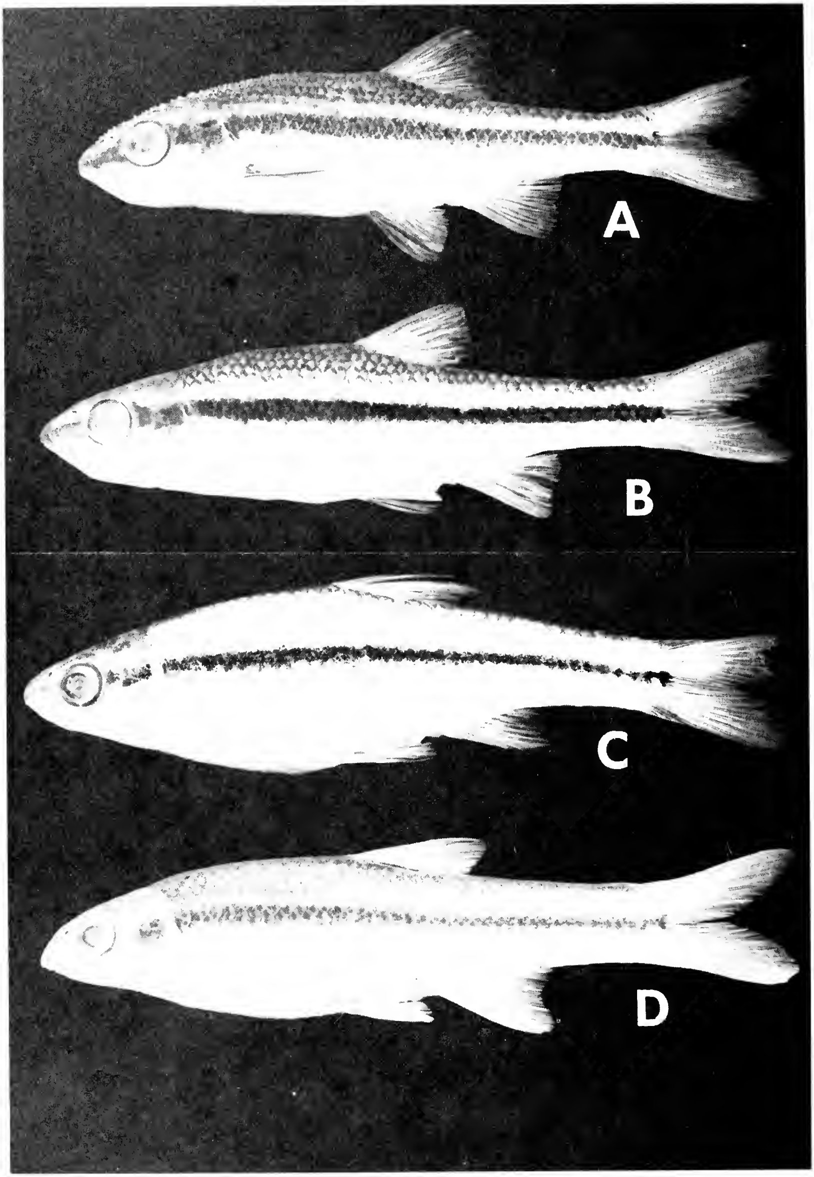


Figure 4. Three species of *Dionda* from Río Pánuco system: **A and B**, nuptial male (51.9 mm SL) and adult female (49.1 mm) of *D. mandibularis* (UMMZ 196703) from marsh 10 km S of Ríoverde, San Luis Potosí. **C**, adult (51.3 mm) of *D. rasconis* (UMMZ 193509) from Río Tamasopo, Tamasopo, San Luis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

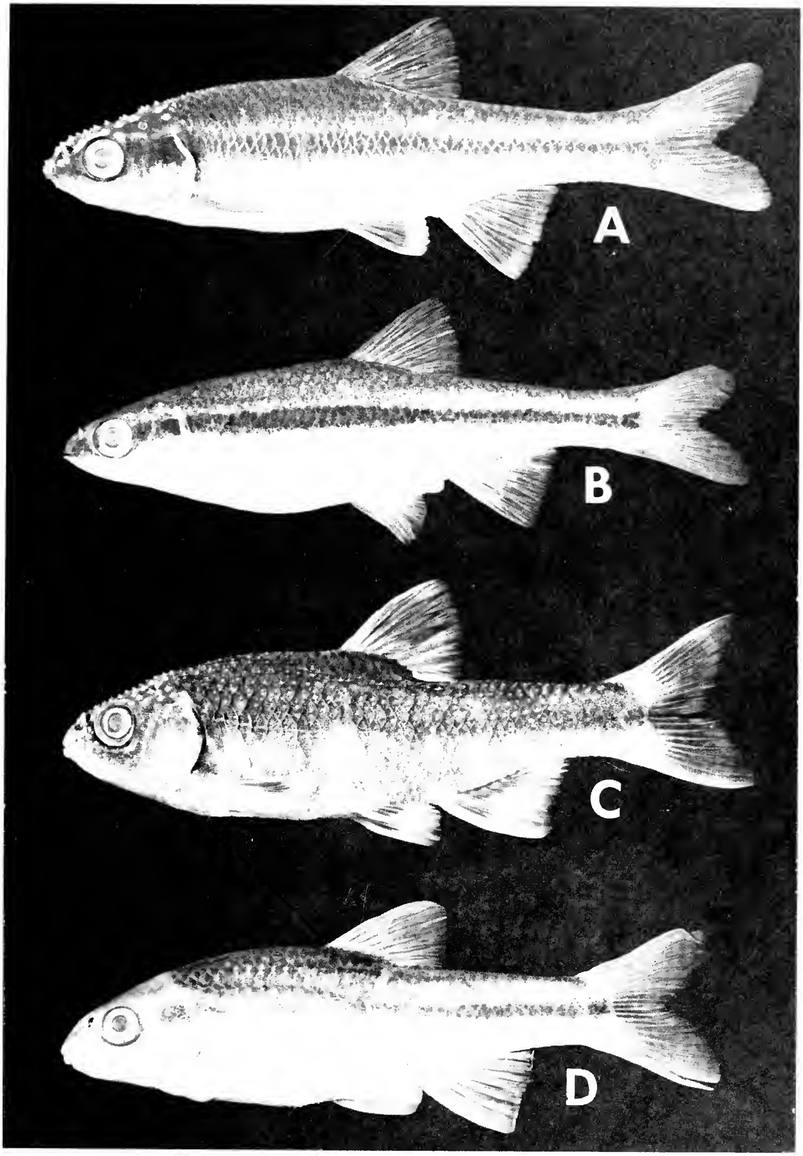


Figure 5. Two species of *Dionda* from Tampico Embayment area: **A and B**, nuptial male holotype (51.7 mm) and female paratype (49.0 mm) of *D. dichroma* (UMMZ 196701–02) from marsh 10 km S of Ríoverde, San Luis Potosí (note large eye). **C and D**, high nuptial male (51.5 mm) and prenuptial male (48.0 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 Ríoverde 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; current 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 Ríoverde, 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 Frío], 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 greately 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 Río 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 symphysial 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 Ríoverde), 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 obscolescent 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-

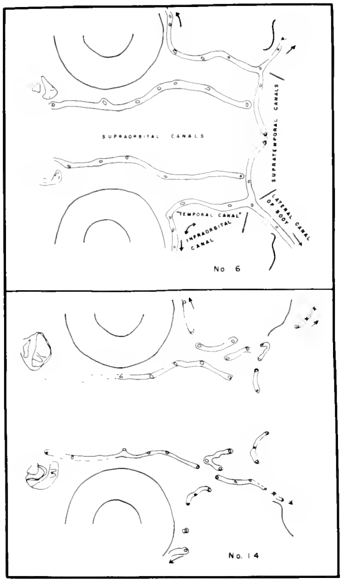


Figure 6. Most nearly normal and most disrupted of eight selected portrayals of the superficial cephalic sensory canal and pore system of the interorbital and upper-postorbital areas (drawn as on a single plane) of *Dionda rasconis* topotypes (UMMZ 196693); selected from the series of 67 specimens.

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-

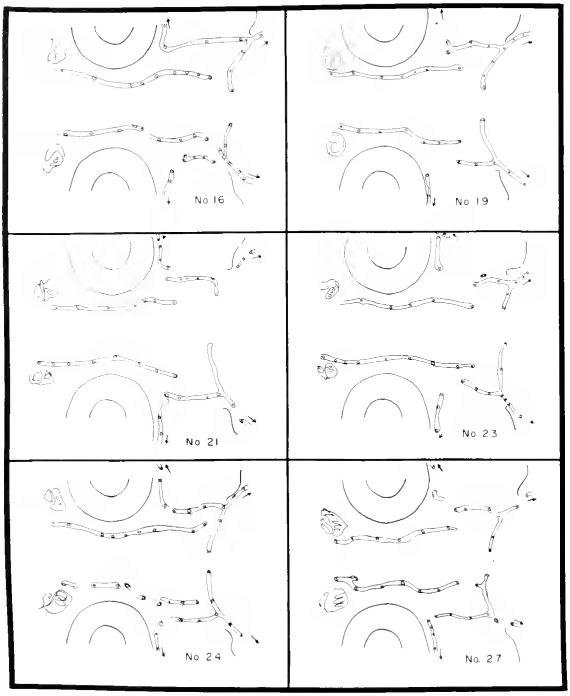


Figure 7. Six additional, less extreme variants in the cephalic sensory canal and pore systems exhibited by *Dionda rasconis* topotypes (UMMZ 196693). The numbers in figures 6 and 7 correspond with those attached to the specimens.

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 procurrent 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* (Frontispiece, 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									
	28-30	31-33	34-36	37-39	40-42	43-45	46-48	49-51	No.	$\overline{X}$ from ungrouped data
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 identation not obliterated by a moderate down-stretching of that fin. Vertebrae normally totalling 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), Rio 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					
	44-49	50-55	56-61	62-67	No.	$\overline{X}$ from ungrouped data
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 moderately 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]
mandibularis (20)	7–9 (8.15)	18–19 (18.95)	12–15 (13.25)	8–9 (8.05)
rasconis (30)	7–8 (7.93)	19 (19.00)	11–15 (13.05)	5–8 (7.77)
catostomops (31)	8 (8.00)	19 (19.00)	12–15 (13.76)	6–9 (8.02)
dichroma (85)[3]	7–9 (8.01)	18–19 (18.97)	12–15 (13.24)	0–9 (7.81)
ipni (48)	8–9 (8.02)	18–19 (18.96)	13–17 (15.08)	7–9 (7.98)
erimyzonops (37–40)	8–9 (8.03)	18–19 (18.97)	12–15 (12.86)	6–9 (8.03)

[1] Counts for anal rays are detailed in Table 4. The paired fins were counted on both sides.

[2] Odd 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.

[3] For 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.	$\bar{X}$
mandibularis	1	42	-	-	-	-	43	7.98
rasconis	3	86	3	-	-	-	92	8.00
catostomops	1	30	-	-	-	-	31	7.97
dichroma	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 Ríoverde	6	197	33	2	-	1	239	8.14
7–10 km S of Ríoverde	2	16	47	5	-	-	70	8.79
16 km SE of Ríoverde	1	21	2	-	-	-	24	8.04
Río Verde, Guayabos	-	23	2	-	-	-	25	8.08
Río Verde, Tanlacú	2	28	1	-	-	-	31	7.97
ipni	-	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
Metztitlán 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
erimyzonops	-	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 puncticulate 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.	$\bar{X}$
mandibularis	-	-	-	-	-	-	2	2	4	6	2	2	1	-	-	19	39.74
rasconis	-	-	1	16	9	3	-	-	-	-	-	-	-	-	-	29	34.48
catostomops	-	-	-	-	-	-	9	16	4	2	-	-	-	-	-	31	37.97
dichroma	-	-	-	-	-	-	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 Ríoverde	-	-	-	-	-	-	-	-	-	-	4	8	6	5	2	25	42.72
16 km S of Ríoverde	-	-	-	-	-	-	-	1	3	7	4	3	2	-	-	20	40.55
Río Verde, Guayabos	-	-	-	-	-	-	-	1	3	6	7	3	-	-	-	20	40.40
Rio Verde, Tanlacú	-	-	-	-	-	-	-	-	6	5	2	1	-	1	-	15	40.13
ipni	-	14	53	55	10	2	1	-	-	-	-	-	-	-	-	135	33.53
erimyzonops	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 puncticulate 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
mandibularis	18-20	17-20	7-8	5-7	4-7	14-16	15-19	31-36	7-9	6-8	15-19
(15-20)	(19.00)	(18.60)	(7.15)	(6.05)	(5.00)	(14.83)	(16.33)	(33.17)	(7.75)	(7.15)	(16.90)
rasconis	16-20	14-18	5-8	4-6	4-5	11-15	13-16	27-32	5-8	5-7	12-17
(21-23)	(17.86)	(15.86)	(6.09)	(4.74)	(4.30)	(12.96)	(14.30)	(29.26)	(6.67)	(5.81)	(14.48)
catostomops	16-21	15-19	6-7	4-6	4-6	13-15	13-16	28-33	7-8	6-7	15-17
(30)	(18.20)	(16.20)	(6.30)	(5.23)	(4.40)	(13.63)	(13.97)	(29.60)	(7.03)	(6.70)	(15.73)
dichroma	17-24	15-23	6-8	5-7	4-7	11-17	13-21	26-39	7-9	5-9	14-20
	172 (20.5)	73 (18.33)	75 (6.77)	75 (5.88)	75 (5.28)	75 (14.46)	75 (16.36)	174 (31.56)	75 (7.37)	75 (6.89)	75 (16.27)
Sta. Catarina	19-24	17-23	6-8	5-7	5-7	13-17	15-21	31-39	7-9	6-9	15-20
(30)	(21.63)	(19.47)	(6.97)	(6.27)	(5.73)	(15.01)	(17.67)	(34.80)	(7.57)	(7.17)	(16.73)
Puerta del Río	17-22	15-20	6-7	5-6	4-5	11-15	13-17	26-34	7-8	5-7	14-17
(18-20)	(18.94)	(17.22)	(6.30)	(5.30)	(4.80)	(13.05)	(15.05)	(29.70)	(7.05)	(6.55)	(15.60)
Vic. Ríoverde	18-24	16-20	6-8	5-7	4-6	13-17	14-18	26-36	7-9	5-8	14-18
(25)[2]	(19.84)	(17.76)	(6.92)	(5.88)	(5.12)	(14.92)	(15.84)	(31.84)	(7.40)	(6.84)	(16.24)
Lower R. Verde	18-23	-	-	-	-	-	-	27-33	-	-	-
(35)[3]	(19.80)	-	-	-	-	-	-	(29.34)	-	-	-
ipni	12-15	11-14	5-7	4-6	3-5	11-13	11-14	24-29	5-7	5-6	12-15
(41-42)	(13.66)	(12.57)	(6.12)	(4.88)	(3.93)	(12.43)	(12.19)	(26.62)	(6.71)	(5.10)	(13.81)
erimyzonops	12-15	11-13	5-6	3-4	3-4	9-13	10-12	21-26	5-6	4-5	11-13
(37-38)	(13.62)	(12.27)	(5.18)	(3.95)	(3.74)	(10.87)	(10.87)	(23.74)	(5.03)	(4.95)	(11.97)

[1] Counts for lateral-line scales are detailed in Table 5.

[2] The predorsal scales and those around the body were enumerated on 89 specimens.

[3] These specimens are from Tanlacú and Guayabos, and are in flabby condition.

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

	Precaudal							Caudal								Total								
Species	**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.**	**$\bar{X}$**
mandibularis	-	23	23	-	-	46	17.50	-	-	21	24	1	-	46	17.57	-	6	31	9	-	-	-	46	35.07
rasconis	-	-	41	26	-	67	18.39	-	22	41	3	-	-	66	16.71	-	6	49	14	-	-	-	69	35.12
catostomops	-	-	-	17	22	39	19.56	-	-	-	9	21	9	39	19.00	-	-	-	-	1	15	23	39	38.56
dichroma	-	-	5	103	68	176	19.36	-	-	20	115	50	1	186	18.17	-	-	-	6	82	69	5	162	37.45
ipni	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
erimyzonops	-	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.	$\bar{X}$
mandibularis	-	-	-	-	-	-	1	8	4	6	-	1	-	20	8.95
rasconis	-	-	-	-	-	-	3	11	9	5	1	1	-	30	8.77
catostomops	-	-	-	-	-	-	-	1	9	15	5	-	-	30	9.80
dichroma	-	-	-	-	-	-	-	4	6	14	11	9	1	45	10.40
ipni	-	-	-	1	8	26	23	11	2	-	-	-	-	71	6.58
erimyzonops	(?)					(?)[1]	-	-	-	-	-	-	-	?	?

[1] The 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 preorbital 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 ωψ, 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*.

	Ratios												
Species	**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**	**No.**	**Range**	$\bar{X}$
mandibularis	-	-	-	-	-	4	13	9	1	2	29	1.82-2.68	2.11
rasconis	-	-	-	-	-	-	9	16	6	2	33	1.96-2.55	2.20
catostomops	-	-	-	-	-	-	3	11	5	1	20	1.99-2.51	2.25
dichroma	-	-	-	1	4	25	18	13	1	1	63	1.49-2.62	1.94
ipni	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
erimyzonops	-	-	-	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 Ríoverde).

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.

	Dionda mandibularis		*Dionda rasconis*		*Dionda catostomops*
	Puerta del Río **UMMZ 196339**	**Marsh 10 km S of Rioverde** **UMMZ 193474, 196703**	**Río Gallinas** **UMMZ 196693**	**Río Tamasopo** **UMMZ 196345**	**Río Tamasopo** **UMMZ 196346-7**
Standard length, mm					Type, ♂, 54.7 mm
Males	40.7-46.7 (44.0) 4	33.0-48.5 (40.4) 10	28.8-43.9 (35.7) 13	This set not sexed	52.5-61.0 (57.0) 10
Females	45.7-57.2 (52.0) 10	32.6-52.7 (44.9) 5	40.5-50.2 (44.5) 7	35.4-52.4 (43.6) 13	56.8-66.1 (61.4) 10
Body depth					Type 265
Males	255-299 (274)	224-276 (256)	225-278 (247)	265-295 (279)	251-279 (263)
Females	260-321 (288)	226-260 (245)	250-280 (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)

Lateral line to D origin					Type 150
Males	147-171 (157)	120-160 (145)	122-155 (140)	145-160 (153)	142-160 (150)
Females	148-170 (160)	127-153 (140)	137-160 (147)		143-161 (151)
Lateral line to P_2 insertion					Type 123
Males	118-137 (129)	108-136 (115)	110-128 (118)	126-162 (140)$_{10}$	112-135 (124)
Females	116-157 (134)	105-116 (111)	113-145 (126)		116-144 (130)
Head length					Type 251
Males	275-287 (281)	278-299 (287)	251-276 (262)	241-275 (256)	238-254 (247)
Females	273-293 (285)	268-291 (283)	248-267 (259)		236-254 (245)
Head depth					Type 173
Males	189-204 (195)	182-213 (197)	171-191 (181)	169—187 (181)	167-179 (174)
Females	187-201 (195)	184-197 (189)	176-186 (180)		161-180 (170)
Head width					Type 136
Males	139-147 (143)	134-153 (142)	118-135 (128)	110-133 (124)	136-153 (144)
Females	139-156 (148)$_9$	130-143 (137)	124-138 (130)		138-150 (147)
Snout length					Type 85
Males	89- 94 (92)	86-102 (91)	72- 94 (80)	72- 90 (81)	83- 90 (87)
Females	88-103 (95)	83- 96 (91)	72- 85 (80)		82- 93 (87)
Orbit length					Type 65
Males	76- 84 (79)	77-102 (90)	77- 94 (86)	76- 88 (82)	59- 65 (62)
Females	77- 90 (82)	74- 98 (88)	71- 84 (80)		57- 65 (62)
Upper-jaw length					Type 69
Males	78- 79 (79)	73- 83 (78)	59- 72 (66)	64- 74 (69)	64- 73 (67)
Females	77- 89 (83)	72- 89 (80)	62- 71 (65)		59- 69 (65)
Suborbital width					Type 39
Males	46- 52 (49)	39- 57 (48)	32- 43 (37)	35- 45 (40)	35- 45 (39)
Females	43- 54 (49)	46- 51 (49)	36- 44 (40)		30- 41 (37)
Least interorbital					Type 89
Males	92-101 (97)	85-106 (96)	78- 96 (85)	79- 94 (86)	83- 91 (87)
Females	81-102 (94)	92- 99 (97)	82- 92 (87)		84- 95 (90)
Mouth overall					Type 65
Males	70- 79 (73)	56- 71 (65)	51- 64 (57)	48- 65 (58)	61- 67 (65)
Females	63- 81 (75)	60- 73 (66)	56- 65 (59)		61- 71 (65)
Mandible length					Type 81
Males	110-115 (112)	108-128 (115)	81- 99 (92)	82- 95 (89)	69- 81 (72)
Females	110-122 (116)	110-131 (119)	89- 97 (88)		70- 78 (73)
Upper-lip symphysis					Type 15
Males	9- 15 (12)	8- 13 (11)	11- 17 (14)	12- 20 (14)	15- 20 (18)
Females	9- 15 (12)	10- 12 (11)	11- 16 (14)		15- 20 (17)

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 Ríoverde. Paratypes: 172195 (251: 16-65) and UF 14575 (10: 46-60), Río Santa Catarina, 65 km W of Ríoverde; 196338 (72: 31-63) and LSUMZ 1216 (7: 47-61), spring at Puerta del Rıo, 20 km SE of Cerritos; 187685 (11: 41-59), La Media Luna, 11 km SSW of Ríoverde; 188800 (13: 30-58), canal in Ríoverde connecting with La Media Luna; 189278 (47: 18-40), Río Verde, 2 km NE of Ríoverde; 189573 (113: 39-64) and UNL 1327 (38: 36-62), Río Verde at bridge just E of Ríoverde; 192511 (4: 28-53), ditch 8 km S of Ríoverde and 4.1 km W of highway; 193448 (24: 13-60), tributary to Río Verde, 16 km SE of Ríoverde; 193473 (19: 33-56), type locality; UNL 1031 (10: 31-55) and 1321 (4: 28-36), arroyo 7 km SSE of Ríoverde. Non-types: FMNH 3877 (16: 25-51), Río Verde at bridge just E of Ríoverde; LSUMZ 23 (3: 17-29), La Media Luna, SSW of Ríoverde; 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 Rioverde, 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 Ríoverde. 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 Ríoverde (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 supratemporal 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 Ríoverde and La Media Luna (including also the Puerta del Rıo 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 Ríoverde, 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 irridescent 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 Ríoverde, read: Outer margins (¼ to ⅓) 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 melanic on body and fins (p. 313, Fig. 5A) and in life their fins become strikingly blue peripherally (see the Frontispiece). 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 Ríoverde 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 postorbital 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 Ríoverde (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

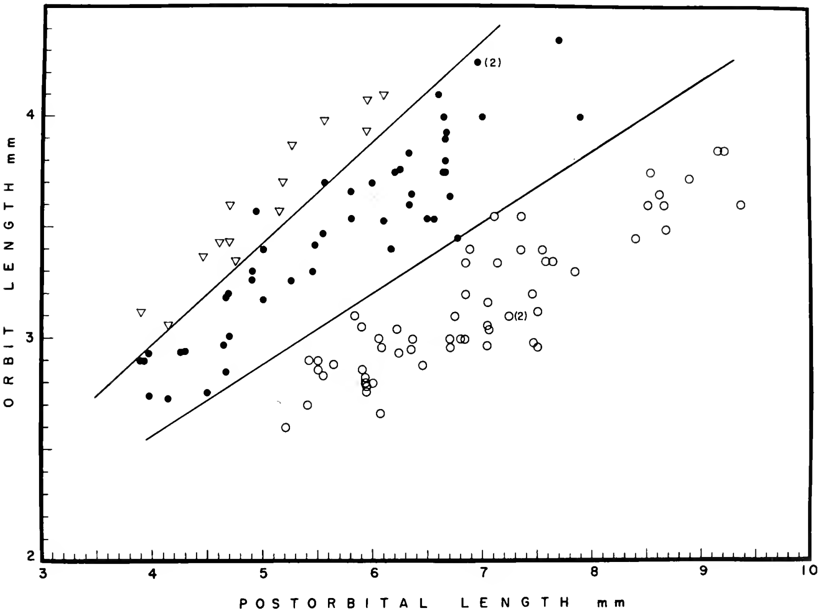


Figure 9. Sharp distinction in size of eye (in relation to postorbital length) between specimens of *Dionda dichroma* from isolated marsh 10 km S of Ríoverde (UMMZ 196702, upper left), and those from the two headwater populations: Puerta del Río (196338, middle) and Río Santa Catarina (172195, lower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

Figure 10. Nuptial male paratype (63.9 mm SL), variant of *Dionda dichroma* (UMMZ 172195, no. 44), from Rio Santa Catarina (Fig. 11), isolated headwater tributary of Río Verde, about 65 km W of Ríoverde, 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 Ríoverde 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 Ríoverde, 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 Rio (1,100 m), of Río Verde, about 45 km NW of the town of Rioverde, 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 Ríoverde, 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 is 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 Ríoverde** **UMMZ 196701-2**	**Río Verde, Tanlacú** **LSUMZ 408**
Standard length, mm			Type, ♂, 51.7 mm	This set not sexed
Males	53.8-64.9 (60.0) 10	44.0-56.3 (50.4) 10	40.9-53.6 (48.5) 7	
Females	49.2-65.0 (56.7) 10	47.2-65.3 (56.2) 10	37.9-49.0 (42.8) 7	46.3-53.7 (51.0) 10
Body depth			Type 264	289-342 (310)
Males	277-327 (300)	293-327 (309)	239-271 (258)	
Females	272-339 (301)	254-328 (296)	247-268 (259)	
C-peduncle depth			Type 115	111-129 (121)
Males	121-135 (126)	111-126 (120)	108-122 (114)	
Females	111-123 (118)	104-126 (113)	99-104 (101)	
C-peduncle length			Type 224	209-236 (221)
Males	216-246 (229)	214-253 (237)	209-236 (219)	
Females	195-246 (219)	206-248 (232)	198-250 (224)	
A origin to C base			Type 353	322-358 (340)
Males	334-362 (347)	326-364 (353)	332-369 (345)	
Females	306-356 (333)	322-371 (347)	329-350 (340)	
Predorsal length			Type 516	516-551 (536)
Males	507-558 (529)	512-538 (530)	516-528 (521)	
Females	511-549 (537)	514-543 (529)	505-540 (524)	
Depressed D fin			Type 230	205-238 (224)
Males	196-230 (218)	208-231 (222)	221-254 (233)	
Females	202-230 (213)	201-234 (217)$_8$	216-231 (222)$_5$	
A-fin base			Type 131	110-125 (116)
Males	106-126 (120)	107-136 (116)	117-134 (127)	
Females	106-121 (114)	103-129 (115)	95-133 (117)	
P_1-fin length			Type 199	186-226 (203)
Males	179-210 (196)	186-208 (196)	197-222 (205)	
Females	171-195 (185)	171-202 (185)	183-192 (186)	
Lateral line to D origin			Type 159	159-182 (169)
Males	158-186 (174)	157-181 (170)	140-166 (153)	
Females	158-183 (169)	136-175 (161)	140-150 (147)	

Lateral line to P_2 insertion			Type 110	
Males	123-144 (134)	135-156 (144)	101-122 (111)	125-156 (137)
Females	128-170 (143)	106-159 (136)	114-133 (120)	
Head length			Type 259	
Males	252-292 (266)	245-268 (257)	248-260 (255)	242-269 (255)
Females	249-264 (255)	235-261 (251)	224-250 (241)	
Head depth			Type 184	
Males	183-217 (202)	178-197 (189)	178-194 (186)	181-200 (190)
Females	185-203 (195)	170-193 (182)	164-182 (175)	
Head width			Type 151	
Males	145-166 (157)$_9$	134-148 (141)	126-151 (137)	125-145 (134)
Females	136-164 (149)	127-154 (138)	122-135 (127)	
Snout length			Type 78	
Males	85- 96 (89)	74- 85 (79)	75- 86 (79)	65- 78 (72)
Females	79- 89 (84)	67- 85 (75)	69- 78 (73)	
Orbit length			Type 79	
Males	54- 65 (58)	69- 86 (75)	75- 82 (79)	66- 73 (70)
Females	58- 62 (60)	68- 77 (72)	78- 82 (80)	
Upper-jaw length			Type 68	
Males	68- 74 (72)	58- 78 (68)	63- 70 (67)	63- 78 (68)
Females	66- 76 (70)	62- 70 (65)	61- 72 (66)	
Suborbital width			Type 36	
Males	41- 49 (44)	35- 49 (39)	34- 42 (37)	27- 36 (32)
Females	33- 45 (41)	28- 41 (34)	30- 37 (34)	
Least interorbital width			Type 93	
Males	97-110 (104)	94-103 (99)	93-109 (99)	80- 95 (87)
Females	94-104 (100)	86-102 (95)	87- 94 (91)	
Mouth overall			Type 64	
Males	68- 80 (76)	61- 72 (66)	60- 69 (66)	58- 67 (62)
Females	68- 80 (73)	55- 69 (62)	54- 67 (60)	
Mandible length			Type 84	
Males	80- 91 (85)	79- 92 (84)	69- 91 (85)	73- 90 (83)
Females	77- 88 (84)	70- 85 (79)	76- 98 (84)	
Upper-lip symphysis			Type 15	
Males	15- 21 (17)	13- 21 (16)	13- 16 (15)	11- 20 (15)
Females	16- 20 (18)	13- 20 (16)	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 (δ ί σ, two), and Χρμα*(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, Cazones, 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 Metztitlán at Barranca de Venados (6 paratypes of *N. ipni*, 21-32); 196682, Río Venados (= Metztitlán), 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 Cazones system, Puebla.—97464, tributary to Río Cazones near Agua Fría, 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 Río 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 P_2 insertion				
Nuptial males	127-141 (134)	120-144 (137)	129-131 (130)	119-140 (128)
Prenuptial 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)
Prenuptial 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)
Prenuptial 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)
Prenuptial 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)
Prenuptial 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)
Prenuptial 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)
Prenuptial 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)
Prenuptial 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)
Prenuptial 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)
Prenuptial 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)
Prenuptial 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)
Prenuptial 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 Cazones 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 Cazones 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, scatteringly, 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 interradial and hardened structure between the first and second rays bears a file of minute slender spinelets, and some also appear on the second interradial structure. On most subsequent strengthened rays rather small hooklets form one row branching once; occasionally, on the second interradial 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).

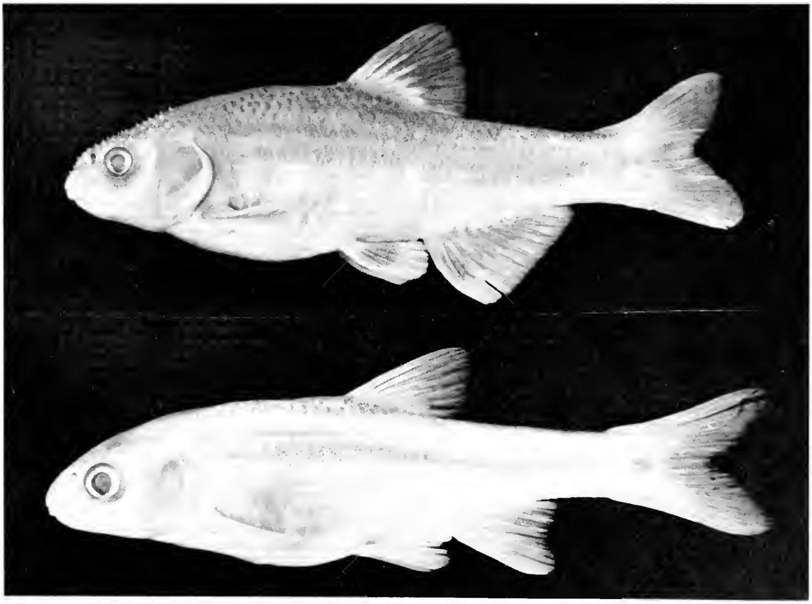


Figure 12. Low nuptial male (62.6 mm SL) and female (48.0 mm) topotypes of *Dionda ipni* (UMMZ 196682), from Rio Venados, Hidalgo.

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 Lasan of the Río Tuxpan system (UMMZ 193502) and from a tributary of Río San Marcos of the Río Cazones 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 fluviatile 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 invididuals 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 Potosi, 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 permillage 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 Ciéncias Biólogicos (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 Autónomo 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, how 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 generaously 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.

LITERATURE CITED

Alvarez, J., 1950. Claves para la determinación de especies en los peces de las aguas continentales Mexicanas. Secretaría de Marina, Dirección General de Pesca e Industrias Connexas, México: 144 p.

Alvarez, J., 1959. Nota preliminar sobre la ictiofauna del estado de San Luis Potosí. Acta Científica Potosina 3 (1): 71-88.

Alvarez, J., 1970. Peces mexicanos (claves). Instituto Nacional de Investigaciones Biológico Pesqueras, Comisión Nacional Consultiva de Pesca, México, Estudio 1: 1-66.

Alvarez, J., and L. Navarro, 1953. Nueva especie de *Notropis* capturada en el río de Metztitlan, estado de Hidalgo. Anales Escuela Nacional Ciencias Biológicas, México, 7 (1-4): 5-8.

Bailey, R. M., and M. O. Allum, 1962. Fishes of South Dakota. Miscellaneous Publications Museum Zoology, University of Michigan 119: 1-133.

Böhlke, J. E., 1953. A catalogue of the type specimens of recent fishes in the Natural History Museum of Stanford University. Stanford Ichthyological Bulletin 5: 1-168.

Contreras-Balderas, S., and J. A. Verduzco-Martínez, 1977. *Dionda mandibularis,* a new cyprinid fish endemic to the upper Río Verde, San Luis Potosí, México, with comments on related species. Transactions San Diego Society of Natural History 18 (16): 259-265.

Cortés, M. T., 1968. Consideraciones sobre el género *Notropis* y descripción de una especie nueva, procedente del Río Atoyac, en Juchatengo, Oax., México. Anales Escuela Nacional Ciencias Biologicas, México 15: 185-192.

CROSS, F. B., 1967. Handbook of fishes of Kansas. University Kansas Museum Natural History, Miscellaneous Publications 45: 1-357.

DARNELL, R. M., 1962. Fishes of the Río Tamesí and related coastal lagoons in east-central Mexico. Publications Institute Marine Science 8: 299-365.

DE BUEN, F., 1940. Lista de peces de agua dulce de México. En preparación de su catâlogo [II] Estación Limnologica de Pâtzcuaro, 1940: 16-31 (mimeo.).

DE BUEN, F., 1946a. Investigaciones sobre ictiología mexicana. I. Atherinidae de aguas continentales de México. Anales Instituto Biología México 16 (2) "1945:" 475-532.

DE BUEN, F., 1946b. Ictiogeografía continental mexicana (I, II, y III). Revista Sociedad Mexicana Historia Natural 7 (1-4): 87-138.

DE BUEN, F., 1947. Investigaciones sobre ictiologia mexicana. I Câtalogo de los peces de la región neártica en suelo mexicano. Anales Instituto Biología Mexico 18 (1): 257-348.

DE BUEN, F., 1956. Contribuciones a la ictiología. XI. El primer represante *(Notropis moralesi* nov. sp.) de la familia Cyprinidae en la fauna neotropical. Anales Instituto Biología México 26 (2): 527-541.

GILBERT, C. R., and R. M. BAILEY, 1972. Systematics and zoogeography of the American cyprinid fish *Notropis (Opsopoeodus) emiliae*. Occasional Papers Museum Zoology, University Michigan 664: 1-33.

HUBBS, C. L., 1955. Hybridization between fish species in nature. Systematic Zoolocy 4 (1): 1-20.

HUBBS, C. L., and G. P. COOPER, 1936. Minnows of Michigan. Cranbrook Institute Science 8: 1-95.

HUBBS, C. L., and R. R. MILLER, 1974. *Dionda erimyzonops*, a new, dwarf cyprinid fish inhabiting the Gulf Coastal Plain of México. Occasional Papers Museum Zoology, University Michigan 671: 1-17.

HUBBS, C. L., and R. R. MILLER, 1975. *Notropis tropicus*, a new cyprinid fish from eastern México. Southwestern Naturalist 20 (1): 121-131.

HUBBS, C. L., R. R. MILLER, and L. C. HUBBS, 1974. Hydrographic history and relict fishes of the north-central Great Basin. Memoirs California Academy Sciences 7: 1-259.

HUBBS, C. L., and C. L. TURNER, 1939. Studies of the fishes of the order Cyprinodontes. XVI. A revision of the Goodeidae. Miscellaneous Publications Museum Zoology, University Michigan 42: 1-80.

HUBBS, CLARK, and W. H. BROWN, 1956. *Dionda diaboli* (Cyprinidae), a new minnow from Texas. Southwestern Naturalist 1 (2): 69-77.

JORDAN, D. S., and B. W. EVERMANN, 1900. The fishes of North and Middle America. Bulletin United States National Museum 47 (Pt. 4): i-ci, 3137-3313.

JORDAN, D. S., and J. O. SNYDER, 1900. Notes on a collection of fishes from the rivers of México, with description of twenty new species. Bulletin United States Fish Commission 19: 115-147.

MEEK, S. E., 1904. The fresh-water fishes of México north of the Isthmus of Tehuantepec. Field Columbian Museum Publication 93, Zoology Series 5: lxii, 1-252.

MILLER, R. R., 1956. A new genus and species of cyprinodontid fish from San Luis Potosí, México, with remarks on the subfamily Cyprinodontinae. Occasional Papers Museum Zoology, University Michigan 581: 1-17.

MILLER, R. R., and J. M. FITZSIMONS, 1971. *Ameca splendens*, a new genus and species of goodeid fish from western México, with remarks on the classification of the Goodeidae. Copeia, 1971 (1): 1-13.

MILLER, R. R., and W. L. MINCKLEY, 1970. *Gambusia aurata*, a new species of poeciliid fish from northeastern México. Southwestern Naturalist 15 (2): 249-259.

MUIR, J. M., 1936. Geology of the Tampico region, México. American Association Petroleum Geologists. 280 p.

REGAN, C. T., 1906-08. Pisces. *In*, Biologia Centrali-Americana 8: i-xxxiii, 1-203.

RENO, H. W., 1969. Cephalic lateral-line systems of the cyprinid genus *Hybopsis*. Copeia, 1969 (4): 736-773.

SNELSON, F. F., Jr., 1971. *Notropis mekistocholas*, a new herbivorous cyprinid fish endemic to the Cape Fear River basin, North Carolina. Copeia, 1971 (3) 449-462.

Scripps Institution of Oceanography, La Jolla, CA 92093, and Museum of Zoology, The University of Michigan, Ann Arbor, MI 48104.