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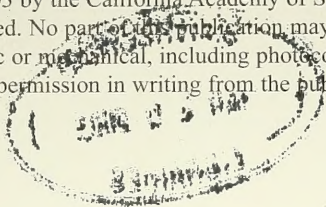
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SCIENTIFIC PUBLICATIONS

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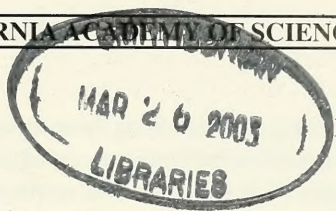
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COVER IMAGE: The "Crew" of the Academy's Galapagos Expedition Schooner *Academy*, taken just before departure from San Francisco, 28 June 1905. (Standing, left to right): Frederick T. Nelson, mate; Alban Stewart, botanist; Ernest S. King, assistant herpetologist; Rollo H. Beck, expedition leader and ornithologist; Joseph S. Hunter, ornithologist; Joseph R. Slevin, herpetologist; Edward W. Gifford, ornithologist; Washington H. Ochsner, geologist and conchologist; Francis X. Williams, entomologist. (Sitting): Captain J.J. Parker, navigator. California Academy of Sciences Archives.

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A New *Calotes* (Squamata: Agamidae) from the Indo-Burman Range of Western Myanmar (Burma)

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A new species of *Calotes* is described from the Indo-Burman Range, western Myanmar. It was found between elevations of 737 m to 1940 m in areas of shifting cultivation and secondary forest. It differs from other species of *Calotes* from Myanmar by a combination of its large size, SVL up to 142.9 mm, relatively small body scales, 59–74 midbody scale rows, the tail in adult males being swollen posterior to base and the presence of head spines. The new species increases the diversity of *Calotes* species in Myanmar to six. A key to the *Calotes* of Myanmar is provided.

The genus *Calotes* Cuvier, 1817 currently contains 20 species (Hallermann 2000), distributed from eastern Iran east to Sumatra, Indonesia (Welch 1994; Manthey and Grossmann 1997) including two isolated species, one in Sabah, Malaysia (*C. kinabaluensis* de Grijis, 1937) and the other on Ambon Island, Moluccas Islands, Indonesia (*C. nigriplicatus* Hallermann, 2000). Five species are known to occur within Myanmar: *Calotes emma*, *C. jerdoni*, *C. kingdonwardi*, *C. mystaceus* and *C. versicolor* (Smith 1935; Welch 1994). *Calotes mystaceus* and *C. versicolor* are widespread. *Calotes emma* although it may occur throughout much of Myanmar, to date the Myanmar Herpetological Survey team has not found it west of the Ayeyarwady River. However, it is known to occur in Bangladesh (CAS 94323) and northeastern India (Smith 1935; Pawar and Birand 2001). *Calotes jerdoni* is known from the Chin Hills of the Indo-Burman Range and along the southern flanks of the eastern Himalayas. *Calotes kingdonwardi* is restricted to the eastern Himalayas (Smith 1935).

MATERIALS AND METHODS

All specimens were hand collected, euthanized, fixed in 10% buffered formalin and later transferred to 70% ethanol. Latitude, longitude and elevation were recorded using a Garmin 12 GPS receiver (datum WGS 84). Museum symbolic codes follow Leviton et al. (1985).

Data for the following meristic characters and measurements were recorded for adult specimens: supralabials (SupL), number of enlarged scales bordering left and right margin of upper lip (not including rostral scale); infralabials (InfL), number of enlarged scales bordering left and right margin of lower lip (not including mental scale); number of scales around midbody (MidB); number of nuchal and dorsal crest spines (DC), enlarged mid-dorsal crest scales from posterior portion of the head to just above anterior margin of vent; number of subdigital lamellae on the right fourth toe (SDL 4th toe), including the last scale on claw base, snout-vent length (SVL); tail length (TailL);

head length (HeadL), distance from tip of snout to rear border of right angle of jaw; head width (HeadW), widest point in the temporal region, anterior to the tympanum; length of third and fourth toes on right foot (3rd Toe and 4th Toe, respectively); width of tail at widest point of swelling in males and the homologous area in females (TailD) and ratios of TailL/SVL, HeadW/HeadL, HeadL/SVL, HeadW/SVL.

Scale counts and observations of external morphology were made using a dissecting microscope. Measurements, except for TailL, were taken with digital calipers and rounded to the nearest 0.1 mm, TailL were measured using a measuring tape with a precision of 1 mm.

Measurements and meristic characters for males and females were compared using the two-tailed independent samples Student's *t*-test. SPSS (version 10.0 for Macintosh) was used for all statistical analysis.

SPECIES DESCRIPTION

Calotes chincollium Vindum, sp. nov.

Figs. 1–5

?*Calotes emma*, Shreve 1940, Proc. New England Zool. Club 18:24.

DIAGNOSIS AND COMPARISONS.— A species of *Calotes* morphologically similar to *C. mystaceus*, head and body robust, slightly compressed dorso-ventrally, snout-vent length to 142.9 mm; body scales relatively small, homogeneous, feebly keeled, arranged in regular rows, upper dorso-lateral scales pointing backwards and upwards and lower flank scales pointing backwards, 59–74 midbody scale rows; dorsal and dorso-lateral scales nearly equal in size to ventrals. Head shape triangular, forehead concave; one enlarged temporal spine on either side of the upper head between the occiput, orbit and tympanum. Nine to 12 supralabial scales and eight to 11 infralabials. Gular scales feebly keeled, males with large gular pouch and cheek pouches. Nuchal crest composed of erect compressed scales, partly overlapping, lanceolate, slightly falcate, directed posteriorly; dorsal crest follows the nuchal crest without a gap, 42–54 nuchal and dorsal crest spines. Distinct oblique fold of skin covered with small granular dark brown scales in front of shoulder. Limbs moderate, fourth toe longer than third, fourth right toe with 23–28 subdigital lamellae. Tail in adult males swollen posterior to base.

Calotes chincollium can be differentiated from all other *Calotes* by a combination of the following characters: its large size at maturity, relatively small body scales, the presence of an oblique fold in front of shoulder, the presence of head spines and the males having a swollen tail posterior to base. *C. chincollium* differs from other Myanmar and northeast India congeners as follows: from the males of all other species, except *C. kingdonwardi*, by males having a swollen tail base; from *C. maria* and *C. jerdoni* by lacking two parallel rows of compressed scales above tympanum and by its larger size (SVL to 120 mm in *C. maria* [Smith 1935]) and to 100 mm in *C. jerdoni* (adult CAS specimens); from *C. mystaceus* by the larger number of midbody scale rows (*C. mystaceus* having 47–57 [CAS specimens]; 48–56 [Hallermann 2000]) and by the gradual reduction in size of the crest scales from the nuchal crest scales to the dorsal crest scales (crest scales in *C. mystaceus* are shorter in the nape area, between the nuchal and dorsal crests); from *C. versicolor* by having an oblique fold in front of shoulder (absent in *C. versicolor*) and larger number of midbody scale rows (*C. versicolor* has 40–50 [Smith 1935]); from *C. emma* by lacking postorbital spines and by having small supraocular scales (*C. emma* has large rectangular supraoculars); and from *C. kingdonwardi* by having more midbody scale rows (45 in *C. kingdonwardi* [Smith 1935] and KIZ specimens), and having scales on the side of the body pointing upwards and backwards and the lower

flank scales pointing backwards (scales in *C. kingdonwardi* pointing backwards and downwards except for upper two to three rows, which point slightly upwards (Smith 1935) or straight backwards [KIZ specimens]) and the presence of head spines and a dorsal crest which are lacking and greatly reduced, respectively, in *C. kingdonwardi* (Smith 1935 and KIZ specimens).

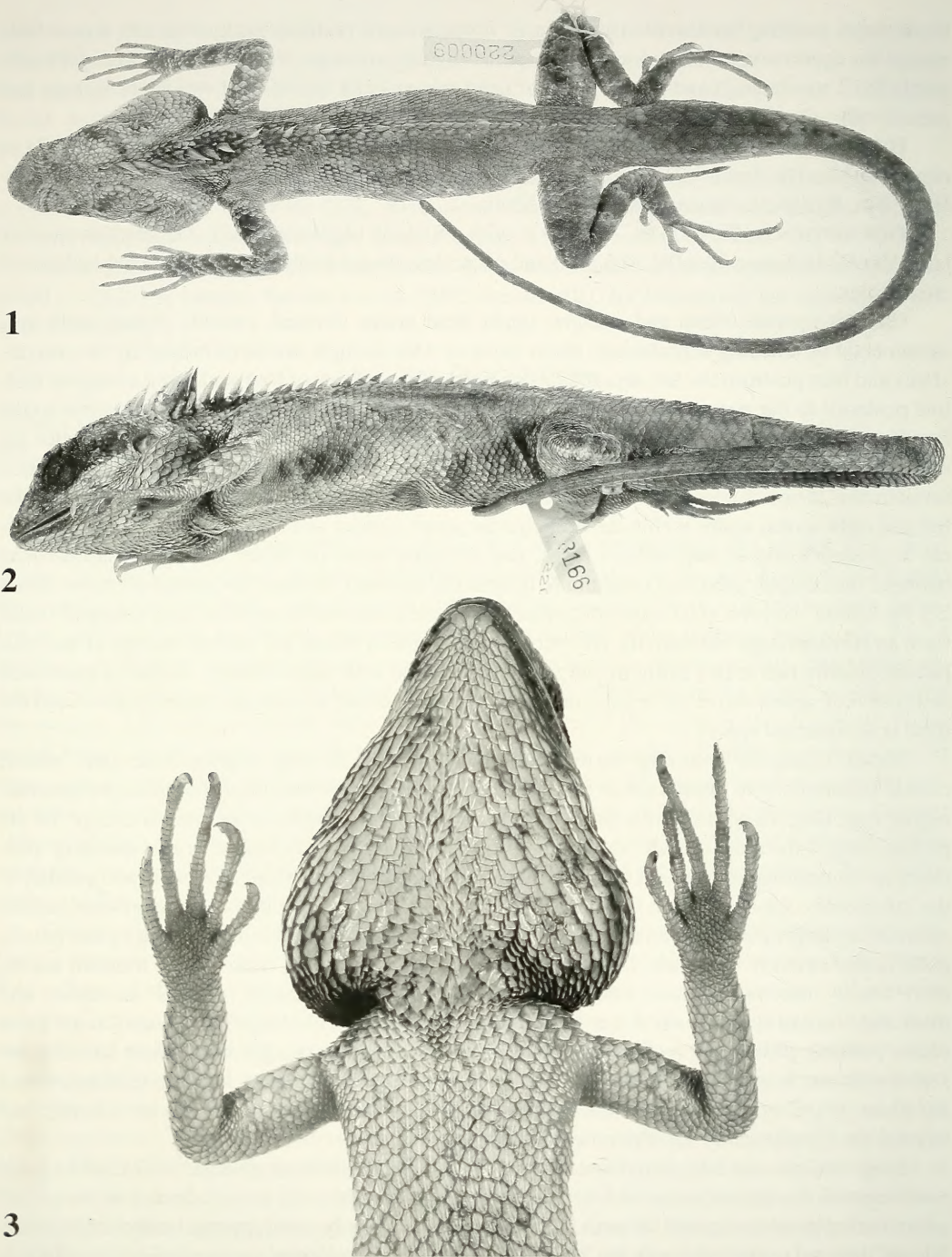
HOLOTYPE.—CAS 220009 (Figs. 1–3), adult ♂, from 21°23'11.2" N, 93°58'15.9" E, 1174 m elevation, Min Dat Township, Min Dat District, Chin State, Myanmar, collected 20 March 2002 by Htun Win, Kyi Soe Lwin and Awan Khwi Shein.

DESCRIPTION OF HOLOTYPE.—Adult ♂ with a SVL of 142.9 mm; TailL 253 mm (incomplete tail); HeadL 48.6 mm; HeadW 30.6 mm; and 68 scales around midbody and 46 nuchal and dorsal crest scales.

Canthus rostralis sharp and straight; upper head scales unequal, smooth; rostral scale low, same height as touching supralabials, about twice as wide as high, bordered behind by two supralabials and four postrostrals; ten supralabials on both sides; a series of four scales run along the midline posterior to the postrostrals, the third and fourth largest and slightly elevated; posterior to the fourth scale, are two scales on either side directed diagonally towards the orbit; the posterior six scales form a weak inverted 'Y'-shaped pattern; the inner border of the supraocular region with a semicircular series of enlarged, feebly keeled scales; at closest point three head scales separate the left and right series; scales within the semicircular series smaller and feebly keeled; a minute tubercle at posterior end of supraciliary ridge; one enlarged spine on either side of the upper head between the occiput, orbit and tympanum; tympanum exposed, 6.8 mm horizontal diameter, about 2/3 the size of the orbit (10.6 mm horizontal diameter); a transverse series of four enlarged scales form an elevated ridge between the posterior margin of the orbit and the anterior margin of the tympanum, middle two scales being the largest and posterior scale most strongly keeled; a transverse series of four scales above the tympanum, anterior scale keeled, second and fourth pointed and the third is an enlarged spine.

Mental triangular becoming narrow posteriorly, as wide as long, slightly wider than rostral; mental followed by an infralabial on either side and two irregular shaped postmentals; postmentals higher than long, in contact with the first infralabials and the length of the mental except for the posterior tip of the mental where the postmentals are separated by two small scales medially; posterior to the postmentals are two chin shields on each side that are longer than wide and parallel to the infralabials, separated from the infralabials by one scale row. The first and second chin shields are scarcely larger than the chin shields following; ten infralabials on both sides; large gular pouch, gular scales strongly imbricate; lateral gular scales form a gradation from almost rounded scales, each weakly mucronate, most smooth or with a slight rise medially to more lanceolate and mucronate medial scales, outer scales wider than long, medial scales longer than wide; lateral gular scales pointing posteriorly and medially, medial scales pointing straight back; most lateral gular scales with one hair receptor at tip or in notch next to tip; cheek pouches large, extending beyond the plane of the temporal region (horizontally from the base of the tympanum) by 6.1 mm, and beyond the tympanum by 9.5 mm on either side.

Large oblique curved fold in front of shoulder, covered with small granular scales; seven scale rows separate the dorsal border of fold from the base of upright scale series adjacent to the nuchal crest; nuchal crest composed of erect compressed scales, partly overlapping, lanceolate, slightly falcate, directed posteriorly, with the 7th to 10th scales being the largest, and a continuous reduction in size anteriorly and posteriorly; dorsal crest follows the nuchal crest without a gap, the gradation of decreasing scale length is continuous posteriorly and does not change from nuchal crest scales to dorsal crest scales; longest nuchal scale extends 15.3 mm from the base of the scale bordering the crest scale; dorsal crest scales do not overlap and become more triangular and gradually lower



FIGURES 1–3. (1) Dorsal view of the holotype of *Calotes chincollium*, sp. nov. (CAS 220009), male, SVL 142.9 mm, from 21°23'11.2" N, 93°58'15.9" E; 1174 m elevation, Min Dat Township, Min Dat District, Chin State, Myanmar; (2) Lateral view of the holotype of *Calotes chincollium*, sp. nov.; (3) Ventral view of anterior portion of the holotype of *Calotes chincollium*, sp. nov. Photographs by Dong Lin, California Academy of Sciences.

posteriorly; 46 mid-dorsal crest scales from the occiput to above the anterior margin of the vent; scales are reduced to a low crest over the sacrum, forming a keeled ridge along the anterior portion of the tail. The nuchal and dorsal crests are bordered on either side by a row of lower erect (pointing dorsally and posteriorly), keeled, mucronate, scales, becoming smaller posteriorly, ending at the sacrum; dorsal and lateral body scales feebly keeled, imbricate, dorsal scales being slightly larger, pointing slightly dorso-posteriorly, lower scales on flanks pointing backwards; dorsal and lateral scales equal in size with ventral scales, the slightly larger dorsal-most scales on sides are about equal to the ventral scales in the chest area, and the lower lateral scales are equal to ventral scales on the abdomen; ventral scales keeled, imbricate, weakly mucronate, pointing posteriorly, 20–22 rows; left hemipenis partially everted.

Forelimbs covered with imbricate, feebly keeled scales, some slightly mucronate; third and fourth, second and fifth, fingers equal in length, first finger smallest; scales under fingers bicarinate, right fourth finger with 23 lamellae (including last scale on claw base); dorsal surface of thigh and dorsal and ventral surfaces of lower leg with imbricate, feebly keeled scales, some slightly mucronate; ventral surface of thigh with smooth rectangular, slightly imbricate scales; scales on posterior portion of thigh imbricate, keeled and mucronate; fourth toe longest (about 1/3 longer than third) followed by third, fifth, second and first; scales under toes bicarinate, right fourth toe with 25 lamellae (including last scale on claw base).

Tail slightly oval in cross-section, swollen posterior to base, with large, strongly keeled, mucronate, scales, arranged in longitudinal rows; tail tip autonomized. Scales of tail larger than dorsal or ventral body scales.

COLORATION IN ALCOHOL.—Upper head grayish, darker on snout; supraciliaries with two parallel light brown bars perpendicular to head axis; irregular brown patch from anterior border of orbit to dorso-anterior border of tympanum, extending dorsally to the supraciliary ridge, slightly bifurcating posteriorly, lower branch ending at the tympanum and the upper extending to the nuchal crest at occiput. Light gray on upper lip extending dorsally to orbit and lower temporal area (below dorsal borders of tympanum), tympanum and cheek pouches. Body grayish with four brownish irregular saddles extending across the back. Anterior-most saddle weak, directly behind occiput, most scales gray with brown at base; second and third saddles brown from base of dorsal crest scales to fourth scale row below dorsal crest (counting crest scale as first). Fourth saddle extends down six scale rows, dorsal portion of saddles the widest, each saddle separated by one or two scales. Tail uniform light olive-brown with dark and light barring toward the tip, darker bars about four transverse scale rows wide, lighter bars two to three scale rows. Dorsal surface of forelimbs grayish with irregular brown bars, gray bars one scale row wide, brown bars two scale rows wide; barring extends on to foot (barring is more prominent on left forelimb). Upper surface of thigh grayish at base with increasing brown proximally, lower leg and foot with gray and brown barring, with brown bars being wider. Gular pinkish from scales posterior to mental and postmentals and extending to ventral portion of cheeks. Inner scales of oblique fold in front of shoulder black. Venter and ventral surface of limbs gray. Ventral side of tail light brownish-gray.

VARIATION.—Body measurements and meristic characters are shown in Tables 1 and 2, respectively, for specimens with a SVL more than 96 mm.

Specimens ranged in size from the smallest juvenile with a SVL of 33.8 mm (CAS 222349) to the largest male SVL 142.9 mm (CAS 220009); and the largest female SVL 123.5 mm (CAS 220120).

Adult males are significantly larger than adult females, having longer snout-vent lengths, tail lengths, head lengths, head widths, and fewer dorsal crest scales (Table 3). The heads of adult males are absolutely and proportionally longer and wider than females of the same snout-vent

TABLE 1. Sex and measurements (in mm) for *Calotes chincollium*
(- indicates incomplete tail and * indicates measurements from left foot)

Catalog Number	SEX	SVL	TailL	TailL/ SVL	HeadL	HeadW	HeadW/ HeadL	HeadL/ SVL	HeadW/ SVL	3rd Toe	4th Toe	TailD
CAS 219972	M	133.3	247	1.85	44.6	27.5	0.617	0.335	0.206	14.3	18.7	17.3
CAS 219973	M	114.3	235	2.06	37.7	22.5	0.597	0.330	0.197	14.0	19.6	13.8
CAS 219974	M	119.0	198-		38.2	22.8	0.596	0.321	0.192	13.4	20.1	15.0
CAS 219976	M	134.7	271	2.01	47.4	28.6	0.603	0.352	0.212	14.0*	21.6*	18.9
CAS 219977	M	120.2	242	2.01	41.2	25.8	0.626	0.343	0.215	14.3	18.5	17.5
CAS 219978	M	112.0	235	2.10	37.5	21.0	0.560	0.335	0.188	14.3	19.6	13.8
CAS 219990	M	117.5	238	2.03	41.0	25.0	0.610	0.349	0.213	13.8	20.7	16.3
CAS 219996	M	120.2	267	2.22	40.3	25.6	0.635	0.335	0.213	13.6	20.5	16.1
CAS 219997	M	101.6	214	2.11	33.6	21.0	0.625	0.331	0.207	14.2	19.2	13.7
CAS 220009	M	142.9	253-		48.6	30.6	0.630	0.340	0.214	17.0	25.0	19.2
CAS 220012	M	134.1	269	2.01	45.4	28.3	0.623	0.339	0.211	13.5*	19.8*	17.5
CAS 220027	M	127.2	269	2.11	44.3	26.3	0.594	0.348	0.207	15.3	22.2	17.3
CAS 220028	M	101.3	201-		33.0	19.7	0.597	0.356	0.194	14.3	19.8	13.3
CAS 220029	M	120.5	288	2.39	44.1	27.2	0.617	0.366	0.226	14.9	22.2	17.5
CAS 220034	M	100.1	211	2.11	33.1	19.9	0.601	0.331	0.199	12.8	17.6	12.5
CAS 220035	M	115.5	238	2.06	38.5	22.9	0.595	0.333	0.198	13.2	17.8	16.3
CAS 220039	M	136.3	293	2.15	49.4	28.8	0.583	0.362	0.211	16.9	23.0	19.8
CAS 220046	M	130.8	281	2.15	42.7	26.3	0.616	0.326	0.201	16.7	24.0	17.2
CAS 220049	M	139.2	306	2.20	49.0	29.4	0.600	0.352	0.211	16.4	22.8	18.1
CAS 220117	M	132.6	287	2.16	48.5	29.8	0.614	0.366	0.225	15.7	21.5	18.8
CAS 220121	M	130.2	290	2.23	46.6	29.6	0.635	0.358	0.227	16.3	23.0	20.1
CAS 220125	M	137.9	297	2.15	45.9	29.8	0.649	0.333	0.216	14.6	20.1	18.2
CAS 220577	M	114.2	265	2.32	37.7	22.2	0.589	0.330	0.194	16.7	19.7	13.7
CAS 220580	M	131.3	266	2.03	46.5	30.8	0.662	0.354	0.235	14.5	19.9	18.6
CAS 220581	M	108.2	244	2.26	37.4	21.4	0.572	0.346	0.198	14.7	20.6	14.1
CAS 220582	M	118.5	248	2.09	38.5	23.7	0.616	0.325	0.2	13.6	18.7	15.0
CAS 220583	M	125.5	265	2.11	44.5	27.4	0.616	0.355	0.218	15.6	22.3	17.9
CAS 222354	M	104.0	216	2.08	34.9	20.7	0.593	0.336	0.199	13.3	17.9	13.6
CAS 222370	M	126.4	261	2.06	43.3	26.6	0.614	0.343	0.21	16.2	21.7	15.4
MCZ 44727	M	113.4	252	2.22	38.9	22.7	0.584	0.343	0.2	15.0	20.6	14.7
MCZ 44728	M	114.7	255	2.22	40.6	22.2	0.547	0.354	0.194	14.7	21.7	14.8
MCZ 44729	M	104.2	222	2.13	35.5	21.3	0.600	0.341	0.204	14.8	18.5	15.4
USNM 547926	M	117.6	232	1.97	40.4	24.3	0.601	0.344	0.207	16.0	21.2	15.4
USNM 547927	M	137.1	299	2.18	49.5	30.8	0.622	0.361	0.225	16.7	24.3	19.8
CAS 219971	F	96.8	206	2.13	30.8	19.0	0.617	0.318	0.196	12.5	16.8	8.8
CAS 219975	F	119.5	234	1.96	35.9	22.2	0.618	0.300	0.186	13.5	18.6	11.9
CAS 220014	F	113.7	251	2.21	36.1	22.0	0.609	0.318	0.193	15.2	20.4	11.6
CAS 220022	F	117.8	220	1.87	35.6	21.6	0.607	0.302	0.183	16.9	24.1	11.0
CAS 220120	F	123.5	251	2.03	38.9	20.9	0.537	0.315	0.169	14.3	19.9	11.0
CAS 220578	F	97.7	204	2.09	30.8	18.4	0.547	0.315	0.188	13.1	18.5	9.6
CAS 220579	F	99.4	224	2.25	32.5	18.7	0.597	0.327	0.188	13.2	19.0	9.9
CAS 220584	F	114.7	229	2.00	38.6	22.0	0.570	0.337	0.192	14.0	21.9	11.8
CAS 220587	F	108.2	221	2.04	34.1	20.0	0.587	0.315	0.185	14.2	18.2	11.0
CAS 222351	F	101.7	230	2.26	32.9	20.2	0.614	0.324	0.199	13.3	19.7	11.2

TABLE 2. Meristic characters for *Calotes chincollum*
(* indicates scale counts from left foot)

Catalog Number	SEX	Mid B	DC	SupL (L/R)	InfL (L/R)	SDL 4th Toe
CAS 219972	M	68	47	11/11	10/10	25
CAS 219973	M	63	46	11/10	10/11	26
CAS 219974	M	59	45	12/11	10/10	25
CAS 219976	M	61	45	9/9	8/11	26*
CAS 219977	M	70	45	11/10	9/9	23
CAS 219978	M	65	45	10/11	9/9	23
CAS 219990	M	65	46	11/10	9/9	26
CAS 219996	M	66	45	11/10	10/9	26
CAS 219997	M	61	44	10/10	9/9	25
CAS 220009	M	68	46	10/10	10/10	25
CAS 220012	M	67	48	10/9	10/10	25
CAS 220027	M	69	45	9/10	10/10	25
CAS 220028	M	63	46	11/10	10/10	27
CAS 220029	M	74	54	12/11	11/11	26
CAS 220034	M	62	45	10/11	9/10	23
CAS 220035	M	66	45	11/10	9/9	26
CAS 220039	M	68	45	11/11	11/9	25
CAS 220046	M	71	45	11/10	10/10	27
CAS 220049	M	69	42	10/10	10/10	26
CAS 220117	M	70	45	10/10	10/11	26
CAS 220121	M	69	45	9/10	9/10	26
CAS 220125	M	67	45	9/11	9/10	25
CAS 220577	M	62	42	11/11	10/10	25
CAS 220580	M	66	48	10/9	10/9	25
CAS 220581	M	62	44	10/9	9/10	27
CAS 220582	M	69	47	10/10	10/11	25
CAS 220583	M	68	46	10/10	9/10	25
CAS 222354	M	70	46	11/11	11/11	26
CAS 222370	M	68	46	10/11	10/9	24
MCZ 44727	M	68	44	10/10	9/9	26
MCZ 44728	M	71	46	10/10	9/10	25
MCZ 44729	M	65	49	9/9	9/9	26
USNM 547926	M	70	47	10/11	11/9	25
USNM 547927	M	67	45	11/10	10/11	28
CAS 219971	F	65	45	11/11	10/10	24
CAS 219975	F	67	47	10/11	9/9	25
CAS 220014	F	68	47	10/11	9/9	26
CAS 220022	F	65	47	9/9	9/9	28
CAS 220120	F	70	48	10/10	10/10	23
CAS 220578	F	66	50	10/10	9/9	28
CAS 220579	F	70	47	11/11	10/10	26
CAS 220584	F	71	49	10/11	8/10	24
CAS 220587	F	65	46	10/10	11/10	23
CAS 222351	F	70	49	10/10	9/9	23

length. Additional sexual characteristics include males having a swollen tail posterior to its base (Table 3) and larger cheek pouches. The dorsal coloration differs between the sexes with the dark saddles in males being lighter or completely faded posteriorly.

COLOR IN LIFE (Fig. 4; based on color transparency of CAS 222354 [♂]): Upper head gray, side of head with distinct dark brown mask from loreal area through orbit and temporal region;

TABLE 3. Body measurements (mm) and meristic characters for male and female *Calotes chincollium* ($X \pm SD$, followed by ranges in parentheses, N=34 for males (except for TailL where N=31) and N=10 for females). Statistically significant results at $0.05 \geq P > 0.01$ are marked with one asterick (*), results at $0.01 \geq P > 0.001$ are marked with two astericks (**) and results at $P \leq 0.001$ are marked with three astericks (***).

	Males	Females
SVL**	121.7 \pm 12.1 (100.1–142.9)	109.3 \pm 9.9 (96.8–123.5)
TailL***	258.2 \pm 26.6 (211–306)	227.0 \pm 15.9 (204–251)
HeadL***	41.7 \pm 5.0 (33.0–49.5)	34.6 \pm 2.9 (30.8–38.9)
HeadW***	25.4 \pm 3.5 (19.7–30.8)	20.5 \pm 1.5 (18.4–22.2)
3rd Toe	14.9 \pm 1.2 (12.8–17.0)	14.0 \pm 1.3 (12.5–16.9)
4th Toe	20.7 \pm 1.9 (17.6–25.0)	19.7 \pm 2.1 (16.8–24.1)
TailD***	16.4 \pm 2.2 (12.5–20.1)	10.8 \pm 1.0 (8.8–11.9)
MidB	66.7 \pm 3.5 (59–74)	67.7 \pm 2.4 (65–71)
DC*	45.7 \pm 2.1 (42–54)	47.5 \pm 1.5 (45–50)
SDL 4th Toe	25.4 \pm 1.1 (23–28)	25.0 \pm 1.9 (23–28)
TailL/SVL	2.12 \pm 0.108 (1.85–2.39)	2.08 \pm 0.129 (1.87–2.26)
HeadL/SVL***	0.343 \pm 0.0122 (0.321–0.366)	0.317 \pm 0.0109 (0.300–0.337)
HeadW/SVL***	0.208 \pm 0.0114 (0.188–0.235)	0.188 \pm 0.00833 (0.169–0.199)

white along the upper lip to the orbit and upper margin of the tympanum and along lower jaw extending onto cheek pouch; nuchal crest bright yellow; gular orange; anterior half of body creamy yellow with flanks spotted with darker yellow, first two dorsal saddles brown; posterior portion of body with light brown and gray mottling; forelimbs banded dark brown and white.

COLORATION IN ALCOHOL (Fig. 5; based on CAS 220022 [♀]): Upper head speckled tan, gray and cream; supraciliaries with two parallel brown bars perpendicular to head; brown patch from anterior border of orbit to dorso-anterior border of tympanum extending dorsally to spines above tympanum; lighter brown (but darker than upper head coloration) between spines over tympanum and occiput spines extending from the posterior supraciliary ridge to the back of the head. Light gray on upper lip extending dorsally to orbit and extending to the lower temporal area including the tympanum. Dorsal coloration cream becoming gray on flanks. Brown triangular patch extending along the anterior margin of the fold in front of the shoulder to the posterior side of the angle of the jaw, extending horizontally between the back of the head (at the level of the upper margin of the tympanum) back to the shoulder fold. From nape to area dorsal to the anterior margin of the vent are seven dark brown irregular bands or saddles, with the coloration extending onto the nuchal and dorsal crest scales. The first four saddles are the most distinct. The anterior most saddle on the nape extends from the nuchal crest onto the back of the head, forming a V-shaped pattern; posterior to the nape the bands are widest along the dorsal crest becoming constricted on the lower portion of the dorsum and then becoming less distinct, irregular and bifurcated on the flank. The sec-

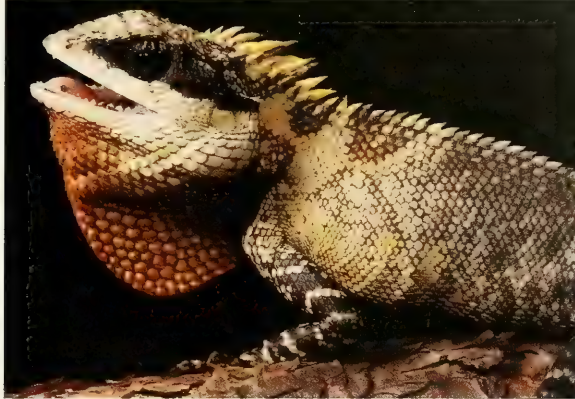


FIGURE 4. Paratype of *Calotes chincollum*, sp. nov. (CAS 222354) a male, SVL 104.0 mm, from 21°11'53.3" N, 94°04'00.5" E, Kanpetlet Township, Min Dat District, Chin State, Myanmar. Photograph by Hla Tun, Forest Department, Ministry of Forestry, Myanmar.

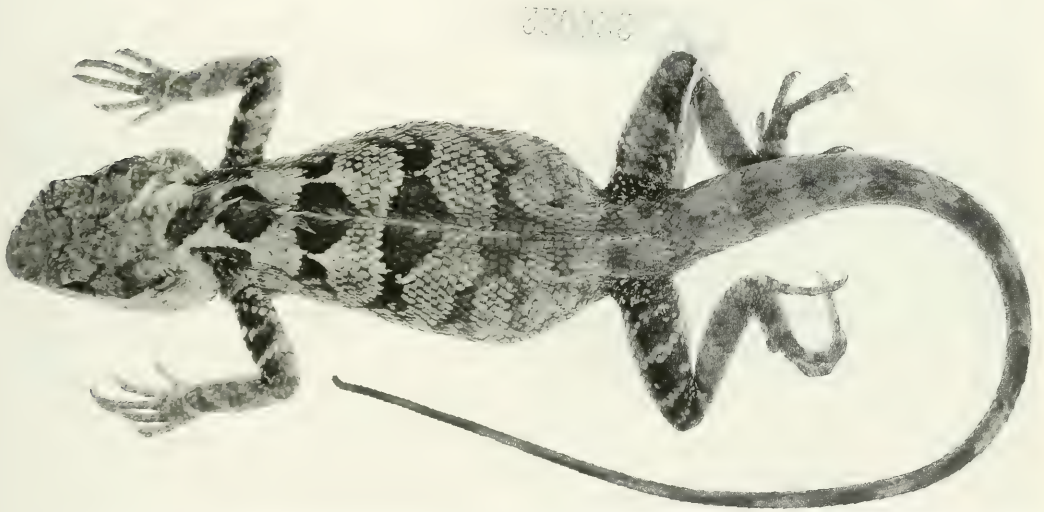


FIGURE 5. Paratype of *Calotes chincollum*, sp. nov. (CAS 220022) a female, SVL 117.8 mm, from 21°22'11.5" N, 93°46'01.7" E, 1,732 m elevation, Min Dat Township, Min Dat District, Chin State, Myanmar. Photograph by Dong Lin, California Academy of Sciences.

ond and third are separated from the brown flank pattern by one scale row giving a faint hint of a lateral stripe. When viewed from above the dorsal bands appear triangular in shape, with the tip of the triangle pointing backwards. The tail is banded throughout with light and dark brown banding, the darker bands being wider. Forelimbs and hindlimbs barred like in holotype. Gular scales pinkish on anterior two-thirds and along the sides; medial posterior third with scales having small dark gray spotting giving an overall grayish appearance. Venter including upper forearms and legs with light gray and dark gray mottling, more so on abdomen. Lower arms and legs with uniform light gray. Underside of tail light and dark gray banding corresponding to the dorsal bands.

CAS 219975, ♀, SVL 119.5 mm, tail length 234 mm, is similar in pattern to CAS 220022 but darker and mottled throughout. Only nape and following two saddles distinct.

COLORATION IN ALCOHOL OF SMALLEST JUVENILE (CAS 222349, SVL 33.8 mm): Upper head gray-brown; supraciliaries with two faint parallel brown bars perpendicular to head; orbit with nine dark brown stripes radiating outwards from eye; brown patch from anterior border of orbit to dorso-anterior border of tympanum extending dorsally to spines above tympanum; lighter brown (but darker than upper head coloration) between spines over tympanum and occiput spines extending from the posterior supraciliary ridge to the back of the head. Light gray on upper lip extending dorsally to orbit and extending to the lower temporal area including tympanum. Dorsal coloration gray. Faint dark brown horizontal stripe extending from the dorsal margin of the fold in front of the shoulder to the back of the head. From nape to area dorsal to the anterior margin of the vent are five brown irregular saddles. The anterior most saddle on the nape extends from the nuchal crest laterally two scale rows. When viewed from above the dorsal bands appear triangular in shape, with the tip of the triangle pointing backwards. The tail is banded throughout with light and brown banding, the lighter bands being wider. Forelimbs and hindlimbs bared. Venter including upper forearms and legs light gray. Lower arms and legs uniform light gray.



FIGURE 6. Map of western Myanmar illustrating the distribution of *Calotes chincollum*. Map prepared by Michelle S. Koo, California Academy of Sciences.

ETYMOLOGY.— The specific epithet refers to the type locality being in the Chin Hills; *chincollum* is a combination of the Anglicized version of a Burmese inscription word for the Chin people and *collium*, Latin in the genitive plural of *collis*, meaning hill.

DISTRIBUTION AND NATURAL HISTORY.— *Calotes chincollum* is known from the Chin Hills, Chin State, and from the Ponnnyaung Range, Sagaing Division, Myanmar (Fig. 6), between elevations of 737 m to 1940 m. The species is most common in areas of shifting cultivation and extends into secondary forest. The species is not found in primary forest. It is primarily found on the ground but climbs onto the base of trees. Htun Win and Awan Khwi Shein observed individuals in recently planted corn fields digging up newly sprouting corn and eating the endosperm tissue of the seedlings.

The holotype was found in sympatry with *Calotes jerdoni*, *C. mystaceus* and *C. versicolor*. Other agamids in the vicinity of *Calotes chincollum* include *Ptyctolaemus gularis*, *Draco maculatus* and *Japalura planidorsata*.

DISCUSSION

The new species superficially resembles the description given by Taylor (1963) for *Calotes emma alticristatus* Schmidt 1925, except that *C. emma alticristatus* has enlarged, elongate scales in the supraocular region; two enlarged chin shields behind each of the postmentals; five postrostral scales; a grayish chin and gular area with black interstitial skin; and tail base is not swollen (Taylor did not give the sex of his specimen, and we have not been able to locate it).

The type locality of *C. emma alticristatus* is "Yunnanfu, Yunnan" (Schmidt 1925), and Taylor

(1963) reported the distribution extending into Chiang Mai Province, Thailand. However, Wermuth (1967), Welch (1994) and Cox et al. (1998) list the distribution of *C. emma alticristatus* as extending northwest into Assam, India. We have found no evidence (either specimens or records in the literature) of *C. emma alticristatus* occurring west of Thailand (namely in Burma, India or Bangladesh). Specimens of *C. emma* from Mon State (CAS 222213), Shan State (CAS 215260) and Mandalay Division (CAS 216395), Myanmar, and Bangladesh (CAS 94323) all have enlarged postorbital spines characteristic of *C. emma emma*.

Recent collections from the lowlands surrounding and the mountains of the Indo-Burman Range, specifically the Rakhine Yoma and Chin Hills have yielded a number of new species: *Lycodon zawi* (Slowinski et al. 2001) from the Rakhine Yoma, Rakhine State, Ponnyadaung Range, Sagaing Division, and the Khasi Hills, India; *Calotes chincollium* from the Chin Hills and the Ponnyadaung Range; *Bufo* sp. (Wogan et al. 2003) and *Chirixalus* sp. (Wilkinson et al. 2003) from the western lowlands of the Rakhine Yoma; and at least three additional new frog species yet to be described from the Rakhine Yoma (pers. commun. G.O.U. Wogan 2002). All new species seem to be endemic to the Indo-Burman Range or limited to the Rakhine Yoma or Chin Hills within the Indo-Burman Range, with the exception of *Lycodon zawi*, which extends into the Khasi Hills, India.

The occurrence of new species being discovered in the Indo-Burman Range is not surprising considering the geological history of the area and the paucity of collections. The Indo-Burman Range (since the late Miocene) was formed by the subduction of the Indian plate causing the obduction of an accretionary prism upon the Indian continental margin (Ni et al. 1989). The resulting mountain ranges consist of deep canyons, ridges, and high peaks, the latter reaching elevations of 1,989 m in Rakhine State, 3109 m in Chin State, and 3,826 m in Sagaing Division. The vegetation types within the Indo-Burman Range includes lowland tropical rain forest along the Bay of Bengal, subtropical lowland forest, subtropical mountain forest and temperate mountain forest at higher elevations (Davis 1964). The formation of the Indo-Burman Range clearly impacted local climate, especially rainfall, and vegetation. With the progressive increase in topographic relief, occasioned by collision tectonics since late-Miocene, vicariant speciation, a consequence of the disruption of gene flow among the closely allied but increasingly fragmented populations of reptiles and amphibians, resulted in a high degree of local species endemism.

As noted above, relatively few collections have been made in the Indo-Burman Range. For instance, other than incidental collections, the only serious collecting forays were made by F.E.W. Venning, who collected in the Hakha area from 1908 to 1910 (Venning 1910a, 1910b), and Gerd Heinrich, who collected in the Mount Victoria area of the Chin Hills in 1938 (Shreve 1940). Thus, the work of the Myanmar Herpetological team, which will return to the Indo-Burman Range in 2003, can be expected to generate exciting new information about the diversity of amphibians and reptiles in this pivotal region of southeast Asia.

KEY TO THE SPECIES OF THE GENUS *CALOTES* OF MYANMAR

- 1. Two parallel rows of compressed spines above tympanum present *C. jerdoni*
Two parallel rows of compressed spines above tympanum absent 2
- 2. Head spines absent *C. kingdonwardi*
Head spines present 3
- 3. Fold in front of shoulder absent *C. versicolor*
Fold in front of shoulder present 4

- 4 Large postorbital spine present *C. emma*
Large postorbital spine absent 5
- 5. 47–57 midbody scale rows, tail not swollen posterior to base in males *C. mystaceus*
59–74 midbody scale rows, tail swollen posterior to base in males *C. chincollium*

MATERIAL EXAMINED

HOLOTYPE:— CAS 220009 (♂), from 21°23′11.2″ N, 93°58′15.9″ E, 1174 m elevation, Min Dat Township, Min Dat District, Chin State, Myanmar, collected 20 March 2002 by Htun Win, Kyi Soe Lwin and Awan Khwi Shein.

PARATYPES (43 specimens, all from Chin State, Myanmar and, except as noted, collected by combinations of Htun Win, Thin Thin, Kyi Soe Lwin, Awan Khwi Shein and Hla Tun).— CAS 219971 (♀), 21°23′26.6″ N, 94°03′31.2″ E, Htin Chaun Village, Min Dat Township, Min Dat District, collected 18 March 2001; CAS 219972–219973 (♂♂), from 21°23′26.6″ N, 94°03′31.2″ E, Htin Chaun Village, Min Dat Township, Min Dat District, collected 18 March 2001; CAS 219974 (♂), CAS 219975 (♀), from 21°22′20.1″ N, 93°58′34.6″ E, 1482 m elevation, Baw Khue Plantation, Htin Chaun Village, Min Dat Township, Min Dat District, collected 18 March 2001; CAS 219976 (♂), from 21°22′52.7″ N, 93°53′43.8″ E, Baw Khue Plantation, Min Dat Township, Min Dat District, collected 19 March 2001; CAS 219977 (♂), CAS 219978 (♀), from 21°22′20.1″ N, 93°58′34.6″ E, 1482 m elevation, Baw Khue Plantation, Htin Chaun Village, Min Dat Township, Min Dat District, collected 19 March 2001; CAS 219990 (♂), from 21°24′08.2″ N, 93°52′45.0″ E, 1920 m elevation, Baw Khue Plantation, Min Dat Township, Min Dat District, collected 19 March 2001; CAS 219996 (♂), from 21°22′15.5″ N, 93°59′13.6″ E, 1418 m elevation, Min Dat Township, Min Dat District, collected 20 March 2001; CAS 219997 (♂), from 21°23′20.9″ N, 93°52′29.0″ E, 1940 m elevation, Baw Khue Plantation, Min Dat Township, Min Dat District, collected 19 March 2001; CAS 220012, USNM 547926 (♂♂), from 21°22′50.1″ N, 93°58′20.6″ E, 1297 m elevation, Min Dat Township, Min Dat District, collected 20 March 2001; CAS 220014 (♀), from 21°22′50.1″ N, 93°58′20.6″ E, 1297 m elevation, Min Dat Township, Min Dat District, collected 20 March 2001; CAS 220022 (♀), from 21°22′11.5″ N, 93°46′01.7″ E, 1732 m elevation, Min Dat Township, Min Dat District, collected 22 March 2001; CAS 220027–220028 (♂♂), from 21°22′18.3″ N, 93°49′00.6″ E, 1787 m elevation, Hee Laung Village, Min Dat Township, Min Dat District, collected 24 March 2001; CAS 220029 (♂), from 21°23′16.1″ N, 93°58′14.9″ E, 1138 m elevation, Min Dat Township, Min Dat District, collected 20 March 2001; CAS 220034 (♂), from 21°22′07.6″ N, 93°49′04.0″ E, 1624 m elevation, Hee Laung Village, Min Dat Township, Min Dat District, collected 25 March 2001; CAS 220035 (♂), from 21°21′33.7″ N, 93°49′13.6″ E, Hee Laung Village, Min Dat Township, Min Dat District, collected 25 March 2001; CAS 220039 (♂), from 21°20′13.3″ N, 93°55′22.1″ E, 1046 m elevation, Che stream, Min Dat Township, Min Dat District, collected 29 March 2001; CAS 220046 (♂), from 21°19′42.6″ N, 93°55′25.2″ E, Che stream, Min Dat Township, Min Dat District, collected 29 March 2001; CAS 220049 (♂), from 21°21′14.9″ N, 93°56′08.3″ E, Che stream, Min Dat Township, Min Dat District, collected 29 March 2001; CAS 220117 (♂), from 21°22′14.2″ N, 93°48′14.1″ E, Che stream, Min Dat Township, Min Dat District, collected 30 March 2001; CAS 220120 (♀), CAS 220121, USNM 547927 (♂♂), from 21°20′53.8″ N, 93°59′56.3″ E, 1112 m elevation, Che stream, Min Dat Township, Min Dat District, collected 31 March 2001; CAS 220125 (♂), from 21°21′02.3″ N, 93°56′00.2″ E, 783 m elevation, Che stream, Min Dat Township, Min Dat District, collected 2 April 2001; CAS 220577 (♂), from 21°11′44.3″ N, 94°04′53.3″ E, Kanpetlet Township, Min Dat

District, collected 25 February 2001; CAS 220578 (♀), from 21°11'23.0" N, 94°01'49.3" E, Kanpetlet Township, Min Dat District, collected 26 February 2001; CAS 220579 (♀), from 21°11'24.2" N, 94°04'11.2" E, Kanpetlet Township, Min Dat District, collected 27 February 2001; CAS 220580 (♂), from 21°13'19.7" N, 93°57'52.5" E, Kanpetlet Township, Min Dat District, collected 11 March 2001; CAS 220581 (♂), from 21°11'55.2" N, 94°03'57.8" E, Kanpetlet Township, Min Dat District, collected 28 February 2001; CAS 220582 (♂), from 21°11'53.5" N, 94°04'00.5" E, Kanpetlet Township, Min Dat District, collected 28 February 2001; CAS 220583 (♂), CAS 220584 (♀), from 21°11'37.1" N, 94°02'58.2" E; 1572 m elevation, Kanpetlet Township, Min Dat District, collected 12 March 2001; CAS 220587 (♀), from 21°23'25.4" N, 94°03'06.9" E, Htin Chaun Village, Min Dat Township, Min Dat District, collected 17 March 2001; CAS 222351 (♀), from 21°11'31.9" N, 94°03'00.8" E, Kanpetlet Township, Min Dat District, collected 26 February 2001; CAS 222354 (♂), from 21°11'53.3" N, 94°04'00.5" E, Kanpetlet Township, Min Dat District, collected 28 February 2001; CAS 222370 (♂), from 21°21'17.3" N, 93°56'11.0" E, 751 m elevation, Che stream, Min Dat Township, Min Dat District, collected 2 April 2001; MCZ R44727–44729 (♂♂s), from Mt. Victoria, Chin State, Myanmar, collected 31 March to 2 July 1938, by Gerd Heinrich.

ADDITIONAL MATERIAL EXAMINED

Calotes chincollium — CAS 222349, 21°11'27.5" N, 94°04'56.9" E, Kanpetlet Township, Min Dat District, Chin State, Myanmar; CAS 222350, 21°11'23.0" N, 94°01'49.3" E, Kanpetlet Township, Min Dat District, Chin State, Myanmar; CAS 222352–222353, 21°11'44.2" N, 94°04'47.5" E, Kanpetlet Township, Min Dat District, Chin State, Myanmar; CAS 222355–222356, 21°15'43.8" N, 93°59'20.3" E, 1734 m elevation, Thui Shwn Village, Kanpetlet Township, Min Dat District, Chin State, Myanmar; CAS 222357, 21°11'45.5" N, 94°03'48.2" E, 1372 m elevation, Kanpetlet Township, Min Dat District, Chin State, Myanmar; CAS 222358, 21°11'32.3" N, 94°05'11.2" E, Kanpetlet Township, Min Dat District, Chin State, Myanmar; CAS 222359–222360, 21°22'00.4" N, 94°00'40.2" E, Htin Chaun Village, Kanpetlet Township, Min Dat District, Chin State, Myanmar; CAS 222361, 21°22'20.1" N, 93°58'34.6" E, 1482 m elevation, Htin Chaun Village, Kanpetlet Township, Min Dat District, Chin State, Myanmar; CAS 222362, 21°23'26.6" N, 94°03'31.2" E, Htin Chaun Village, Kanpetlet Township, Min Dat District, Chin State, Myanmar; CAS 222363, 21°22'20.1" N, 93°58'34.6" E, Baw Khue Plantation, Min Dat Township, Min Dat District, Chin State, Myanmar; CAS 222364, 21°22'18.3" N, 93°49'00.6" E, 1787 m elevation, Hee Laung Village, Min Dat Township, Min Dat District, Chin State, Myanmar; CAS 222365–66, 21°20'13.3" N, 93°55'22.1" E, 1047 m elevation, Che stream, Min Dat Township, Min Dat District, Chin State, Myanmar; CAS 222367, 21°18'52.4" N, 93°54'48.7" E, 1308 m elevation, Che stream, Min Dat Township, Min Dat District, Chin State, Myanmar; CAS 222368, 21°22'14.2" N, 93°48'14.1" E, Che stream, Min Dat Township, Min Dat District, Chin State, Myanmar; CAS 222369, 21°21'14.9" N, 93°56'08.3" E, Che stream, Min Dat Township, Min Dat District, Chin State, Myanmar; CAS 222371, 21°21'13.1" N, 93°56'03.3" E, 738 m elevation, Che stream, Min Dat Township, Min Dat District, Chin State, Myanmar; MCZ 44730, Mt. Victoria, Chin State, Myanmar; CAS 215505–215507, 22°15'18.0" N, 94°16'46.5" E, Lesha Chaung camp, Alaungdaw Kathapa National Park, Sagaing Division, Myanmar.

Calotes emma — CAS 94323, Lawachera Forest, Srimangal, Bangladesh; CAS 172718, ca. 1200 m elevation, park headquarters complex, Doi Suthep National Park, Chiang Mai Province, Thailand; CAS 172764, ca 1500 m elevation, ca 3.5 km above upper ranger station, on trail to peak, Doi Inthanon National Park, Chiang Mai Province, Thailand; CAS 215260, 20°41'47.5" N, 96°30'17.5" E, Wat Phu Ye camp, Kalaw Township, Shan State, Myanmar; CAS 216395,

22°57'16.8" N, 96°14'26.5" E, Ondan Village, Shwe U Daung Wildlife Sanctuary, Moe Kok Township, Pyin Oo Lwin District, Mandalay Division, Myanmar; CAS 222213, 17°31'23.8" N, 97°03'00.9" E, near Kyauk Phyar Village, Kyaik-Hti-Yo Wildlife Sanctuary, Kyaik-Hti-Yo Township, Mon State, Myanmar.

Calotes jerdoni — CAS 94324, 11.6 km S of Pynursla, Assam, India; CAS 219992–219993, 21°23'01.5" N, 93°53'55.9" E, 1788 m elevation, Baw Khue Plantation, Min Dat Township, Min Dat District, Chin State, Myanmar; CAS 220020, 21°11'08.3" N, 93°45'33.8" E, 1938 m elevation, Min Dat Township, Min Dat District, Chin State, Myanmar; CAS 220026, 21°26'04.6" N, 93°49'29.6" E, 1663 m elevation, Min Dat Township, Min Dat District, Chin State, Myanmar; CAS 221514, 27°26'28.4" N, 97°55'07.5" E, Rabaw, Naung Mon Township, Putao District, Kachin State, Myanmar; CAS 221551, 27°17'23.8" N, 97°51'30.5" E, road between Ahtonga and Rabaw, Machanbaw Township, Putao District, Kachin State, Myanmar.

Calotes kingdonwardi — KIZ 730010 (holotype of *C. kingdonwardi bapoensis*), KIZ 730036, Bapo, Gongshan Xian, Yunnan Province, China.

Calotes mystaceus — CAS 208441, 21°38'36.3" N, 96°00'28.8" E, fields west of Kyauk Se, Shan Ywa Village, Kyauk Se Township, Mandalay Division, Myanmar; CAS 208446, 21°34'05.4" N, 96°09'43.7" E, fields and hills just east of Kyauk Se Village, Kyauk Se Township, Mandalay Division, Myanmar; CAS 213960, 20°57'14.4" N, 95°11'23.6" E, Popa Mountain Park, Kyauk Pan Tawn Township, Mandalay Division, Myanmar; CAS 214092, 20°52'43.7" N, 95°09'56.3" E, Popa Mountain Park, Kyauk Pan Tawn Township, Mandalay Division, Myanmar; CAS 214097, 20°53'01.8" N, 95°10'29.9" E, Popa Mountain Park, Kyauk Pan Tawn Township, Mandalay Division, Myanmar; CAS 214117, 20°58'06.7" N, 95°14'32.4" E, Popa Mountain Park, Kyauk Pan Tawn Township, Mandalay Division, Myanmar; CAS 214168, 21°07'21.3" N, 94°51'29.6" E, Nyaung Oo Township, Lawka Nanda Park, Mandalay Division, Myanmar; CAS 215321, 215323–215326, 20°46'07.3" N, 96°20'05.5" E, Forest Department office, Yin Mar Bin Village, Thazi Township, Mandalay Division, Myanmar; CAS 215930, 21°24'53.2" N, 95°46'55.0" E, Shout Taw Yoe camp, Minsontaung Wildlife Sanctuary, Na Htoe Gyi Township, Mandalay Division, Myanmar; CAS 215970, 21°24'09.8" N, 95°48'06.0" E, Shout Taw Yoe camp, Minsontaung Wildlife Sanctuary, Na Htoe Gyi Township, Mandalay Division, Myanmar; CAS 216014, 21°22'44.4" N, 95°48'05.8" E, Kat Lan Dam, Minsontaung Wildlife Sanctuary, Mandalay Division, Myanmar; CAS 216031, 21°24'43.4" N, 95°49'54.1" E, Htan Taw Village, Minsontaung Wildlife Sanctuary, Na Htoe Gyi Township, Mandalay Division, Myanmar; CAS 215766, 22°14'36.1" N, 94°38'59.1" E, Pwint Kyi camp, Alaungdaw Kathapa National Park, Sagaing Division, Myanmar; CAS 210705, 21°33'43.5" N, 95°12'43.9" E, near Pakokku, Magwe Division, Myanmar; CAS 215895, 21°35'47.5" N, 95°07'18.1" E, Yar Gyi Gone Village, Shin Ma Taung Reserve, Ye Sa Gyo Township, Pakokku District, Magwe Division, Myanmar; CAS 220574–220576, 21°14'45.5" N, 94°09'53.6" E, Forest Department, Saw Town, Saw Township, Gan Gaw District, Magwe Division, Myanmar; CAS 220016, 21°23'16.1" N, 93°58'14.9" E, 1138 m elevation, Min Dat Township, Min Dat District, Chin State, Myanmar; CAS 220586, 21°23'26.6" N, 94°03'31.2" E, Htin Chaun Village, Kanpetlet Township, Min Dat District, Chin State, Myanmar.

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A New Species of *Chirixalus* (Anura: Rhacophoridae) from Western Myanmar (Burma)

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A new species of the rhacophorid genus *Chirixalus* is described from western Myanmar. As with other members of *Chirixalus*, this species possesses a hand in which the two outer fingers oppose the inner fingers. This species differs from other members of this genus by a dorsal pattern of many dark brown spots on a lighter background of the head, trunk, and legs.

Chirixalus is a relatively small genus of 13 species from Asia (Frost 2002). Members of this genus closely resemble species of *Philautus*, except that they possess opposable fingers (Boulenger 1893). Of the 13 species, three are known from Myanmar (*Chirixalus doriae*, *C. nongkhorensis*, and *C. vittatus*). Here, we report a fourth species collected in June of 2001 in western Myanmar near the Bay of Bengal (Fig 1).

Specimens are housed in the collection of the Department of Herpetology, California Academy of Sciences (CAS), the Myanmar Biodiversity Museum (MBM), and the Division of Amphibians and Reptiles, National Museum of Natural History, Smithsonian Institution (USNM). Museum acronyms follow Leviton et al. (1985). Tissues were removed from some specimens, then all were fixed in 10% buffered formalin before preserving in 70% ethanol. Latitude and longitude were recorded with a Garmin 12 GPS, set to datum WGS84.

The preserved specimens were examined, measured, and compared with available specimens and all published descriptions of currently recognized (Frost 2002) species of *Chirixalus* (Boulenger 1887, 1893; Boettger 1895; Annandale 1915; Smith 1924; Cochran 1927; Bourret 1942; Smith 1953; Roonwal and Kripalani 1961; Kuramoto and Wang 1987; Chanda and Ghosh 1989; Ray 1992). Measurements were taken using dial calipers to the nearest 0.1 mm as follows: snout-vent length (SVL); head length (HL); head width (HW); internarial distance (IND); interorbital distance (IOD); snout length (SL); distance from nostril to eye (DNE); forelimb length (FLL); hand length (HLT); thigh length (THL); tibia length (TIL); foot length (FL); width of disk of third finger (3FDW); and width of disk of fourth toe (4TDW).

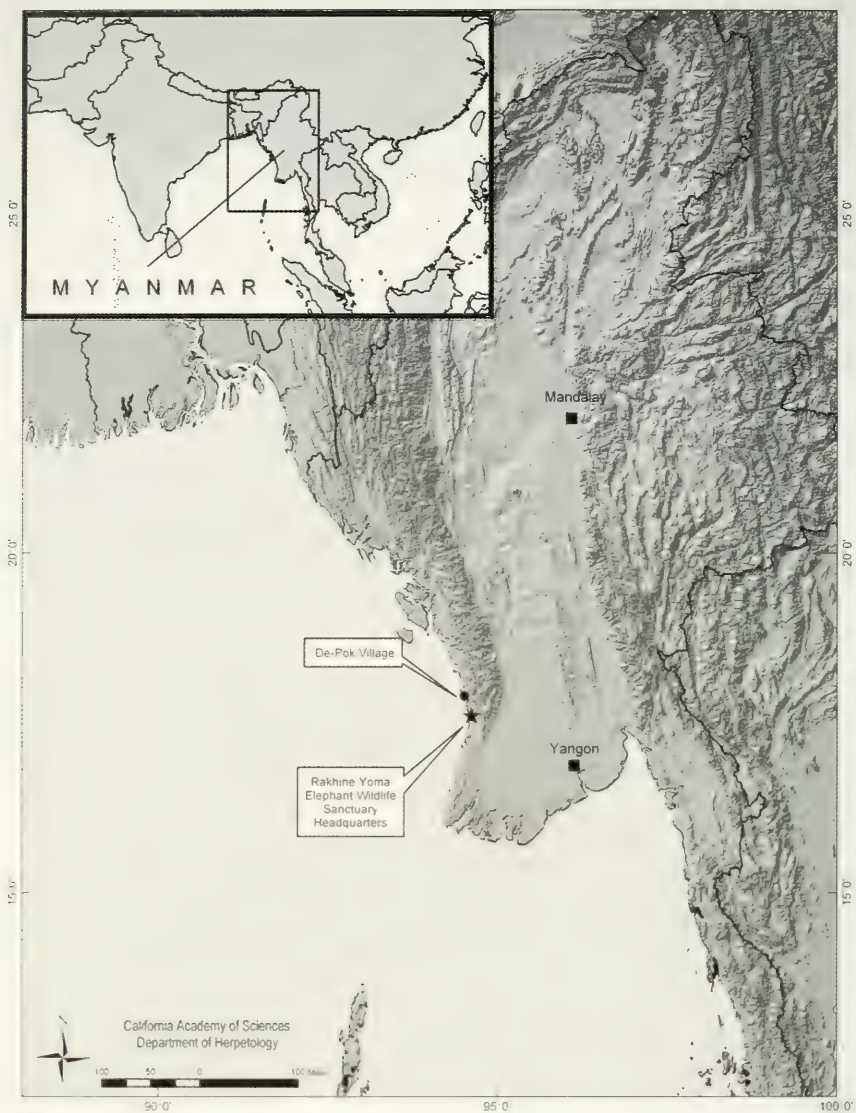


FIGURE 1. Distribution of *Chirixalus punctatus* in Myanmar with type locality indicated by a star.

SPECIES DESCRIPTION

Chirixalus punctatus Wilkinson, sp. nov.

Myanmar spotted treefrog

DIAGNOSIS.— Because *Chirixalus punctatus* is a relatively small frog that possesses expanded discs on the fingers and toes, an intercalary element between the penultimate and terminal phalanges, a flange on the distal end of the third metacarpal, and opposable fingers, it has been placed within *Chirixalus*. It can be distinguished from all other species of *Chirixalus* by a relatively uniform pattern of dark brown spots on a lighter ground color of the dorsal aspect of the head, trunk,

and legs. In addition, *C. punctatus* differs from all other Myanmar species of *Chirixalus* as follows: from *C. doriae* by an indistinct tympanum, a more pointed and elevated snout (Fig. 3), an external vocal sac, webbing only at the base of the third and fourth fingers and absence of webbing on the remainder, and the absence of dark stripes along the head and dorsum (Fig. 4); from *C. nongkhorensis* by the absence of a prominence at the end of the snout (Fig. 3), the absence of small tubercles on the dorsum, the absence of striping on the dorsal aspect of the thighs (Fig. 5), an indistinct canthus rostralis, and an indistinct tympanum; and from *C. vittatus* by a stockier body, a broader head, and larger toe pads (Fig. 6).

HOLOTYPE.— CAS 221555 (Fig. 2), an adult male, collected at the Rakhine Yoma Elephant Wildlife Sanctuary Headquarters (17°36'48.8" N, 94°36'50.2" E), Gwa, Gwa Township, Rakhine State, Myanmar, collected 3 June 2001 by Htun Win, Thin Thin, Kyi Soe Lwin, and Awan Khwi Shein.

DESCRIPTION OF HOLOTYPE.— Habitus moderately stocky; 22.9 mm SVL; head as long as broad, head length 33.8% of SVL; head width 34.5% of SVL; snout pointed in lateral view (Fig. 3), slightly longer than the diameter of the eye, sloping anteroventrally, projecting beyond the mouth; canthus rostralis is rounded, not distinct; loreal region is slightly oblique and concave; nostrils are slightly protuberant and nearer to the tip of the snout than the eye; internarial space is slightly smaller than interorbital space; interorbital space is wider than upper eyelid; eyes are moderately large, diameter of eye 41% of head length; tympanum not distinct, slightly dorsoventrally oval with slight posterior inclination, less than half the diameter of eye; tympanic annulus anteroventrally raised, obscured posterodorsally by slightly raised supratympanic fold.

Vomerine teeth absent; choanae oval partially hidden by edge of jaw when viewed ventrally; tongue, attached anteriorly, V-shaped notch posteriorly; external vocal sac and vocal slits present; premaxilla and maxilla with minute straight teeth.

Third finger longest; followed by the fourth finger, second finger, and the first finger is the shortest; expanded disks on fingers with circummarginal grooves; disk on the third finger largest, approximately the same size as the tympanum; the webbing between the first and second, and second and third fingers is absent, between the third and fourth fingers only at base; the two outer fingers distinctly separated from the two inner fingers (opposable); subarticular tubercles between penultimate and adjoining proximal phalange oval and well developed.

Hindlimbs relatively short, the tibio-tarsal articulation reaches to between the eye and the tip of the snout; heels overlapping when thighs and tibia are placed at right angles to body; length of tibia 51.4% of SVL; foot length 45.1% of SVL; fourth toe longest, fifth toe a little longer than third, second much shorter than third and slightly longer than first; all toes with disks with circummarginal grooves, a little smaller than those of fingers; the webbing on the toes extends to more than two-thirds the length of the toe with a webbing pattern of I 11/2-2 II 1-2 III 1-2 IV 2-11/2 V following Myers and Duellman (1982); the subarticular tubercles are moderately developed (oval); the inner metatarsal tubercle is small indistinct and oval; no outer metatarsal tubercle. The skin on



FIGURE 2. The holotype of *Chirixalus punctatus* (CAS 221555).

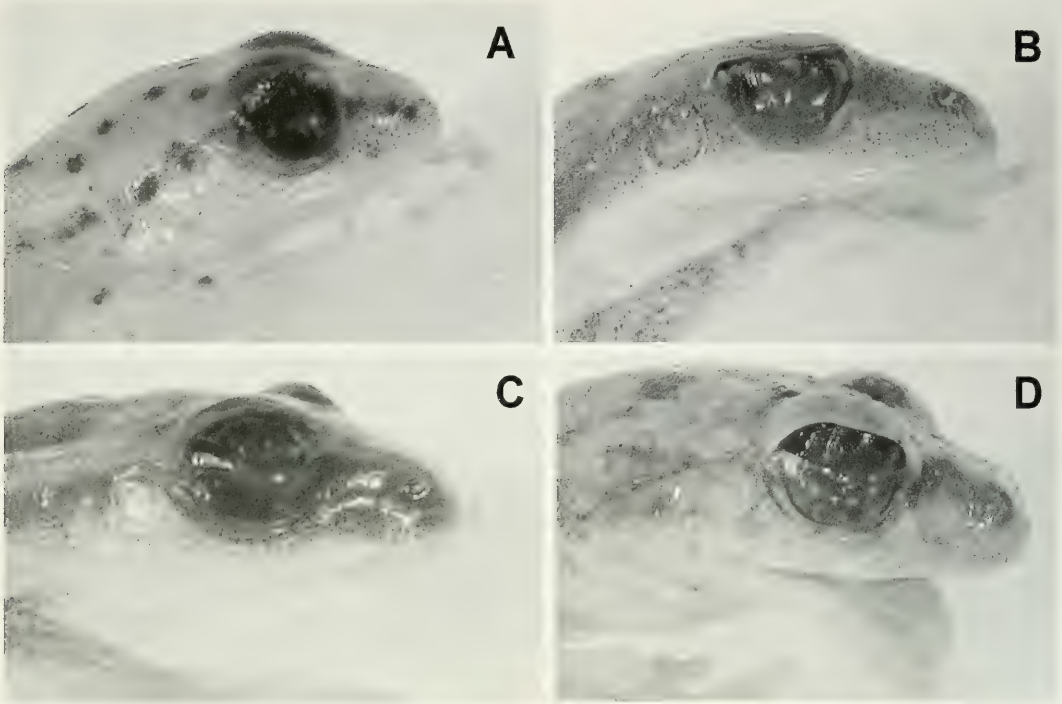


FIGURE 3. Lateral views of the heads of A) *Chirixalus punctatus* (CAS 221555), B) *C. doriae* (CAS 210088), C) *C. viratus* (CAS 221114), and D) *C. nongkhorensis* (FMNH 172569).

the dorsum is smooth, on the throat with small granules, on the abdomen and underside of thighs with larger granules.

COLORATION IN ALCOHOL.—A uniform pattern of minute dark flecks with larger dark (brown) spotting on a lighter background over the head, dorsum, and legs, spotting merges together to form a broken line from snout to eye across the canthus rostralis and from the eye dorsolaterally to groin; a light dorsolateral stripe beginning well behind the eye and ending well before the hindlimbs; there is no pattern or striping on the legs or groin.

VARIATION.—The females are larger than the males (Table 1) but the tibio-tarsal articulation reaches only to the posterior end of the eye, whereas, in the males it reaches to the eye or between the eye and the tip of the snout. The tympanum is more obscure in some individuals than in others. Also, the amount of spotting varies, being sparser in some individuals, restricted primarily to the dorsal aspect of the head whereas in others to the entire dorsum. In some individuals, there is no merging together of the spots to form a broken dorsolateral line from the eye to the groin and no light dorsolateral stripe after preservation, as in the holotype. In life [based on a color transparency of a paratype (JBS 9274); Fig. 7], the dorsal color is a yellowish brown and the ventrum is brownish pink; a pale yellow dorsolateral stripe extends from the snout to just before the vent; the iris is bicolored, with a light upper color meeting the dorsolateral stripe as if the stripe extends through the eye; the fingers are a lighter yellowish brown appearing almost translucent. After preservation in ethanol the dorsal and ventral ground color is white and the dorsolateral stripe fades.

ETYMOLOGY.—The name *punctatus*, from the Latin meaning of having spots, because of the dorsal spotting that distinguishes this species from all other species of *Chirixalus*.



FIGURES 4–6. Dorsal views of (4) *Chirixalus doriae* (CAS 210088); (5) *Chirixalus nongkhorensis* (FMNH 172569); (6) *Chirixalus vittatus* (CAS 221114).

DISTRIBUTION AND NATURAL HISTORY.— At present, *Chirixalus punctatus* is known only from the southwestern foothills of Rakhine Yoma, Gwa Township, Rakhine State, in western Myanmar (Fig. 1). All individuals were found in disturbed habitat between mountain evergreen forests and agricultural land, 1 to 2 m off the ground in bushes. Searches of the evergreen forests failed to find any individuals. The males were calling at the time of collection. The call consisted of a series of a short “dat” separated by 3–4 second intervals. Amplectant pairs were also observed in the plants, where the female would select an oviposition site to build a foam nest for egg deposition on leaves overhanging standing water. The foam nests were found only in a particular plant of the genus *Arum* in the family *Araceae*.

Other frogs collected in the vicinity of the localities of *Chirixalus punctatus* were *Amolops* sp., *C. nongkhorensis*, *Occidozyga* sp., *Philautus* sp., *Polypedates leucomystax*, *Rana alticola*, *R. erythracea*, *R. lateralis*, *R. cf. limnocharis*, and *R. nigrovittata*.

TABLE 1. Measurements of type series of *Chirixalus punctatus*. Mean (in mm) followed by range (in parenthesis). Please see text for abbreviations.

	Males (N=21)	Females (N=6)
SVL	22.9 (21.5–25.0)	26.7 (24.7–28.4)
HL	8.0 (7.4–8.8)	9.2 (8.1–10.0)
HW	7.8 (7.1–9.5)	8.7 (7.5–9.6)
IND	2.4 (2.0–2.8)	2.7 (2.2–3.0)
IOD	3.1 (2.9–3.4)	3.5 (3.0–3.9)
SN	3.2 (2.8–3.5)	3.9 (3.4–4.2)
DNE	1.8 (1.5–2.7)	2.1 (1.6–2.4)
FLL	10.5 (9.6–11.9)	12.2 (10.8–12.9)
HL	6.6 (6.0–7.5)	7.5 (6.5–8.2)
THL	11.1 (9.8–12.6)	12.1 (11.3–12.6)
TIL	11.3 (10.5–12.3)	12.8 (11.9–13.8)
FL	9.6 (8.9–10.6)	10.9 (9.4–11.8)
3FDW	1.3 (0.9–1.7)	1.4 (1.3–1.6)
4TDW	0.9 (0.6–1.1)	1.0 (0.7–1.2)

DISCUSSION

As stated earlier, species of the genus *Chirixalus* are distinguished from other Asian rhacophorids by the presence of opposable fingers. Liem (1970) also suggested that the combination of an elongated vertebral column (2.4 times the width) and the absence of vomerine teeth, along with opposable fingers, can distinguish *Chirixalus* from other rhacophorids. However, many species of *Philautus* also lacked vomerine teeth and all possessed an elongated vertebral column (1.6 to 2.4 times the width) in Liem’s study. The close resemblance of species within *Chirixalus* to those within *Philautus* has prompted some researchers to either move some of the 13 species of *Chirixalus* into *Philautus* or not recognize *Chirixalus* as a genus separate from *Philautus* (Cochran 1927; Pope 1931; Bourret 1942; Taylor 1962). For example, *C. palpebralis* was originally assigned to *Philautus* by Smith (1924), even though he noted that the “first two fingers [were] partially opposed to the others” and though he considered it “most nearly related to *C. doriae*”. Based on these statements, Cochran (1927) and Pope (1931) did not recognize *Chirixalus* as a genus separate from *Philautus*. Taylor (1962) followed suit though he did suggest that *Chirixalus* may be recognized as a genus separate from *Philautus* based on the presence of opposable fingers. However, Bourret (1942) recognized *Chirixalus* as a genus separate from *Philautus*, but he did not place all current species into *Chirixalus* (i.e., *laevis* and *vittatus*). Finally, *C. palpebralis* was again assigned to *Chirixalus* by Inger et al. (1999), based on the presence of opposable fingers.

Recently, Bossuyt and Dubois (2001) tentatively assigned *C. cherrapunjiae* (Roonwal and Kripalani), *C. romeri* (Smith), and *C. shyamrupus* (Chanda and Ghosh) to *Chirixalus* based on the presence of a tadpole stage in *C. cherrapunjiae* and *C. romeri*, since, all species of *Philautus* are thought to be direct developers (Dring 1987), and because *C. shyamrupus* has longitudinal lines on the body, which they contend are not present in species of *Philautus*. Upon examining the figures and reviewing the text from the original descriptions, it is our view that *C. shyamrupus* is the only species to possess opposable fingers (Chanda and Ghosh 1989, Fig. 1) and thus should be assign to *Chirixalus*. *Philautus romeri* and *P. cherrapunjiae* appear to lack opposable fingers (Smith 1953;



FIGURE 7. Paratype of *Chirixalus punctatus* (JBS 9274).

Roonwal and Kripalani 1961; Karsen and Lau 1986; Fei 1999). *Philautus romeri* may be a member of the new genus *Kurixalus* Ye, Fei, and Dubois, whereas *P. cherrapunjiae* may be a member of *Rhacophorus* but a determination will require examinations of the type specimens and observations of individuals in the field.

In a recent study of rhacophorid phylogeny, *Chirixalus* was the only paraphyletic genus (Wilkinson et al. 2002). Of five species of *Chirixalus* sampled (*C. doriae*, *C. eiffingeri*, *C. idiootocus*, *C. palpebralis*, and *C. vittatus*), *C. eiffingeri* and *C. idiootocus* formed a strong sister taxon relationship, separate from *C. doriae* and *C. vittatus*. The (*C. eiffingeri*, *C. idiootocus*) clade formed a weaker relationship with members of *Philautus*, however, these two taxa shared only a few molecular and morphological characters with *Philautus* species (Wilkinson et al. 2002). Fei (1999) recently placed *C. eiffingeri* into the new genus *Kurixalus*, and assigned *C. idiootocus* to *Philautus*. The results of the Wilkinson et al. (2002) study and the absence of opposable fingers in *C. eiffingeri* and *C. idiootocus* led Wilkinson and colleagues to assign *C. idiootocus* along with *C. eiffingeri* to *Kurixalus*. Their results also suggest a close relationship of *Philautus* and *Kurixalus*.

Chirixalus doriae formed a strong clade with *Chiromantis*, whereas *C. vittatus* formed a weak clade with *Polypedates* in the Wilkinson et al. (2002) study. *Chirixalus palpebralis* did not form a clade with any rhacophorid genus suggesting that it may be a representative of a heretofore unnamed genus.

It is interesting to note that as with species of *Chiromantis*, *Polypedates*, and *Rhacophorus*, *Chirixalus doriae* (the type species for this genus) constructs a foam nest. *Chirixalus punctatus* also constructs a foam nest. We therefore place *C. punctatus* within *Chirixalus* due to the presence of opposable fingers, the foam-nesting behavior, and other characters as described above but recognize the need for a systematic study of this genus that includes all known species and further evaluates their relationships with other rhacophorid genera.

We provide the following key to distinguish between ten species of *Chirixalus* (minus *P. cherapunjiae*, *K. eiffingeri*, *K. idiootocus*, and *P. romeri*) based on specimens we examined and original descriptions. We could not distinguish between *C. hansenae* and *C. vittatus*. One difference according to the original descriptions is a distinct tympanum in *C. hansenae* (Cochran 1927) and an indistinct (hidden) tympanum in *C. vittatus* (Boulenger 1887). However, we observed the tympanum to be indistinct in half of the specimens of *C. hansenae* that we examined, and we observed the tympanum to be distinct in one specimen of *C. vittatus* (MVZ 222098). We observed the tympanum on a paratype of *C. hansenae* (USNM 70110) to be distinct. Cochran (1927) based her description of *C. hansenae* on nine specimens. Of these nine, she reported that the tympanum in two specimens "is not so distinct because it is more nearly the color of the surrounding skin, although it can be readily outlined when the frog is placed in a different light". In addition, she compared these specimens with specimens of *C. palpebralis* and *C. doriae* but not with *C. vittatus*. Therefore, *C. hansenae* may be a junior synonym of *C. vittatus*, and the following key should be used with that caveat.

KEY TO THE SPECIES OF *CHIRIXALUS*

1. Longitudinal stripes on dorsum present 2
 Longitudinal stripes on dorsum absent 9
2. Dorsolateral stripes present 3
 Several dark longitudinal stripes present, distinct dorsolateral stripes absent 8
3. Tympanum distinct 4
 Tympanum indistinct 7
4. Inner metatarsal tubercle present 5
 Inner metatarsal tubercle absent, found in Arunachal Pradesh, India *shyamrupus*
5. Third and fourth fingers 1/4 webbed, found in Uttar Pradesh, India *dudhwaensis*
 No or very slight webbing on fingers 6
6. Disk on third finger as large as tympanum, 1/2 to 2/3 webbing on toes, indistinct
 metatarsal tubercle, found in east-central Thailand *hansenae*
 Disk on third finger smaller than tympanum, 1/3 webbing on toes, distinct oval
 metatarsal tubercle, found in Annam, Vietnam *laevis*
7. Dark spots on dorsum present, stocky body, broader head, larger toe disks, found in
 western Myanmar *punctatus*
 Dark spots on dorsum absent, slender body, narrower head, smaller toe disks, found
 throughout Southeast and East Asia *vittatus*
8. Snout obtusely pointed, skin smooth, glandular fold between eye and shoulder absent,
 found throughout South, Southeast, and East Asia *doriae*
 Snout truncated, skin of head with small round scattered warts, glandular fold between
 eye and shoulder present, found in northeastern India *simus*
9. Tympanum distinct, interorbital space broader than upper eyelid, fingers distinctly
 opposable, blotched pattern on dorsum, white patch on side of upper jaw absent, found
 in Southeast Asia *nongkhorensis*
 Tympanum indistinct, interorbital space as large as upper eyelid, fingers only partially
 opposable, hourglass pattern on dorsum, white patch on side of upper jaw present,
 found in Annam, Vietnam and Yunnan, China *palpebralis*

MATERIAL EXAMINED

HOLOTYPE.— CAS 221555, adult male, collected at the Rakhine Yoma Elephant Wildlife Sanctuary Headquarters (17°36'48.8" N, 94°36'50.2" E), Gwa, Gwa Township, Rakhine State, Myanmar, 3 June 2001, by Htun Win, Thin Thin, Kyi Soe Lwin, and Awan Khwi Shein.

PARATYPES.— CAS 221553–221554, CAS 221556–221559, USNM 547928–547929, Joseph B. Slowinski (JBS) field numbers to be deposited in the MBM, JBS 8996, 8998–8999, 9201 seven adult males and five adult females, collected at the same locality and date as the holotype; CAS 221560, an adult male, from the De-Pok Village camp (17°53'35.5" N, 94°30'30.8" E), Gwa Township, Rakhine State, Myanmar, collected 4 June 2001 by Htun Win, Thin Thin, Kyi Soe Lwin, and Awan Khwi Shein; CAS 221561, 221964–221965, JBS 9231–9232, 9234, six adult males, from the De-Pok Village camp (17°53'50.1" N, 94°30'31.7" E), Gwa Township, Rakhine State, Myanmar, collected 4 June 2001 by Htun Win, Thin Thin, Kyi Soe Lwin, and Awan Khwi Shein; CAS 221562–221563, 221966, JBS 9237 four adult males, from the De-Pok Village camp (17°53'44.6" N, 94°30'30.8" E), Gwa Township, Rakhine State, Myanmar, collected 4 June 2001 by Htun Win, Thin Thin, Kyi Soe Lwin, and Awan Khwi Shein, and JBS 9274, 9276, two males, from the De-Pok Village camp (17°53'5" N, 94°30'23" E), Gwa Township, Rakhine State, Myanmar, collected 6 June 2001 by Htun Win, Thin Thin, Kyi Soe Lwin, and Awan Khwi Shein.

ADDITIONAL MATERIAL EXAMINED

Chirixalus doriae: China, NMNS 3183; Myanmar, CAS 210078–210083, 210085–210088, 210091–210094; Vietnam, ROM 32762, 32764, 32782–32783, 32884, 32915, 32951–32952, 33006, 33008. *Chirixalus eiffingeri*: Japan, CAS 211453–211458; Taiwan, CAS 211527–211531. *Chirixalus hansenae*: Thailand, FMNH 182568, 182572–182575, 182577, 182580–182584, 182586–182588, 182590–182591, USNM 70110. *Chirixalus idiotocous*: Taiwan, CAS 166031–166034, 211366, 211524–211526. *Chirixalus laevis*: Vietnam, ROM 30282. *Chirixalus nongkhorensis*: Myanmar, CAS 215915, 221564; Thailand, FMNH 172562–172563, 172567–172570, 182596, 182598–182602, 182607, 182610, 187518, 187519. *Chirixalus palpebralis*: China, NMNS 3104; Vietnam, MVZ 221980–221982, 221986–221987, 221989, 222008, 222010–222011, 222014. *Chirixalus vittatus*: China, NMNS 3184; Myanmar, CAS 221114–221115, 221212–221213, 221266–221267, 221293, 221565–221566; Vietnam, MVZ 222098, ROM 30338–30339, 30341, 30349, 30352, 30362–30363, 30369, 30381.

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Diatom Biostratigraphy of the Neogene Milky River Formation, Alaska Peninsula, Southwestern Alaska

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The Milky River Formation of the Alaska Peninsula, southwestern Alaska, contains more than 100 marine diatom and three silicoflagellate taxa in more than 50 samples from the 263-m-thick (863-foot-thick) Sandy Ridge stratigraphic section. Age-diagnostic diatoms include *Neodenticula kamschatica*, *Thalassiosira oestrupii* and *Cosmiodiscus insignis*, whose co-occurrence characterizes the latest Miocene to early Pliocene subzone b of the North Pacific *Neodenticula kamschatica* diatom Zone of Barron and Gladenkov (1995). The occurrence of additional biostratigraphically-important diatoms, including *Thalassiosira temperei* and *Thalassiosira latimarginata*, is the basis for refining the age of different parts of the formation. Diatoms occur directly within the shells of the bivalve *Astarte* and other marine mollusks of the Milky River Formation. The first appearance of *Astarte* in North Pacific stratigraphic sections signals the earliest opening of Bering Strait, because the genus otherwise dwelled only in the North Atlantic-Arctic region. Diatoms from the stratigraphically lowest *Astarte*-bearing horizon in the Milky River Formation indicate an age range of 5.5–5.4 Ma for the strait's earliest opening. Data on the age of Neogene diatom-bearing sediments resulting from this study also contribute to the stratigraphic framework of Alaska and to refined regional correlations.

Fossil diatoms occur widely in deep-sea and onshore stratigraphic sequences in the middle to high latitudes of the North Pacific and are the primary biostratigraphic tool for the precise dating and correlation of marine sediments in this region. The current high-resolution North Pacific Neogene diatom zonation includes numerous biohorizons based on datum levels, which have been directly correlated to the magnetostratigraphy of the late early Miocene to Quaternary (Barron 1980, 1992a; Koizumi and Tanimura 1985; Koizumi 1992; Barron and Gladenkov 1995; Yanagisawa and Akiba 1998). However, even though Cenozoic marine diatoms of different ages are well represented in sea floor sediments (Kanaya and Koizumi 1966; Jousé et al. 1969; Sancetta 1981a-b, 1982; Sancetta and Silvestri 1986) and deep-sea cores in the eastern part of the Bering Sea and the Gulf of Alaska (Schrader 1973; Barron and Gladenkov 1995), they are extremely rare or absent in onshore sequences of Alaska. As a result, it is often difficult to determine the precise ages and correlations of these sediments. A relatively diverse Neogene diatom flora has previously been studied only from the Pribilof Islands, southern Bering Sea, Alaska (Hanna 1919, 1970), and sparse remains of poorly preserved marine diatoms have also been reported from the Middleton Island section of the Yakataga Formation along the northeastern Gulf of Alaska margin (Plafker and Addicott 1976). Assigning precise ages to these floras has proved difficult, owing to

the absence of biostratigraphically significant taxa. The present study of diatoms from the Milky River Formation, including age-diagnostic species, is the first description of a Cenozoic diatom assemblage from the Alaska Peninsula, southwestern Alaska. These diatoms are present in stratigraphically well-controlled samples and are highly significant for age, regional correlations, and paleoenvironmental reconstruction of the Milky River Formation.

PREVIOUS STUDIES, MATERIALS AND METHODS

Certain diatom species in the Milky River marine diatom flora have been the basis for documenting the earliest opening of Bering Strait (Marincovich and Gladenkov 1997, 1999, 2001; Gladenkov and Marincovich 1998, 1999). Part of the present diatom flora was first discovered within five mollusk shells from two stratigraphic levels in the Sandy Ridge stratigraphic section that were housed in the California Academy of Sciences, San Francisco. These samples had been collected from Sandy Ridge in the course of petroleum geological field work by Mobil Oil Company geologists in the 1970s. At that time, this sequence was assigned to the upper part of the Bear Lake Formation (Detterman et al. 1996). Initial study of the diatoms showed them to be characteristic of Subzone b of the North Pacific *Neodenticula kamschatica* diatom Zone of Barron and Gladenkov (1995), with an age range of 5.5–4.8 Ma based on correlations with the time scale of Berggren et al. (1995). Even though these diatoms and mollusks (*Astarte*) were the basis for dating the earliest opening of Bering Strait (Marincovich and Gladenkov 1999, 2001; Marincovich 2000), the precise location of these fossils in the Sandy Ridge stratigraphic section was unknown. In order to place these fossils within a stratigraphic, geological and paleontological context, field work at Sandy Ridge was conducted in August 1998 and July 1999 under the leadership of L. Marincovich, Jr., and supported by National Science Foundation grant OPP 9806461 (Marincovich et al. 2002; Gladenkov et al. 2002). This additional sampling at Sandy Ridge was critical to more precisely dating the first occurrence of Arctic-Atlantic mollusks within the North Pacific diatom biostratigraphic scheme, especially since diatoms were absent or extremely rare in the enclosing matrix but relatively abundant in the mollusk shells. Sampling the interiors of mollusk shells was done because in some cases fossil diatoms are present in fine sediment within shells and are thereby protected from abrasion and dissolution (Barron and Mahood 1993). Fine grained sediments containing diatoms might also be protected from winnowing by bottom currents if they are within molluscan shells.

A total of 56 samples for diatom analysis were collected during field work at the Sandy Ridge stratigraphic section (Figure 1). These strata had previously been assigned to the Bear Lake Formation (Detterman et al. 1996). However, in the course of field work it was discovered that the main part of these rocks contain, exclusively, late Miocene mollusks, in contrast to the early middle Miocene mollusks known from the Bear Lake Formation (Marincovich et al. 2002; Gladenkov et al. 2002). These strata were therefore reassigned to the Milky River Formation, which had been proposed by Galloway (1974) for volcanic and sedimentary rocks that overlies the Bear Lake Formation on the Alaska Peninsula. A profound angular unconformity separates these two formations at Sandy Ridge, with semi-isoclinally folded non-marine conglomerate, sandstone and coal beds of the lower middle Miocene Bear Lake Formation underlying subhorizontal shallow-marine sediments of the upper Miocene Milky River Formation. It is now clear that all previously studied marine diatoms and mollusks from this stratigraphic section came not from the upper part of the Bear Lake Formation, as supposed by Marincovich and Gladenkov (1997, 1999, 2001), but from the overlying Milky River Formation. The stratigraphic horizon with the first appearance of *Astarte*, which is the signal of an open Bering Strait, is 28 meters above the angular unconformity

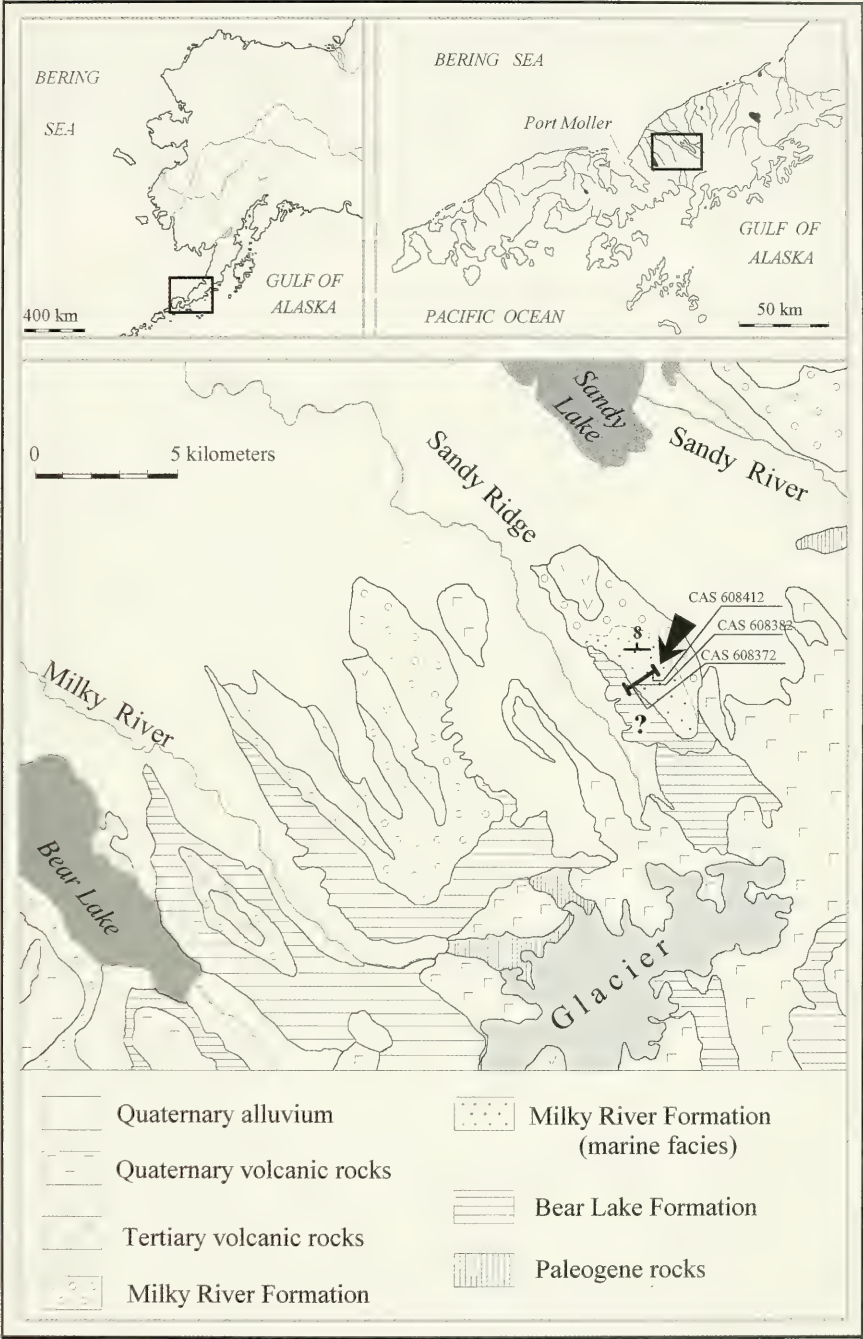


FIGURE 1. Location of the study area on the Alaska Peninsula and geological map of the Sandy Ridge area (modified after Detterman et al. 1996), with arrow showing the Sandy Ridge stratigraphic section of the Milky River Formation (after Gladenkov et al. 2002). Localities of the stratigraphically lowest (CAS 608372) and highest (CAS 608412) samples in the Sandy Ridge stratigraphic section yielding diatoms are shown. CAS 608382 indicates the locality of sample collected from the stratigraphically lowest *Astarte*-bearing horizon in the Milky River Formation.

and within the lower part of the Milky River Formation (Marincovich et al. 2002; Gladenkov et al. 2002). In the course of field work at Sandy Ridge, 52 samples for diatom analysis were collected from the 263-m-thick (863-ft-thick) section of the Milky River Formation and four samples were collected from the uppermost part of the underlying Bear Lake Formation (Figures 1–2; Table 1).

Due to the induration of the sediments and the low concentration of diatoms, the following procedure was used to process the samples. Samples were preliminary crushed and then placed in acetic acid for several days. The acid-treated material was then made pH-neutral by repeatedly filling and decanting the beakers with distilled water, allowing 3 hr or more for each rinse. The material was then processed by boiling it in a solution of water and sodium pyrophosphate ($\text{Na}_4\text{P}_2\text{O}_7 \times 10\text{H}_2\text{O}$), followed by repeated washing with distilled water, and then a centrifuge (at 2500 rpm for 10 min) was used with heavy liquid (specific weight = 2.3) to separate a suspension fraction. To remove the heavy liquid, both the suspension and residue were again rinsed in distilled water. Finally, strewn slides were prepared by placing the material in a vial, adding distilled water, agitating the vial, and removing part of the upper suspension with a pipette. Strewn slides¹ were prepared by spreading the pipette suspension onto a cover slip (size 24×24 mm), drying on a hot plate, and mounting in Naphrax (index of diffraction = 1.74). Slides prepared from both fractions obtained after centrifuging were studied as a control. The slides were examined in their entirety under a Jeneval (Zeiss) light microscope at 400×, with identifications routinely checked at 1000×. Whenever possible, all diatom taxa were counted up to a maximum of 200 specimens (other than *Chaetoceros* spores). *Chaetoceros* spores were tabulated separately while counting the other taxa. After counting, slides were scanned to record the presence of other diatom species missed among the first 200 specimens. When fewer than 200 diatom valves were encountered on a slide, all of the taxa were tabulated. Silicoflagellates, if present, were tabulated for the entire slide. The preservation of diatoms is listed as G (good), M (moderate), and P (poor) depending on the degree of destruction and dissolution of valves. The relative abundance is evaluated as A (abundant, more than 1500 diatom valves per slide), C (common, 400–1500 valves), F (few, 250–400 valves), and R (rare, 250–50 valves), and VR (very rare, less than 50 valves).

Numerical ages have been updated herein according to the geochronologic and geomagnetic polarity scales after Berggren et al. (1995). The correlation of geological epochs and periods also follows Berggren et al. (1995), with the exception of the Pliocene subepochs. The Pliocene epoch

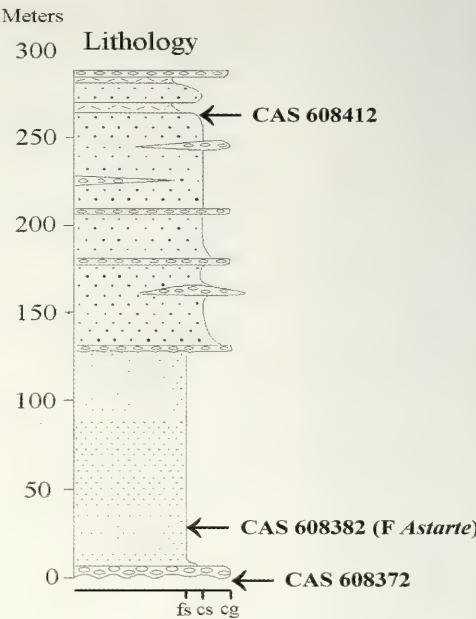


FIGURE 2. Generalized stratigraphic column of the Milky River Formation at the Sandy Ridge stratigraphic section (after Gladenkov et al. 2002)

The wavy line indicates an angular unconformity separating the Milky River Formation and the Bear Lake Formation. Arrows show stratigraphically lowest (CAS 608372) and highest (CAS 608412) samples levels possessing diatoms, and the sample level (CAS 608382) coinciding with the stratigraphically lowest Astarte-bearing horizon (F Astarte). Abbreviations used: fs—fine-grained sandstones, cs—coarse grained sandstones, cg—conglomerate.

¹The original set of slides are in Gladenkov's laboratory in Moscow. A duplicate set of slides has been deposited in the Diatom Collection at the California Academy of Sciences.

is divided into early, middle, and late subepochs that are equivalent to the European Zanclean, Piacenzian, and Gelasian stages, respectively. As a result, the former late Pliocene is divided into middle and late subepochs, as was adopted at the 30th International Geological Congress (Beijing, China, 1996). The boundary between middle and late Pliocene is at 2.58 Ma coinciding with the top of Chron C2An. The North Pacific Neogene diatom zonation follows Barron and Gladenkov (1995) (Figure 3).

RESULTS AND DISCUSSION

OCCURRENCE OF BIOSTRATIGRAPHICALLY SIGNIFICANT TAXA.— Three of 4 samples from the Bear Lake Formation are barren of siliceous microfossils. Rare diatoms representing only a few taxa were found only in sample CAS 608372 (1.5 m below the unconformity) (Figures 1–2). Determining a precise age for the poorly preserved assemblage in sample CAS 608372, from the uppermost part of the Bear Lake Formation at Sandy Ridge, has proven difficult owing to the absence of co-occurring, biostratigraphically significant taxa characteristic of the *Neodenticula kamtschatica* Zone or older diatom zones (Table 1). About 100 species and varieties of diatoms and three taxa of silicoflagellates were identified in the 52 samples examined from the 263-m-thick section of the Milky River Formation exposed above the unconformity at the Sandy Ridge stratigraphic section. Their occurrences are shown in Table 1. In addition, because of its importance, the richest diatom-bearing sample (CAS 60269-s) of five samples reported by us previously (Marincovich and Gladenkov 1999, 2001) is included in the occurrence chart here. Its stratigraphic position approximately coincides with that of sample CAS 608382 (about 28 m above the unconformity), which was collected from the horizon characterized by the first appearance of mollusks *Astarte* in the Milky River Formation. The Appendix gives taxonomic citations for the taxa encountered.

In general the diatom flora of the Milky River Formation consists of boreal and subarctic species typical of high to middle latitudes (Plates 1–7; Table 1; Appendix). The North Pacific diatom zonations of Akiba (1986), Koizumi (1992), Barron and Gladenkov (1995), and Yanagisawa and Akiba (1998) are most applicable to this study. A version of the Cenozoic diatom zonation proposed by Barron and Gladenkov (1995) for the North Pacific (Figure 3) is used here. In Figure 4 the stratigraphic ranges of selected diatoms are used to correlate micropaleontological assemblages from the Sandy Ridge section with diatom zones and subzones.

Overall, diatoms are rare to abundant and well preserved to poorly preserved throughout the

TABLE 1. Stratigraphic occurrences and relative abundances of selected diatoms from the Sandy Ridge stratigraphic section

Notes: Stratigraphic interval is in meters above the base of the Milky River Formation, which is marked by an angular unconformity at Sandy Ridge. The location of sample CAS 60269-s coincides approximately with that of sample CAS 608382, which was collected from the horizon containing the stratigraphically lowest occurrence of the bivalve mollusk *Astarte*. Sample CAS 608372 is from the uppermost part of the Bear Lake Formation at Sandy Ridge.

Preservation (G = good, M = moderate, P = poor) and relative abundance (A = abundant, C = common, F = few, R = rare, VR = very rare). Plus sign (+) indicate diatom specimens recorded after the count.

A total number of valves of all diatom taxa counted in each sample are shown. However, because of space limitations, only occurrences for stratigraphically important marine diatoms and taxa having a most importance for paleoenvironments are included in Table 1. Other taxa (primary nonmarine and benthic) were also tabulated, however they are not treated here. Identified taxa of silicoflagellates are also not included. Interested persons may contact the author for a complete chart of taxonomic occurrences in the Sandy Ridge stratigraphic section.

Partial boxes within the table indicate the first or/and last occurrences of the biostratigraphically most important species in the Milky River Formation at Sandy Ridge stratigraphic section.

Elevation above the unconformity (m)	263.0	246.0	246.0	237.4	222.2	207.9	188.7	172.8	155.5	147.2	146.6	139.9	139.9	134.1	133.2	121.3	114.6	103.0	96.6	95.1	94.8
Sample #CAS-	608412	608411	608410	608409	608408	608407	608406	608405	608404	608403	608402	608401	608400	608399	608398	608397	608396	608395	608427	608426	608394
Preservation	M	P	P	M	M	P	P	P	P	M	P	M	G	P	P	P	P	P	P	M	P
Abundance	R	VR	R	VR	F	VR	VR	VR	R	R	VR	F	A	F	F	F	F	R	R	C-F	R
<i>Actinocyclus curvatus</i>					1				1		+	1	1							2	
<i>A. ochotensis</i>	1				+						+	1	1	1			+			+	
<i>A. octonarius</i>					1			1			+	1	1	+	+					1	1
<i>Actinocyclus</i> spp.					1			2			1	1									
<i>Actinoptychus senarius</i>					1			1			3	8	2	3	4	11				2	1
<i>A. splendens</i>											+	1	+	+				1			
<i>Adoneis pacifica</i>																				+	
<i>Bacteriastrum varians</i>													+								
<i>Bacterosira fragilis</i>	2				9			1	4	1	10	5	13	9	11	17	1	1	20	2	
<i>Cladogramma dubium</i>					+						+			+	+				1	+	
<i>Coscinodiscus marginatus</i>	3	1			8			7	1	1	20	26	25	15	34	9	12	5	8	3	
<i>Cosmiodiscus insignis</i>					1			1	4	1	22	34	15	12	36	18	17	3	3	4	
<i>Cymatosira debvi</i>									1				1	2	1	1				2	
<i>Delphineis angustata</i> group					2			1			3	+	2	5	1	1				4	
<i>D. sachalinensis</i>					+						+	+			1	1				3	
<i>D. simonsenii</i>																					
<i>D. surirella</i>					+			1		1	+	1	+	2	1					3	
<i>Detonula confervacea</i>								1		1		+		+	+	1				2	
<i>Dicladia capreolus</i>					+								1			+				+	
<i>Fragilariopsis cylindrus</i>																+				+	
<i>F. oceanica</i>																	+			+	
<i>Hyalodiscus obsoletus</i>					3						2	1		+		2				1	
<i>Hyalopyxis concava</i> + <i>Trochosira spinosa</i>	1	1			6			1	3	1	12	3	4	17	24	35	2			12	2
<i>Lithodesmium minusculum</i>											+	+								1	
<i>Neodenticula kamtschatica</i>				1	+			1			+	+		1	1					3	
<i>Nitzschia rolandii</i>								1	1		1	1				1	1			2	
<i>Odoniella aurita</i>	1																				
<i>Paralia sulcata</i>	1	1	1		18		3	16	2	3	34	58	37	38	44	45	28	7	15	4	
<i>Porosira punctata</i>									1		+	+									
<i>Pseudopyxilla americana</i>					1						+	+									
<i>Pyxidicula zabelinae</i>	1	3	3	1	26		3	15	1		12	13	9	8	2	3	4	3	3	1	
<i>Rhaphoneis angularis</i>					1			1			+	1	1	1	1	2	2		1	1	
<i>Rhizosolenia hebetata</i> group											+				1						
<i>Stephanogonia hanzawae</i>															1					+	
<i>Thalassionema nitzschioides</i>	4	1	1		68		2	13	8	2	47	23	38	43	8	24	3	2	64	3	
<i>Thalassiosira antiqua</i>					+			1		1	1			1		1			8	1	
<i>Thalassiosira</i> sp. cf. <i>T. convexa</i>																					
<i>T. dolmatovae</i>	2				2			2	1	9	8	7	7	2	7	2			2	3	
<i>T. eccentrica</i>								1		1	+			+	1				4	1	
<i>T. gravida</i>					+					1	+	1	4						1		
<i>T. hvalina</i>										+	+				1	1			1		
<i>T. jacksonii</i>																					
<i>T. jouseae</i>					7					1	1	3	2	1	2				6	1	
<i>T. kryophila</i>																			+		
<i>T. latimarginata</i>					1														+		
<i>T. leptopus</i>																					
<i>T. manifesta</i>								1													
<i>T. marujamica</i>																					
<i>T. nativa</i> + <i>T. sp. cf. nativa</i>			2	1	2			5			+	1			1	1			1		
<i>T. oestrupii</i>	1				2			1	1		1	1	1	1	+	1			1	1	
<i>T. orientalis</i>					1						1	+							1		
<i>T. praeoestrupii</i>																					
<i>T. sheshukovae</i>					1						+	+	+	1	1					2	
<i>T. temperlei</i>																					
<i>T. tertiaria</i>													+							+	
<i>T. undulosa</i> + <i>Porosira glacialis</i>											1	4	+	+	+	2				2	
<i>Thalassiothrix longissima</i>					2						1	+	+	2	+	+				3	
<i>T. robusta</i>					8			1	2		4	3	8	10	1	5	1		9	1	
Resting spores of <i>Chaetoceros</i>	1	4	3		25		1	8	2	1	19	8	6	23	3	25	3	2	53	2	
Total number of valves counted	87	30	77	44	200	34	18	22	132	64	17	200	200	200	200	200	200	109	65	200	66

608425	608424	608393	608392	608423	608391	608422	608390	608389	608421	608388	608420	608387	608386	608419	608418	608385	608384	608417	608383	60269	608382	617357	608381	608371	608380	608379	608378	608377	608376	608375	617358	608372	
M	P	M	M	M	P	P	P	M	P	P	M	P	P	P	P	M	P	M	P	M	G	P	P	M	M	M	M	M	M	P	M	P	
F	F	C	C	F	C	R	R	C	R	F	F	R	V	R	V	F	F	F	F	C	A	R	R	C	C	F	C	C	C	V	C	R	
2	1	1	2					+			+	1				+	+	+	+	2	+		+	+	+	1	2	1	1		2		
+	+	1	1			+								1		+	+	+	+	+	+	+	+	+	+	2	+	+	1				
2	1	+	1	+				+			+					+	+	+	1	+	1	+	1	+	1	3	+	+	+				
4	3	20	10	3	3	3	4	9		5	4	3		+	1	4	3	2	1	2	2	2	2	2	1	3	2	2	2	1			
		+	+	+		1	1	+			+						3	7	4	4	4	1			3	2	3	4		1			
+	+	+	+								+								+	+	+		+			+	+						
25	22	9	9	20	2	4	7	16		15	7	3		+	1	15	29	18	7	12	20	1	15	12	13	22	8	11	31	1	20		
+	+	1	+	+	+	+					+				1	1	1	+	+	1	2		+	+	1	+	+	+	+				
8	9	24	16	5	7	32	5	5	7	6	19			29	1	18	9	13	20	3	19	13	10	29	5	21	3	17	5	2			
6	3	14	11	4	21	54	11	6	7	7	22	1		47		7	5	5	14	6	18	12	15	5	20	10	29	19	5	8			
1	2	+	2	5				3	1	2						4	3	8	2	5	+	+	2	4	1	8	2	4	7				
2	5	2	3	3		+	2	1		4	2					2	2	1	3	6	1	1	4	3	1	4	3	6	5				
1	1	1	+	+		+		+		1	+					1	+	+		4	+			1	+	+	1	1	+				
+	1	3	4	2	1	+	6	5		7	4					3	11	9	3	4	3	+	4	5	+	7	+	2	8				
1	2	+	3	2	1	1	2	3		2	1					1	1	1	+	2	+		+		1	+		1					
								+												+	+				+	+	+						
		+	1	2				+		1	+					+	+	+		2	+		+			1		3					
+	+	+	+	+												+	+	+		+	+			+	+	+	+	+	+	+			
10	11	14	28	13	4	3	12	32	1	37	19	4		6		49	43	35	11	19	7	9	41	32	18	48	21	18	41		31		
1	+	+	+							+										+	+						+	+	+				
2	1	+	1	2				1		+	1					+	2			2	+		1	3	+	+	+	+	3				
+	+	+															+	+	+	+	+					+	+	+					
3	1	+	1	5	1	+		1		1	+					+	2	1	2	2	3	+	1	3		2	2	2	1		7		
28	18	31	30	31	34	65	47	41	19	41	56	3	2	93		33	31	23	62	12	40	97	42	45	61	29	37	32	21	10	31		
		+						+		+						+	+	+	+	1			+	+	1	+	+	+					
6	4	2	6	6	7	3	2	5	2	5	28	1		5	1	4	3	5	15	3	13	16	8	11	17	2	7	9	2	2	4		
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48	57	21	20	56	11	12	18	31	1	21	16	+		11		27	21	24	6	72	16	27	14	15	14	19	20	28	13	4	24		
8	8	1	1	4	1		2	8			2					1	+	+		5	+					+	1	+	+				
		+															+	+	+	+	+		+				1	+	+				
4	6	17	9	3	3	4	2	8		9	1	1		3		5	11	8	9	4	11	1	10	8	9	11	10	17	11		16		
5	5	3	6	1		+	1	4		1	2					+	2	2	2	2	3		1	3	+	+	1	1	3		3		
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2	3	+	2	2		+	1			+	+					1	1	+		1	+	+					+	+	+			1	
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1	1	1	1	1		1		2		+	+					+	2	2	4	1	11	1	2	2	2	2	4	5	3	3		3	
1	1	+	+	6				+			+					+	+	+		+	4	1	+			3	3	2	1		+		
6	7	5	5	6	1	1	1	3		+	+	1		+		4	3	2	1	5	2	5	1	1	2	5	6	19	2	1		5	
32	37	11	23	41	5	7	12	33		23	15	45		5		24	31	21	13	16	28	8	14	12	6	38	13	27	25		37		
200	200	200	200	200	132	200	148	200	66	200	200	130	3	200	22	200	200	200	200	200	200	200	200	200	200	200	200	200	200	33	200	12	

Milky River Formation at Sandy Ridge. The first occurrences of *Thalassiosira oestrupii*, *T. antiqua*, *T. jouseae*, *T. marujamica*, *T. sheshukovae*, *Neodenticula kamtschatica*, *Bacterosira fragilis*, *Detonula confervacea* and *Rhaphoneis angularis* are in sample CAS 617358 from the basal part of the Milky River Formation (0.9 m above the base). *Thalassiosira oestrupii* ranges to the top of the section in sample CAS 608412 (263.0 m). The last occurrences of *Neodenticula kamtschatica* and *Cosmiodiscus insignis* are below the stratigraphic top, in samples CAS 608410 (246.0 m) and CAS 608408 (222.2 m), respectively. The last consistent occurrence of *Cosmiodiscus insignis* is in sample CAS 608405 (172.8 m). *Lithodesmium minusculum* is present in the interval from sample CAS 608376 (3.4 m) to sample CAS 608401 (139.9 m). *Delphines simonsenii* occurs from sample CAS 608379 (8.8 m) to sample CAS 608392 (85.3 m), and *Nitzschia rolandii* from sample CAS 608382 (28.0 m) to sample 608425 (93.0 m). *Thalassiosira jacksonii* and *Thalassiosira* sp. cf. *T. convexa* range from sample CAS 608376 (3.4 m) to sample CAS 608425 (93.0 m), including sample CAS 608393 (88.4 m). *Thalassiosira temperei* is present in samples CAS 608378 (5.5 m) and CAS 608382 (28.0 m), while sample CAS 60269-s (about 28.0 m) contains *Thalassiosira praeoestrupii*. Samples CAS 608426 (95.1 m) and CAS 608408 (222.2 m) yield *Thalassiosira latimarginata*, while *Thalassiosira tertiaria* was found in samples CAS 608426 and CAS 608400 (139.9 m).

AGE OF THE DIATOM FLORA.—As noted above, determining a precise age for the poorly preserved assemblage in sample CAS 608372, from the uppermost part of the Bear Lake at Sandy Ridge, has proven difficult owing to the absence of co-occurring, biostratigraphically significant taxa characteristic of any North Pacific diatom zone. The co-occurrence of *Thalassiosira oestrupii*, *Cosmiodiscus insignis* and *Neodenticula kamtschatica* in the Milky River Formation allows recognition of the latest Miocene to early Pliocene subzone b of the North Pacific *Neodenticula kamtschatica* Zone of Barron and Gladenkov (1995) in the Sandy Ridge stratigraphic section. The *Neodenticula kamtschatica* Zone is the interval from the first occurrence (FO) of *N. kamtschatica* to the FO of *N. koizumii* (Figure 3). This zone is divided into subzones a, b, and c by the FO of *Thalassiosira oestrupii* and the last occurrence (LO) of *Cosmiodiscus insignis*, following Barron (1980). Thus, based on the find of *Cosmiodiscus insignis* in sample CAS 608408 (222.2 m), most of the Milky River Formation at Sandy Ridge section can be correlated with subzone b of the *N. kamtschatica* Zone. The boundaries of the *N. kamtschatica* Zone and its subzones, based on diatom datum levels, are calibrated with the magnetostratigraphic record in the North Pacific (Barron and Gladenkov 1995). According to the geochronologic and chronostratigraphic scale of Berggren et al. (1995), Subzone b has an age range of 5.5 to 4.8 Ma. The Miocene/Pliocene boundary is currently placed at 5.32 Ma by Berggren et al. (1995). Diatoms from the uppermost part of the Milky River section, above sample CAS 608405 (172.8 m), however, are rare and generally exhibit poor preservation. So, it is uncertain whether *Cosmiodiscus insignis* has its true last occurrence in sample CAS 608408 (222.2 m), which is its final occurrence, or in sample CAS 608405 (172.8 m), which is its last consistent occurrence but where this species is represented by a single, possibly reworked specimen. On the other hand, the absence of *Cosmiodiscus insignis* above 222.2 m due to paleoecological changes cannot be excluded. Therefore, a tentative upper boundary of subzone b, marked by the LO of *Cosmiodiscus insignis* at level 172.8 m, is proposed for the Sandy Ridge section.

The occurrence of additional biostratigraphically important diatoms allows refining the age for the different parts of the stratigraphic section. Not all horizons in this section are characterized by the consistent occurrence of diatoms, including age-diagnostic marine taxa, but analysis of the species still is valuable. The most important species for biochronology in the lower part of Milky River Formation is *Thalassiosira temperei* (Figure 4). The last occurrence of this species is a useful Neogene biohorizon marker in the North Pacific, including onshore sequences in Japan and

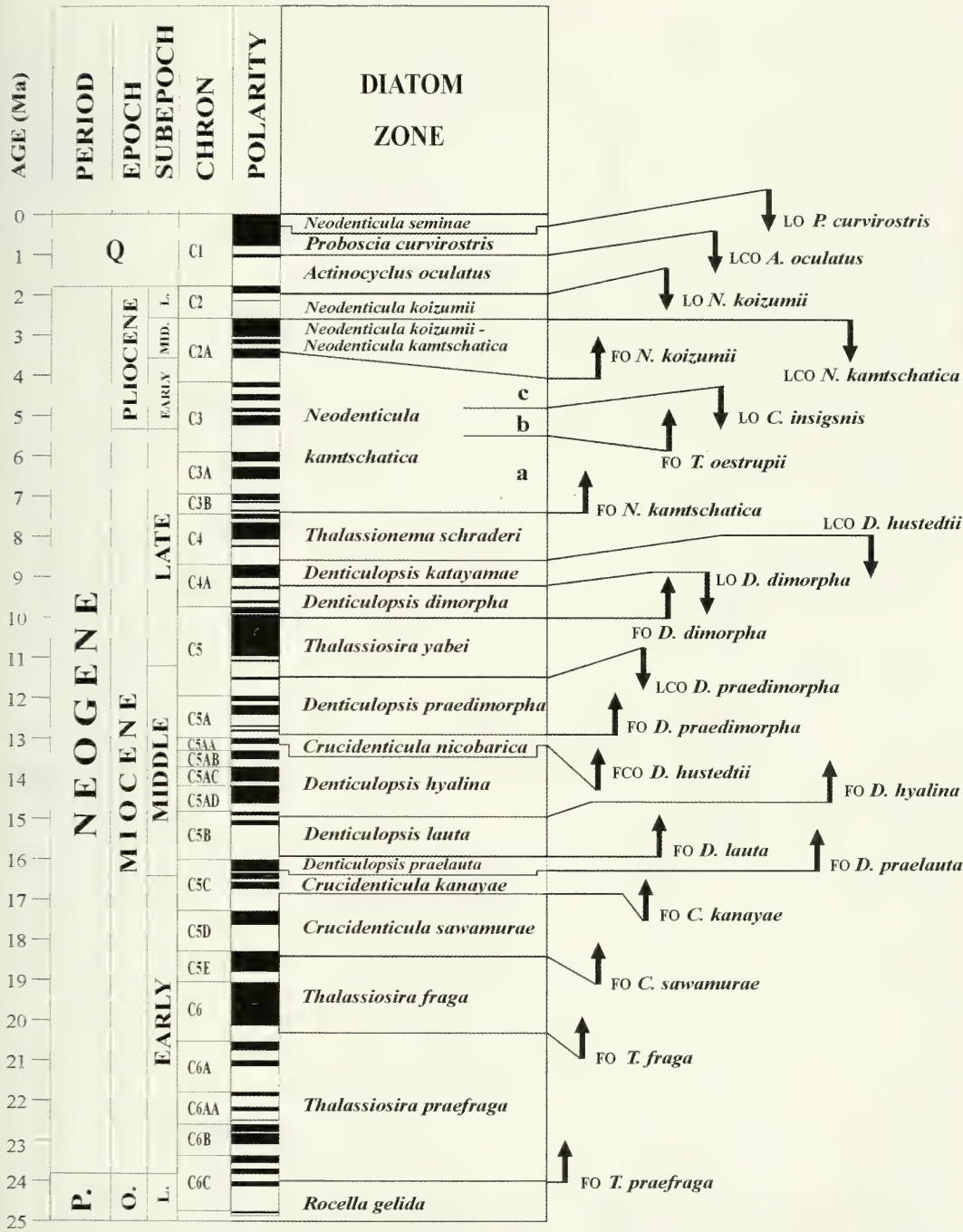
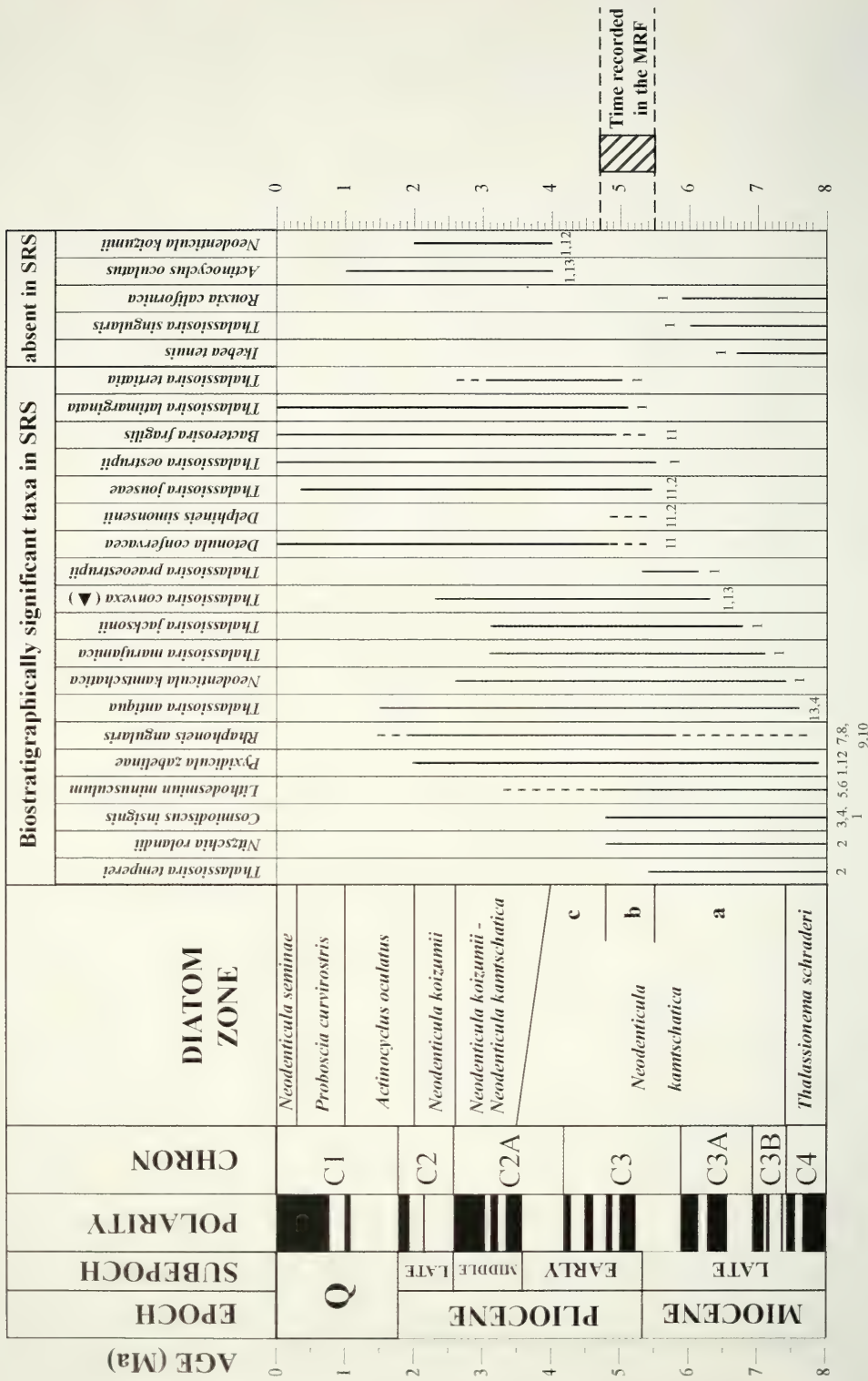


FIGURE 3. The North Pacific Neogene diatom zonation after Barron and Gladenkov (1995) correlated to the geomagnetic polarity time scale and chronostratigraphic subdivisions of Berggren et al. (1995) (see text for additional explanation). Abbreviations used: FO, first occurrence; LO, last occurrence; FCO, first common occurrence; LCO, last common occurrence; a-c, subzones; Q, Quaternary; P, Paleogene; O, Oligocene; L, late.



Kamchatka. It occurs within the interval corresponding to the lowermost part of subzone b of the *Neodenticula kamtschatica* diatom Zone (Barron 1980, 1992a; Akiba et al. 1982; Oreshkina 1985; Akiba 1986; Akiba and Yanagisawa 1986; Yanagisawa 1990, 1998). The most recent data, based on extrapolated sedimentation rates and occurrences in deep-sea cores, indicates that *Thalassiosira temperei* had its last occurrence at 5.4 Ma in the middle- to high-latitude North Pacific (Yanagisawa and Akiba 1998) (Figure 4). Therefore, the co-occurrence of *Thalassiosira temperei*, *T. oestrupii*, and *Cosmiodiscus insignis* indicates a narrow age interval of 5.5 to 5.4 Ma for the lower part of the Milky River Formation at Sandy Ridge.

The presence of secondary marker species, including *Delphines simonsenii*, *Bacterosira fragilis*, *Detonula confervacea*, and *Thalassiosira jouseae*, are useful for evaluating the lower age limit of the Milky River Formation at Sandy Ridge. According to Akiba (1986), the first occurrences of all of these species at DSDP Site 584 off northeastern Japan, are within the interval corresponding to subzone b of the *Neodenticula kamtschatica* Zone of Barron and Gladenkov (1995). More precisely, these species first occur within a narrow interval just above the FO of *Thalassiosira oestrupii*. The total occurrence of *Delphines simonsenii* is restricted to subzone b at DSDP Site 584 (Akiba 1986). These datum levels have not been directly correlated to magnetostratigraphy, but the presence of these species in the Sandy Ridge section supports a lower limit for the Milky River Formation of not more than 5.5 Ma.

As shown in Table 1, *Rhaphoneis angularis* is typical of diatom assemblages from the Milky River Formation. In the Harris Grade section, California, this species ranges from between the first occurrences of *Thalassiosira oestrupii* and *Thalassiosira praeoestrupii*, i.e. from about 5.3–5.4 Ma (Barron and Baldauf 1986; Dumont and Barron 1995). On the other hand, in sequences from the Oregon continental shelf *Rhaphoneis angularis* ranges from an older interval corresponding to the uppermost part of the *Thalassionema schraderi* Zone (Whiting and Schrader 1985). So, the datum from California may not apply in more northern regions such as Alaska.

In summary, diatoms imply an age range for lower 28 m of the Milky River Formation, below sample CAS 608382 (which has the last co-occurrence of *Thalassiosira temperei*, *T. oestrupii*, *Neodenticula kamtschatica*, and *Cosmiodiscus insignis*) of 5.5–5.4 Ma.

The most biochronologically important species in the upper part of Milky River Formation are *Thalassiosira latimarginata* and *Thalassiosira tertiaria*. As noted above, *T. latimarginata* is present in samples CAS 608426 (95.1 m) and CAS 608408 (222.2 m), and *T. tertiaria* in samples CAS 608426 and CAS 608400 (139.9 m). The FO of *T. latimarginata* has been calibrated with the magnetostratigraphic record of deep-sea cores in the subarctic North Pacific at about 5.1 Ma (Barron and Gladenkov 1995). The FO of *T. tertiaria* has been correlated with magnetostratigraphy in ODP

FIGURE 4. Published biostratigraphic ranges of selected diatom taxa present in the Sandy Ridge stratigraphic section (SRS), indicating a latest Miocene to early Pliocene age for the Milky River Formation (MRF).

Black triangle in parentheses indicates that *Thalassiosira* sp. cf. *T. convexa* is present in the Milky River Formation (see Appendix).

Key to published ranges: 1. Barron and Gladenkov (1995*), ODP sites in the subarctic North Pacific. 2. Yanagisawa and Akiba (1998), DSDP Hole 438A, off northeastern Japan. 3. Barron (1980), DSDP sites, off northeastern Japan. 4. Barron (1992a*), DSDP and ODP sites in the North Pacific. 5. Barron (1992b), California. 6. Oreshkina (1985; personal communication, 1998), DSDP Site 192, off northeastern Kamchatka. 7. Barron and Baldauf (1986), California. 8. Dumont and Barron (1995), California. 9. Whiting and Schrader (1985), the Oregon continental shelf. 10. Schrader (1973), DSDP sites in the Gulf of Alaska. 11. Akiba (1986), DSDP Site 584, off northeastern Japan. 12. Koizumi (1992*), ODP sites in the Japan Sea. 13. Koizumi and Tanimura (1985*), DSDP sites in the northwestern Pacific. Asterisks (*) indicate a paleomagnetic calibration.

The North Pacific diatom zonation of Barron and Gladenkov (1995) for the last 8 myr correlated to the geomagnetic polarity time scale and chronostratigraphic subdivisions of Berggren et al. (1995).

Abbreviations used: Q, Quaternary; a-c, subzones; DSDP, Deep Sea Drilling Project; ODP, Ocean Drilling Program.

Site 884 in the western part of the subarctic North Pacific, where it has an age of 5.0 Ma (Barron and Gladenkov 1995). Thus, the presence of these species in the Milky River Formation indicates an age not older than 5.1–5.0 Ma for the horizons overlying the 95.1-m level.

Lithodesmium minusculum (occurring from 3.4 m to 139.9 m) could have served as an additional useful age marker for the upper portion of the section studied. The age range of the last occurrence of this species in California is 4.6–4.8 Ma (Barron 1992b; Dumont and Barron 1995). However, the presence of *Lithodesmium minusculum* is documented in younger horizons of the *Neodenticula koizumii*-*Neodenticula kamtschatica* Zone at DSDP Site 192, off northeastern Kamchatka (T. Oreshkina 1985, personal communication 1998). These data suggest that the datum from California may not apply in more northerly regions, such as Alaska.

COMPARISON WITH THE DIATOM FLORA OF THE PRIBILOF ISLANDS.— As noted in the Introduction, a relatively well-preserved and diverse fossil marine diatom flora from an onshore sequence in Alaska has previously been documented and studied only from the Pribilof Islands, Bering Sea (Hanna 1919, 1970). Overall, this diatom assemblage is comprised of relatively long-ranging forms with little or no precise age significance. In contrast to the flora from the Sandy Ridge section, this diatom assemblage lacks most of the biostratigraphically-important taxa typical of the Milky River Formation, such as *Neodenticula kamtschatica*, *Thalassiosira oestrupii*, *T. latimarginata*, *Bacterosira fragilis*, *Detonula confervacea*, *Thalassiosira jouseae*, and *Delphineis simonsenii*. However, both floras have a few species in common, including *Cosmiodiscus insignis* and *Thalassiosira temperei* (referred to as *Cymatotheca weissflogii* by Hanna 1970). These latter species suggest that the flora from the Pribilof Islands is older than the one at Sandy Ridge and has an age older than 5.5 Ma. This conclusion is supported by data from L. Burckle and N. Opdyke, who studied diatoms and magnetostratigraphy from sequences in the Pribilof Islands (Burckle and Opdyke, unpublished data). Diatom-bearing sediments exposed in outcrops on St. Paul Island exhibit the normal polarity of Chron C3A (Burckle, personal communication 2002), which ranges in age from 6.57 Ma to 5.89 Ma (Berggren et al. 1995). This age range implies that the diatom flora from the Pribilof Islands is possibly assignable to the older part of the North Pacific *Neodenticula kamtschatica* diatom Zone, which is Subzone a that has an age range of 7.4–5.5 Ma. The absence of the zonal species *Neodenticula kamtschatica* in the Pribilof Islands flora is possibly due to paleoecological exclusion. However, the absence of *Neodenticula kamtschatica* due to the possible difference of preparation methods, including the procedures of processing of samples, between Hanna (1970) and this study also cannot be excluded.

DIATOM PALEOENVIRONMENTS.— In general, the diatom flora from the Milky River Formation is composed by boreal and subarctic species typical of high to middle latitudes. Overall, the assemblages are dominated by marine neritic-planktic and sublittoral taxa (including *Paralia sulcata*, *Chaetoceros* spores and *Delphineis* spp.) that are accompanied by benthic and nonmarine forms, which implies deposition in productive shallow water (shallower than 100 m) of the Alaskan continental shelf (Sancetta 1981a–b; Sancetta and Silvestri 1986). The persistence and occasionally common occurrence of *Thalassionema nitzschioides* accompanied by oceanic planktic elements suggests incursions of transitional water from the outer shelf zone, where shelf and oceanic waters are incompletely mixed. The presence of *Fragilariopsis oceanica* and *F. cylindrus*, which commonly live near sea ice, as well as some marine arctoboreal species (*Bacterosira fragilis*, *Detonula confervacea*, *Porosira glacialis*, *Thalassiosira kryophila*, *T. hyalina*, *T. gravida*) imply periods of bloom associated with melting ice near the continental margin of southwestern Alaska. Sparse occurrences of subtropical or transitional planktonic taxa such as *Thalassiosira leptopus*, *T. lineata*, *T. temperei*, *T. oestrupii*, *Bacteriastrum varians*, *Auliscus* and *Azpeitia* spp. suggest possible episodes of relatively warmer conditions.

SUMMARY

The 263-m-thick stratigraphic section of the Milky River Formation at Sandy Ridge contains Neogene marine diatom assemblages of different preservation and abundance. A total of about 100 species and varieties of diatoms were identified in the samples examined. The presence of the marker species *Neodenticula kamtschatica*, *Cosmiodiscus insignis*, and *Thalassiosira oestrupii* throughout the section allows recognition of the latest Miocene to early Pliocene subzone b of the *Neodenticula kamtschatica* Zone of Barron and Gladenkov (1995), which has an age range of 5.5 to 4.8 Ma. Additional age-diagnostic diatoms, including *Thalassiosira temperei* and *T. latimarginata*, allow refining the age for the basal part of the Milky River Formation to 5.5 Ma to 5.4 Ma, and to 5.1 Ma to 4.8 Ma for the upper part of the formation at Sandy Ridge. This information, from stratigraphically well-controlled samples, is the basis for dating mollusks that occur directly with the diatoms, including the biogeographically important bivalve *Astarte*. Diatoms in the stratigraphically lowest *Astarte*-bearing horizon at Sandy Ridge have an age range of 5.5–5.4 Ma, which is the basis for dating the earliest opening of Bering Strait (Marincovich and Gladenkov 1999, 2001; Marincovich et al. 2002; Gladenkov et al. 2002).

Both the dominant and common elements of the Milky River Formation flora imply deposition on a productive continental shelf, with some incursions of transitional waters from the outer shelf zone. The presence of species living with sea ice, along with marine arctoboreal species, suggests periods of bloom associated with the melting of ice near the continental margin of southwestern Alaska. Sparse occurrences of subtropical or transitional planktonic taxa suggest transient warmer conditions.

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APPENDIX

Taxonomic Notes and References to Good Figures

Taxonomic references to marine diatom and silicoflagellate taxa from the Milky River Formation, including those illustrated on Plates 1–7, are listed below. In general, only references to good figures are listed following a semicolon. Thus, with few exceptions, the reader should look to these references for the original citation of the taxon. Important synonyms and brief remarks are included.

In most cases, only generic distinctions were made for nonmarine diatoms encountered in the Milky River Formation samples. This group includes *Achnanthes* Bory, *Amphora* Ehrenberg ex Kützing, *Asterionella* Hassal (tabulated together with *Tabellaria* Ehrenberg ex Kützing), *Aulacosira* Thwaites, *Cyclotella* Kützing ex Brebisson, *Cymbella* Agardh, *Dimerogramma* Ralfs, *Diatoma* De Candolle, *Eunotia* Ehrenberg, *Fragilaria* Lyngbye, *Gomphonema* Agardh, *Gyrosigma* Hassal, *Melosira* Agardh, *Meridon* Agardh, *Navicula* Bory, *Nitzschia* Hassal, *Pinnularia* Ehrenberg, *Surirella* Turpin, *Synedra* Ehrenberg, *Tetracyclus* Ralfs, and *Tryblionella* Smith.

Marine Diatoms

- Actinocyclus curvatulus* Janisch; Koizumi, 1973, pl. 1, figs. 1–6; Sancetta, 1982, pl. 1, figs. 1–3. Synonyms: *Actinocyclus divisus* (Grunow) Hustedt; *Coscinodiscus curvatulus* Grunow; *Coscinodiscus divisus* Grunow. (Plate 5, Figs. 11–12)
- Actinocyclus ochotensis* Jousé, 1968: pp. 17–18, pl. 2, figs. 2–5; Donahue, 1970, pl. 1, figs. a–b, d; Koizumi, 1973, pl. 2, figs. 3, 6–7; Sancetta, 1982, pl. 1, figs. 4–6. (Plate 5, Fig. 9)
- Actinocyclus octonarius* Ehrenberg; Wornardt, 1967, fig. 49. **Synonym:** *Actinocyclus ehrenbergii* Ralfs. (Plate 5, Fig. 5)

- Actinocyclus* Ehrenberg spp. **Remarks:** Some species of *Actinocyclus* have been not identified precisely. They have not been described or tabulated specifically here.
- Actinoptychus senarius* (Ehrenberg) Ehrenberg; Kanaya, 1959, pl. 7, fig. 17; Hanna, 1970, figs. 38–39; Sancetta, 1982, pl. 1, fig. 7; Akiba, 1986, pl. 29, fig. 2. **Synonym:** *Actinoptychus undulatus* (Bailey) Ralfs. (Plate 5, Fig. 8)
- Actinoptychus splendens* (Shadbolt) Ralfs; Sheshukova-Poretskaya, 1967, pl. 29, fig. 1; Hanna, 1970, figs. 25–26, 40, 44. **(Plate 5, Fig. 1)**
- Actinoptychus vulgaris* Schumann; Sheshukova-Poretskaya, 1967, pl. 28, figs. 2a–d; Sancetta, 1982, pl. 1, fig. 8; Akiba, 1986, pl. 29, fig. 1.
- Adoneis pacifica* Andrews et Rivera, 1987: pp. 2, 9, figs. 1–26. **(Plate 1, Fig. 2)**
- Arachnoidiscus* Bailey ex Ehrenberg spp. **Remarks:** Only scarce fragments of valves with the typical structure of *Arachnoidiscus* were observed. No attempt has been made to subdivide this group.
- Aulacodiscus* Ehrenberg spp. **Remarks:** No specific generic distinctions were made for rare specimens of *Aulacodiscus* and their fragments found in the material studied.
- Auliscus* sp. cf. *A. grunowii* Schmidt. **Remarks:** Only rare fragments of valves have been found. However, their structure resembles that of specimens illustrated by Wornardt (1967, figs. 92–94).
- Azpeitia* Peragallo spp. **Remarks:** The rare specimens observed here are similar in part to *Azpeitia nodulifera* (Schmidt) Fryxell et Sims and *Azpeitia tabularis* (Grunow) Fryxell et Sims, but they differ to some extent from these species by a character of valves structure.
- Bacteriasrtum varians* Lauder; Barron, 1975, pl. 4, fig. 8. **(Plate 2, Figs. 8–9)**
- Bacterosira fragilis* (Gran) Gran; Sheshukova-Poretskaya, 1967, pl. 33, figs. 2a–b; Schrader, 1973, pl. 16, fig. 7; Sancetta, 1982, pl. 2, figs. 1–4; Akiba, 1986, pl. 4, figs. 1–4; Dzinoridze and Makarova, 1988, pl. 60, figs. 7–12. **(Plate 3, Fig. 19; Plate 4, Fig. 18)**
- Chaetoceros cinctus* Gran (spore); Sheshukova-Poretskaya, 1967, pl. 33, fig. 9. **Remarks:** Because of the similarity of *Chaetoceros cinctus* and *Chaetoceros incurvus* spores, they have been combined and counted together.
- Chaetoceros furcellatus* Bailey (spore); Sheshukova-Poretskaya, 1967, pl. 33, fig. 8; Sancetta, 1982, pl. 2, figs. 7, 9.
- Chaetoceros incurvus* Bailey (spore); Sheshukova-Poretskaya, 1967, pl. 33, fig. 10. **Remarks:** See Remarks for *Chaetoceros cinctus*.
- Chaetoceros septentrionales* Oestrup (spore); Sancetta, 1982, pl. 2, fig. 8.
- Chaetoceros subsecundus* (Grunow) Hustedt (spore); Sancetta, 1982, pl. 2, figs. 5–6. **Synonym:** *Chaetoceros diadema* (Ehrenberg) Gran.
- Cladogramma dubium* Lohman; Sheshukova-Poretskaya, 1967, pl. 24, figs. 6 a–b, pl. 29 figs. 4 a–c; Schrader, 1973, pl. 13, figs. 17–18, 21; Barron, 1975, pl. 5, fig. 10. **(Plate 7, Figs. 3, 6)**
- Cocconeis antiqua* Tempère et Brun; Hanna, 1970, fig. 48; Barron, 1975, pl. 5, fig. 11
- Cocconeis californica* Grunow; Sheshukova-Poretskaya, 1967, pl. 43, fig. 11; Yanagisawa et al., 1989, pl. 6, fig. 13.
- Cocconeis costata* Gregory; Sheshukova-Poretskaya, 1967, pl. 44, figs. 4 a–c; Barron, 1975, pl. 5, fig. 12; Sancetta, 1982, pl. 6, figs. 6–7.
- Cocconeis placentulla* Ehrenberg; Barron, 1975, pl. 5, fig. 17.
- Cocconeis pribiloefformis* Hanna, 1970: p. 184, fig. 34.
- Cocconeis scutellum* Ehrenberg; Sheshukova-Poretskaya, 1967, pl. 44, fig. 7; Barron, 1975, pl. 5, fig. 19.
- Cocconeis vitrea* Brun; Sheshukova-Poretskaya, 1967, pl. 45, figs. 3a–c; Wornardt, 1967, figs. 183–184; Barron, 1975, pl. 5, fig. 23.
- Coscinodiscus asteromphalus* Ehrenberg; Sheshukova-Poretskaya, 1967, pl. 21, fig. 2; Wornardt, 1967, figs. 14–18; Schrader and Fenner, 1976, pl. 34, figs. 2–3.
- Coscinodiscus marginatus* Ehrenberg; Kanaya, 1959, pl. 4, figs. 4–6; Wornardt, 1967, figs. 27–28; Hanna, 1970, figs. 1–2; Barron, 1975, pl. 7, fig. 1; Akiba, 1986, pl. 1, figs. 1–4. **(Plate 2, Figs. 4–5)**
- Coscinodiscus oculus-iridis* Ehrenberg; Kanaya, 1959, pl. 4, fig. 7; Sheshukova-Poretskaya, 1967, pl. 21, fig. 1; Wornardt, 1967, figs. 34–35; Hanna, 1970, fig. 18; Barron, 1975, pl. 7, fig. 9; Sancetta, 1982, pl. 2, fig. 11.
- Coscinodiscus* Ehrenberg spp. **Remarks:** Rare fragments of different *Coscinodiscus* having indistinct charac-

ters for identification were assigned to this category.

Cosmiodiscis insignis Jousé, 1961: pp. 67–68, pl. 2, fig. 8; Sheshukova-Poretskaya, 1967, pl. 25, figs. 2 a–c; Hanna, 1970, figs. 9–11, 31, 32; Koizumi, 1973, pl. 4, figs. 7–11; Barron, 1980, pl. 4, fig. 1; Barron, 1985, fig. 9.9; Akiba, 1986, pl. 17, fig. 1. **Synonym:** *Thalassiosira insigna* (Jousé) Harwood et Maruyama sensu Barron and Gladenkov (1995). **Remarks:** Harwood and Maruyama (1992) transferred this taxon from *Cosmiodiscis* to *Thalassiosira* and proposed the new combination *Thalassiosira insigna* (Jousé) Harwood et Maruyama, based on observations of Antarctic forms bearing a central structure (dimple or bubble). Following Harwood and Maruyama (1992), in some cases this new combination has also been used for North Pacific forms (Barron and Gladenkov 1995; Marinovich and Gladenkov 1999, 2001; and others). However, recently, specimens of *Cosmiodiscus insignis* collected by G D. Hanna from the Pribilof Islands were studied with a SEM by E. Fourtanier (Fourtanier, personal communication, 2001), who observed that the non-areolate center of the valve does not possess a central process, and that a ring of labiate processes is located on the boundary between the mantle and valve face. I also observed the same features when studying specimens of this taxon from the Milky River Formation with a SEM at the California Academy of Sciences in 2001. These observations indicate that this North Pacific taxon cannot be included in *Thalassiosira*, and that perhaps forms from the North Pacific and Antarctic regions belong to different taxa. Further study of the Antarctic forms under a SEM should clarify their taxonomic position. (**Plate 4, Fig. 16; Plate 6, Figs. 2–3, 5**)

Cosmiodiscis intersectus (Brun) Jousé, 1961: p. 68, pl. 2, figs. 9–10; Sheshukova-Poretskaya, 1967, pl. 25, figs. 1 a–b; Koizumi, 1973, pl. 4, figs. 12–13.

Cymatosira debyi Tempère et Brun; Sheshukova-Poretskaya, 1967, pl. 40, fig. 7, pl. 41, fig. 6; Akiba, 1986, pl. 19, figs. 19–20; Yanagisawa et al. 1989, pl. 5, fig. 31. (**Plate 3, Figs. 3–4; Plate 4, Fig. 8**)

Delphineis angustata (Pantocsek) Andrews group. **Remarks:** Specimens of *Delphineis* range from elliptical to elongate with rounded apices, and resemble *Delphineis angustata* (Pantocsek) Andrews, 1977, *Delphineis ischaboensis* (Grunow) Andrews, 1988, and *Delphineis karstenii* (Boden) Fryxell et Miller have been placed in this group in part following the example of *Delphineis* cf. *angustata* of Akiba (1986). (**Plate 4, Figs. 3–6, 10–11**)

Delphineis sachalinensis (Sheshukova) Barron et Baldauf, 1986: p. 363. **Synonym:** *Rhaphoneis sachalinensis* Sheshukova; Sheshukova-Poretskaya, 1967, p. 242, pl. 42, fig. 2. (**Plate 4, Fig. 13**)

Delphineis simonsenii (Mertz) Akiba, 1986: p. 439, pl. 20, figs. 12–13. (**Plate 5, Figs. 6–7**)

Delphineis surirella (Ehrenberg) Andrews, 1980: pp. 83–85; pl. 1, figs. 1–5, pl. 2, figs. 6–7; Akiba, 1986, pl. 20, figs. 2–3.

Detonula confervacea (Cleve) Gran; Dzinoridze and Makarova, 1988, p. 88, pl. 60, figs. 14–15, text figs. 6.1–6.3. **Synonym:** *Melosira albicans* Sheshukova, 1964; Sheshukova-Poretskaya, 1964, p. 69, 71, text figs. 1–2, pl. 1, fig. 3; 1967, pl. 10, figs. 2a–b, pl. 11, figs. 1a–b; Akiba, 1986, pl. 4, figs. 11–12; Yanagisawa et al., 1989, pl. 3, fig. 7. (**Plate 1, Fig. 9; Plate 5, Fig. 10**)

Di cladia capreolus Ehrenberg; Kanaya, 1959, pl. 11, figs. 1–2; Sheshukova-Poretskaya, 1967, pl. 34, figs. 1a–c. **Synonyms:** *Di cladia capreola* Ehrenberg; Hanna, 1970, fig. 63; *Di cladia pylea* Hanna et Grant; *Chaetoceros di cladia* Castracane. (**Plate 2, Figs. 2–3**)

Diploneis smithii (Brebisson) Cleve; Barron, 1975, pl. 8, fig. 17; Sancetta, 1982, pl. 6, fig. 21.

Fragilariopsis cylindrus (Grunow) Krieger; Koizumi, 1973, pl. 7, figs. 1–2; Hasle, 1993, p. 316. **Synonyms:** *Nitzschia cylindrus* (Grunow) Hasle; Koizumi, 1975, pl. 1, fig. 49; *Nitzschia cylindra* (Grunow) Hasle; Sancetta, 1982, pl. 3, figs. 6–7. (**Plate 3, Figs. 13–15**)

Fragilariopsis oceanica (Cleve) Hasle; Hasle, 1993, p. 317; **Synonym:** *Nitzschia grunowii* Hasle; Sancetta, 1982, pl. 3, figs. 8–10; Akiba, 1986, pl. 24, figs. 19–21. (**Plate 3, Fig. 16–17**)

Grammatophora Ehrenberg spp. **Remarks:** Observed specimens resemble *G. angulosa* Ehrenberg and *G. arcuata* Ehrenberg and occur very sporadically.

Hercotheca mamillaris Ehrenberg; Barron, 1975, pl. 9, fig. 13.

Hyalodiscus obsoletus Sheshukova, 1964; Sheshukova-Poretskaya, 1964, p. 71, pl. 1, fig. 1; 1967, pl. 12, fig. 2; Akiba, 1986, pl. 29, fig. 15; Yanagisawa et al., 1989, pl. 3, fig. 12. (**Plate 1, Fig. 11**)

Hyalopyxis concava (Sheshukova) Makarova, 1989: p. 35, pl. 1, figs. 1–7, pl. 2, figs. 1–6. **Synonym:** *Trochosira concava* Sheshukova; Sheshukova-Poretskaya, 1967, p. 138, pl. 11, figs. 7a–b, pl. 13, fig. 3.

Remarks: Specimens of *Hyalopyxis concava* were tabulated together with specimens of *Trochosira spinosa* Kitton. (**Plate 3, Fig. 21–22**)

Liradiscus ellipticus Greville; Barron, 1975, pl. 9, fig. 19.

Lithodesmium minusculum Grunow; Wornardt, 1967, fig. 132; Schrader, 1973, pl. 12, figs. 15, 17; Barron, 1975, pl. 10, fig. 4; Oreshkina, 1985, pl. 3, fig. 15. (**Plate 7, Figs. 7, 11**)

Navicula glacialis Cleve; Sheshukova-Poretskaya, 1967, pl. 46, fig. 8.

Neodenticula kamtschatica (Zabelina) Akiba et Yanagisawa, 1986: pp. 490–491, pl. 21, figs. 7–21, pl. 22, figs. 1–12; Akiba, 1986, pl. 25, figs. 7–27; Yanagisawa and Akiba, 1990, pl. 7, figs. 27–37. **Synonyms:** *Denticula kamtschatica* Zabelina; Sheshukova-Poretskaya, 1967, pl. 47, figs. 9a–b, pl. 48, figs. 4a–d; Koizumi, 1973, pl. 5, figs. 14–17; Schrader, 1973, pl. 2, figs. 1–13; Koizumi, 1975, pl. 1, figs. 13–20; Barron, 1980, pl. 1, figs. 5–8; *Denticulopsis kamtschatica* (Zabelina) Simonsen; Barron, 1985, fig. 13.16; Oreshkina, 1985, pl. 1, figs. 16–20; Whiting and Schrader, 1985, pl. 6, figs. 15–16, 18–20. (**Plate 5, Figs. 2–4; Plate 6, Fig. 4**)

Nitzschia extincta Kozyrenko et Sheshukova group. **Remarks:** Specimens having a similarity in shape and structure to *Nitzschia extincta* Kozyrenko et Sheshukova (in Sheshukova-Poretskaya, 1967, pp. 303–304, pl. 47, fig. 12) have been placed in this group.

Nitzschia rolandii Schrader; Akiba and Yanagisawa, 1986, pl. 21, figs. 1–6; Akiba, 1986, pl. 25, figs. 1–6; Yanagisawa and Akiba, 1990, pl. 7, figs. 17–26. (**Plate 3, Fig. 20**)

Odontella aurita (Lyngbye) Agardh; Sancetta, 1982, pl. 3, figs. 11–12; Akiba, 1986, pl. 17, figs. 2–3. (**Plate 2, Figs. 7, 10**)

Opephora schwartzii (Grunow) Petit; Wornardt, 1967, figs. 161–165; Barron, 1975, pl. 11, fig. 10.

Paralia sulcata (Ehrenberg) Cleve; Sancetta, 1982, pl. 3, figs. 13–15; Akiba, 1986, pl. 29, figs. 4–5. (**Plate 7, Figs. 12–13**)

Pleurosigma Smith spp. **Remarks:** No specific generic distinctions were made for rare specimens of *Pleurosigma* and their fragments found in the material studied.

Porosira glacialis (Grunow) Jørgensen; Koizumi, 1973, pl. 4, figs. 15–18; Barron, 1980, pl. 6, fig. 13; Dzinoridze and Makarova, 1988, pl. 60, figs. 1–6. **Remarks:** Specimens of *Porosira glacialis* were counted together with specimens of *Thalassiosira undulosa* (Mann) Sheshukova. (**Plate 7, Fig. 5**)

Porosira punctata (Jousé) Makarova, 1988: Makarova, 1988a, p. 1184, pl. 1, figs. 1–16; Dzinoridze and Makarova, 1988, pl. 59, figs. 1–10. **Synonym:** *Thalassiosira punctata* Jousé, 1961: p. 64, pl. 1, figs. 7–8, pl. 3, fig. 3; Sheshukova-Poretskaya, 1967, pl. 14, fig. 10, pl. 17, figs. 1a–b; Hanna, 1970, figs. 5–6; Koizumi, 1973, pl. 8, figs. 7–9; Schrader and Fenner, 1976, pl. 19, fig. 10; Barron, 1980, pl. 6, fig. 3; Akiba, 1986, pl. 9, figs. 5–6. (**Plate 2, Fig. 1; Plate 6, Fig. 12**)

Proboscia alata (Brightwell) Sundström; Jordan et al., 1991, figs. 1–9; **Synonym:** *Rhizosolenia alata* Brightwell; Schrader, 1973, pl. 10, fig. 12; Koizumi, 1975, pl. 1, fig. 38; Akiba, 1986, pl. 18, fig. 6.

Proboscia barboi (Brun) Jordan et Priddle, 1991: p. 56, figs. 1–2; **Synonyms:** *Rhizosolenia barboi* (Brun) Tempère et Peragallo; Schrader, 1973, pl. 24, figs. 4, 7; Barron, 1980, pl. 2, fig. 17; Barron, 1985, fig. 4.5; Akiba and Yanagisawa, 1986, pl. 42, figs. 3–5, 7, 10–11, pl. 44, figs. 1–8; *Rhizosolenia curvirostris* var. *inermis* Jousé; Donahue, 1970, pl. 1, figs. b–c; Koizumi, 1973, pl. 5, figs. 32–33.

Pseudopyxilla americana (Ehrenberg) Forti; Sheshukova-Poretskaya, 1967, pl. 39, figs. 2a–b; Schrader, 1973, pl. 10, fig. 22; Barron, 1975, pl. 11, fig. 12. (**Plate 7, Fig. 4**)

Pseudopyxilla Forti sp. **Remarks:** Only scarce fragments of *Pseudopyxilla* having some similarity to *Pseudopyxilla rossica* (Pantoscsek) Forti have been observed.

Pyxidicula zabelinae (Jousé) Makarova et Moiseeva; Makarova and Moiseeva, 1986, p. 244–245, pl. 1, figs. 1–15, pl. 2, figs. 1–15. **Synonyms:** *Thalassiosira zabelinae* Jousé, 1961: p. 66–67, pl. 2, figs. 1–7; Sheshukova-Poretskaya, 1967, pl. 16, figs. 2 a–d; *Thalassiosira usatschevii* Jousé, 1961: pp. 64, 66, pl. 1, fig. 10; Sheshukova-Poretskaya, 1967, pl. 15, figs. 3 a–d. (**Plate 1, Figs. 13, 15–16**)

Rhabdonema japonicum Tempère et Brun; Hanna, 1970, figs. 92–95; Schrader, 1973, pl. 12, fig. 10.

Rhaphoneis amphiceros Ehrenberg; Sheshukova-Poretskaya, 1967, pl. 41, fig. 9; Schrader, 1973, pl. 25, figs. 2–3; Whiting and Schrader, 1985, pl. 6, figs. 4–5; Akiba, 1986, pl. 20, fig. 19.

Rhaphoneis angularis Lohman, 1938: pp. 92–93, pl. 22, figs. 6–8; Schrader, 1973, pl. 26, figs. 9–10; Whiting and Schrader, 1985, pl. 6, figs. 22–24; Yanagisawa et al., 1989, pl. 5, fig. 38. **Synonym:** *Rhaphoneis amph-*

- iceros* var. *angularis* (Lohman) Wornardt, 1967: p. 78, figs. 169–170. (**Plate 4, Figs. 1–2, 7; Plate 6, Figs. 6, 10**)
- Rhizosolenia hebetata* (Bailey) Gran group. **Remarks:** All scarce specimens having a similarity with *Rhizosolenia hebetata* f. *hiemalis* Gran (Akiba, 1986, pl. 17, figs. 10–11, pl. 18, figs. 9–10) and *Rhizosolenia hebetata* f. *semispina* (Hensen) Gran (Akiba, 1986, pl. 18, fig. 8) were placed in this group. (**Plate 4, Fig. 12**)
- Rhizosolenia setigera* Brightwell; Akiba, 1986, pl. 18, fig. 5.
- Rhizosolenia styliformis* Brightwell; Sancetta, 1982, pl. 4, figs. 7–8; Akiba, 1986, 18, fig. 4.
- Stellarima microtrias* (Ehrenberg) Hasle et Sims; Hasle et al., 1988, figs. 1–25. **Synonym:** *Coscinodiscus symbolophorus* Grunow; Sheshukova-Poretskaya, 1967, pl. 22, figs. 3 a–e; Akiba, 1986, pl. 2, fig. 1.
- Stephanogonia hanzawae* Kanaya, 1959: pp. 118–119, pl. 11, figs. 3–7; Schrader and Fenner, 1976, pl. 12, figs. 10, 12, pl. 13, figs. 5, 7–8; Akiba et al., 1982, pl. 2, fig. 36. **Synonym:** *Pterotheca kittoniana* var. *kamtschatica* Gaponov; Sheshukova-Poretskaya, 1967, pl. 39, figs. 3a–f. (**Plate 1, Fig. 14**)
- Stephanopyxis turris* (Greville et Arnott) Ralfs; Kanaya, 1959, pl. 2, figs. 5–7; Koizumi, 1973, pl. 6, figs. 13–16; Schrader, 1973, pl. 15, figs. 1–7; Sancetta, 1982, pl. 4, figs. 9–10.
- Stephanopyxis* (Ehrenberg) Ehrenberg spp. **Remarks:** All scarce specimens not referable to *Stephanopyxis turris* were assigned to this category.
- Thalassionema nitzschioides* (Grunow) H. et M. Peragallo; Sancetta, 1982, pl. 4, figs. 11–13; Akiba, 1986, pl. 21, fig. 11. **Remarks:** No attempt was made to separate varieties of this species. (**Plate 3, Figs. 9–10**)
- Thalassiosira antiqua* (Grunow) Cleve-Euler; Sheshukova-Poretskaya, 1967, pl. 14, figs. 3a–b; Schrader, 1973, pl. 11, fig. 25, pl. 25, fig. 25; Barron, 1980, pl. 5, fig. 5; Barron, 1985, fig. 11.2; Akiba, 1986, pl. 12, figs. 1, 3–4. (**Plate 3, Figs. 1–2**)
- Thalassiosira* sp. cf. *T. convexa* Mukhina, 1965: pp. 22–24, pl. 2, figs. 1–2. **Remarks:** Specimens resemble *T. convexa* but they differ to some extent from typical form by more flat valve, arrangement of areolae and character of the marginal zone. (**Plate 6, Figs. 11, 13–17; Plate 4, Fig. 15**)
- Thalassiosira decipiens* (Grunow) Jørgensen; Sancetta, 1982, pl. 5, figs. 1–3.
- Thalassiosira delicata* (Barron) Akiba, 1986: p. 440. **Synonym:** *Thalassiosira nidulus* var. *delicata* Barron, 1980: p. 671, pl. 6, figs. 1, 4.
- Thalassiosira dolmatovae* Oreshkina in Gladenkov et al., 1992: p. 129, pl. 40, figs. 7–8. **Synonym:** *Thalassiosira* sp. 9 of Dolmatova in Volobueva et al., 1992: p. 86, pl. 30, figs. 1–5. (**Plate 1, Fig. 1; Plate 3, Fig. 24**)
- Thalassiosira eccentrica* (Ehrenberg) Cleve; Makarova, 1988b, pl. 20, figs. 1–9; pl. 21, figs. 1–12; Makarova, 1988c, pl. 40, figs. 1–9. (**Plate 4, Fig. 14; Plate 6, Fig. 9**)
- Thalassiosira gravida* Cleve; Schrader and Fenner, 1976, pl. 16, figs. 5–6, pl. 17, fig. 2; Barron, 1980, pl. 6, figs. 11, 14; Akiba, 1986, pl. 10, figs. 1–4. **Remarks:** No separation of the species from *Thalassiosira gravida* f. *fossilis* Jousé (1961: p. 63, pl. 1, fig. 9) was done in the material studied. (**Plate 2, Fig. 6**)
- Thalassiosira hyalina* (Grunow) Gran; Sancetta, 1982, pl. 5, figs. 4–5; Akiba, 1986, pl. 5, fig. 9; Makarova, 1988b, pl. 45, figs. 1–10. (**Plate 3, Figs. 7–8, 18**)
- Thalassiosira jacksonii* Koizumi et Barron in Koizumi, 1980: p. 396, pl. 1, figs. 11–14; Barron, 1980, pl. 6, figs. 2, 6; Akiba, 1986, pl. 11, fig. 2. **Synonym:** *Thalassiosira* sp. b of Schrader and Fenner, 1976, pl. 17, figs. 5, 10. (**Plate 6, Figs. 7–8**)
- Thalassiosira* sp. cf. *T. jacksonii* Koizumi et Barron. **Remarks:** Specimens resemble *T. jacksonii* but differ from the latter by lacking a distinct central hyaline area with a process.
- Thalassiosira jouseae* Akiba, 1986: p. 440, pl. 6, figs. 8–10. (**Plate 1, Figs. 3, 7, 10**)
- Thalassiosira kryophila* (Grunow) Jørgensen; Sheshukova-Poretskaya, 1967, pl. 14, fig. 6; Koizumi, 1973, pl. 8, fig. 3; Makarova, 1988b, pl. 35, fig. 3. (**Plate 2, Fig. 11**)
- Thalassiosira latimarginata* Makarova; Makarova, 1988b, pl. 30, figs. 1–12; Makarova, 1988c, pl. 40, figs. 11–17. **Synonym:** *Thalassiosira trifulta* Fryxell in Fryxell and Hasle, 1979: pp. 16–19, pls. 1–5, figs. 1–24; Sancetta, 1982, pl. 5, figs. 10–12, pl. 6, figs. 1–2; Akiba, 1986, pl. 10, figs. 5–7. (**Plate 1, Fig. 4; Plate 6, Fig. 1**)
- Thalassiosira leptopus* (Grunow) Hasle et Fryxell; Akiba, 1986, pl. 9, figs. 3–4; Makarova, 1988b, pp. 49–50; Makarova, 1988c, pl. 42, fig. 12. (**Plate 4, Fig. 17**)

Thalassiosira lineata Jousé, 1968: p. 13, pl. 1, figs. 1–2; Akiba, 1986, pl. 14, figs. 7, 9.

Thalassiosira manifesta Sheshukova, 1964: Sheshukova-Poretskaya, 1964, p. 72, pl. 1, figs. 6–7; 1967, pl. 14, figs. 9a–b; Akiba, 1986, pl. 9, figs. 1–3. (**Plate 7, Figs. 8, 10**)

Thalassiosira marujamica Sheshukova emend. Makarova, 1988: Makarova, 1988b, pp. 51–52, pl. 24, figs. 1–13; 1988c, pl. 41, figs. 13–21. **Synonyms:** *Thalassiosira decipiens* (Grunow) Jørgensen sensu Sheshukova-Poretskaya, 1964, pl. 1, fig. 2; 1967, pl. 14, fig. 2; *Thalassiosira borealis* Koizumi, 1980: p. 395, pl. 1, figs. 7–10. (**Plate 3, Figs. 25, 27**)

Thalassiosira nativa Sheshukova, 1964: Sheshukova-Poretskaya, 1964, p. 75, pl. 1, figs. 4–5; 1967, pl. 14, figs. 7 a–c. (**Plate 1, Figs. 5–6**)

Thalassiosira sp. cf. *T. nativa* Sheshukova. **Remarks:** Small specimens resemble *T. nativa* having some indistinct characters for the precise identification were assigned to this category and tabulated together with specimens of *T. nativa*.

Thalassiosira nidulus (Tempère et Brun) Jousé; Akiba, 1986, pl. 6, figs. 5–7.

Thalassiosira oestrupii (Ostenfeld) Proshkina-Lavrenko; Barron, 1980, pl. 5, fig. 4; Barron, 1985, figs. 11.5–11.6; Akiba, 1986, pl. 14, figs. 1–6; Makarova, 1988b, pl. 25, figs. 1–9; Makarova, 1988c, pl. 42, figs. 13–17. (**Plate 3, Figs. 11–12**)

Thalalassiosira orientalis Sheshukova emend. Makarova, 1988: Makarova, 1988b, p. 77, pl. 50, figs. 1–9; 1988c, pl. 52, figs. 13–17. **Synonyms:** *Thalalassiosira margaritae* (Frenguelli et Orlando) Kozlova sensu Sheshukova-Poretskaya, 1964, pl. 2, figs. 1–3; *Thalalassiosira* aff. *margaritae* (Frenguelli et Orlando) Kozlova sensu Sheshukova-Poretskaya, 1967, pl. 14, figs. 5a–c. (**Plate 7, Fig. 9**)

Thalassiosira praeoestrupii Dumont et al., 1986 emend. Bodén, 1993: pp. 67–68, pl. 1, figs. H–J, pl. 2, figs. C–G, pl. 3, figs. H, J. (**Plate 7, Figs. 1–2**)

Thalassiosira sheshukovae Makarova, 1988: Makarova, 1988a, p. 1185, pl. 2, figs. 1–11. **Synonym:** *Pseudopodosira elegans* Sheshukova: Sheshukova-Poretskaya, 1964, p. 75–76, text fig. 3, pl. 2, figs. 4–5; 1967, pl. 24, fig. 3; Pl. 25, fig. 4; Sancetta, 1982, pl. 4, figs. 1–2; Akiba, 1986, pl. 4, figs. 5–7. (**Plate 1, Fig. 8**)

Thalassiosira temperei (Brun) Akiba et Yanagisawa, 1986: p. 493, pl. 31, figs. 1–7; Yanagisawa, 1990, pl. 1, figs. 16, 25. **Synonyms:** *Coscinodiscus temperei* Brun; Kanaya, 1959, pl. 4, fig. 8; Barron, 1980, pl. 4, fig. 5; Akiba et al., 1982, pl. 1, fig. 5; *Cymatothea weissflogii* (Grunow) Hendey sensu Sheshukova-Poretskaya, 1967, pl. 26, fig. 1; sensu Hanna, 1970, figs. 15–16. (**Plate 3, Fig. 23**)

Thalassiosira tertiaria Sheshukova, 1967: Sheshukova-Poretskaya, 1967, p. 148, pl. 15, fig. 2.

Thalassiosira undulosa (Mann) Sheshukova, 1967: Sheshukova-Poretskaya, 1967, pp. 148–149, pl. 16, figs. 1 a–c; Koizumi, 1973, pl. 8, figs. 5–6; Akiba, 1986, pl. 9, fig. 4. **Synonym:** *Coscinodiscus undulosus* Mann; Hanna, 1970, fig. 3. (**Plate 4, Fig. 19**)

Thalassiosira Cleve spp. **Remarks:** The precise identification of *Thalassiosira* species having sublinear, tangential or fasciculated areolae pattern, with an indistinct structure of the marginal and central zones, was not attempted. These specimens were not tabulated separately in the occurrence table.

Thalassiothrix longissima Cleve et Grunow; Schrader, 1973, pl. 23, figs. 7, 17–18; Akiba, 1986, pl. 21, fig. 18.

Thalassiothrix robusta (Schrader) Akiba, 1986: p. 441, pl. 21, fig. 4. (**Plate 3, Figs. 5–6; Plate 4, Fig. 9**)

Trochosira spinosa Kitton; Sheshukova-Poretskaya, 1967, pl. 11, figs. 6a–b, pl. 13, figs. 4a–b. **Remarks:** See Remarks for *Hyalopyxis concava* (Sheshukova) Makarova.

Xanthiopyxis globosa Ehrenberg; Barron, 1975, pl. 15, figs. 8–9.

Xanthiopyxis ovalis Lohman, 1938: p. 91, pl. 20, fig. 6, pl. 22, fig. 12; Hanna, 1970, fig. 70; Barron, 1975, pl. 15, fig. 13.

Xanthiopyxis (Ehrenberg) Ehrenberg spp. **Remarks:** All scarce specimens not referable to *X. globosa* or *X. ovalis* were assigned to this category.

Silicoflagellates

Distephanus crux s. ampl. (Ehrenberg) Haeckel; Perch-Nielsen, 1985, figs. 18.7–18.10.

Distephanus speculum pentagonus Limmermann; Perch-Nielsen, 1985, fig. 20.1.

Distephanus speculum speculum (Ehrenberg) Glezer; Perch-Nielsen, 1985, figs. 20.8–20.9.

PLATES 1-7

Plate 1

Fig. 1: *Thalassiosira dolmatovae* (a–c: valve in different focus). Fig. 2: *Adoneis pacifica*. Figs. 3, 7, 10: *Thalassiosira jouseae*. Fig. 4: *Thalassiosira latimarginata*. Figs. 5–6: *Thalassiosira nativa*. Fig. 8: *Thalassiosira sheshukovae*. Fig. 9: *Detonula confervacea*. Fig. 11: *Hyalodiscus obsoletus*. Fig. 12: *Actinocyclus* sp. Figs. 13, 15–16: *Pyxidicula zabelinae*. Fig. 14: *Stephanogonia hanza-wae*.

Light microscope (LM). Magnification $\times 1000$ except of Fig. 4 ($\times 1250$).

Figs. 1–3, 7–9, 11–14: CAS 608382. Fig. 4: CAS 608426. Figs. 5, 10: CAS 617358. Fig. 6: CAS 608378. Fig. 15: CAS 608376. Fig. 16: CAS 608426.

PLATE 1

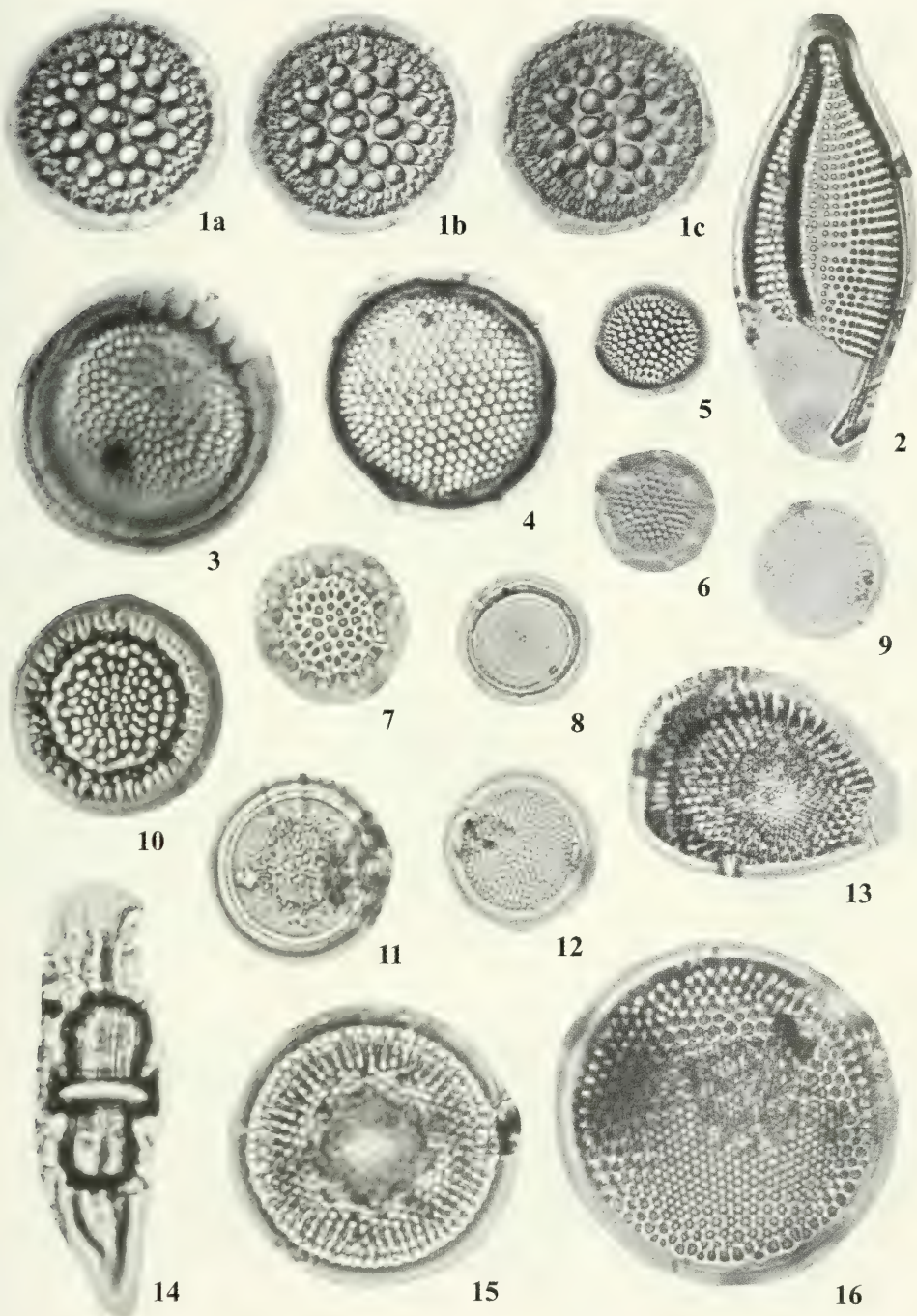


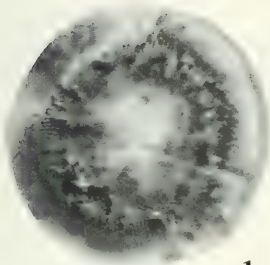
Plate 2

Fig. 1: *Porosira punctata*. Figs. 2–3: *Dicladia capreolus*. Figs. 4–5: *Coscinodiscus marginatus*. Fig. 6: *Thalassiosira gravida*. Figs. 7, 10: *Odontella aurita*. Figs. 8–9: *Bacteriastrum varians*. Fig. 11: *Thalassiosira kryophila* (a–b: valve in different focus).

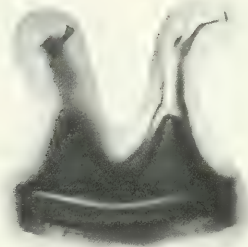
LM. Magnification $\times 1000$.

Fig. 1: CAS 608378. Figs. 2, 8: CAS 608400. Figs. 3, 5–7, 9–11: CAS 608382. Fig. 4: CAS 608397.

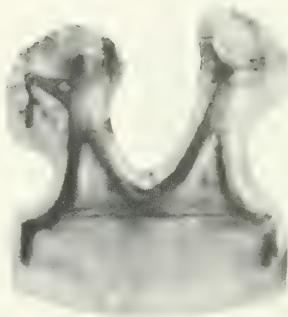
PLATE 2



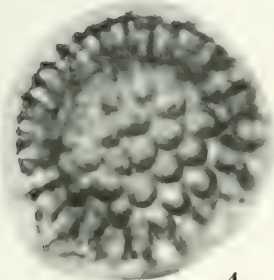
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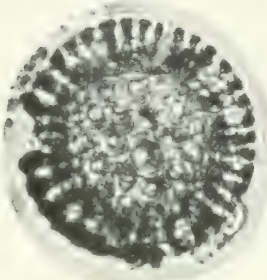
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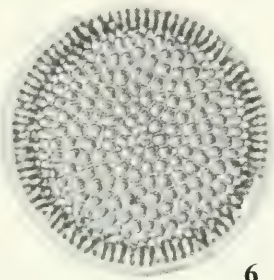
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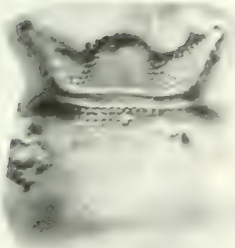
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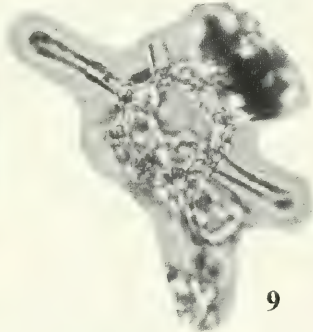
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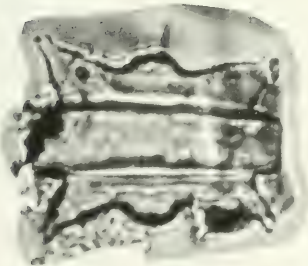
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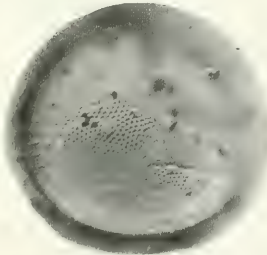
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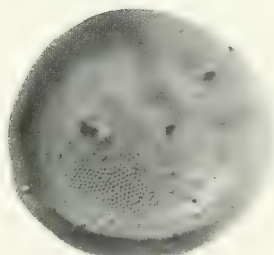
9



10



11a



11b

Plate 3

Figs. 1–2: *Thalassiosira antiqua*. Figs. 3–4: *Cymatosira debyi*. Figs. 5–6: *Thalassiothrix robusta*. Figs. 7–8, 18: *Thalassiosira hyalina*. Figs. 9–10: *Thalassionema nitzschioides*. Figs. 11–12: *Thalassiosira oestrupii*. Fig. 13–15: *Fragilariopsis cylindrus*. Figs. 16–17: *Fragilariopsis oceanica*. Fig. 19: *Bacterosira fragilis* (a–b: valve in different focus). Fig. 20: *Nitzschia rolandii*. Figs. 21–22: *Hyalopyxis concava*. Fig. 23: *Thalassiosira temperei*. Fig. 24: *Thalassiosira dolmatovae*. Figs. 25, 27: *Thalassiosira marujamica*. Figs. 26, 28: *Chaetoceros* resting spores.

LM. Magnification $\times 1000$ except of Figs. 11–12 ($\times 600$).

Figs. 1, 6, 8, 10–11, 20, 23–24, 28: CAS 608382. Figs. 2, 18: CAS 60269–s. Figs. 3–4, 13–14, 19: CAS 608376. Figs. 5, 9: CAS 608424. Figs. 7, 12, 26: CAS 617358. Figs. 15–16: CAS 608393. Fig. 17: CAS 608376. Figs. 21–22, 25, 27: CAS 608371.

PLATE 3

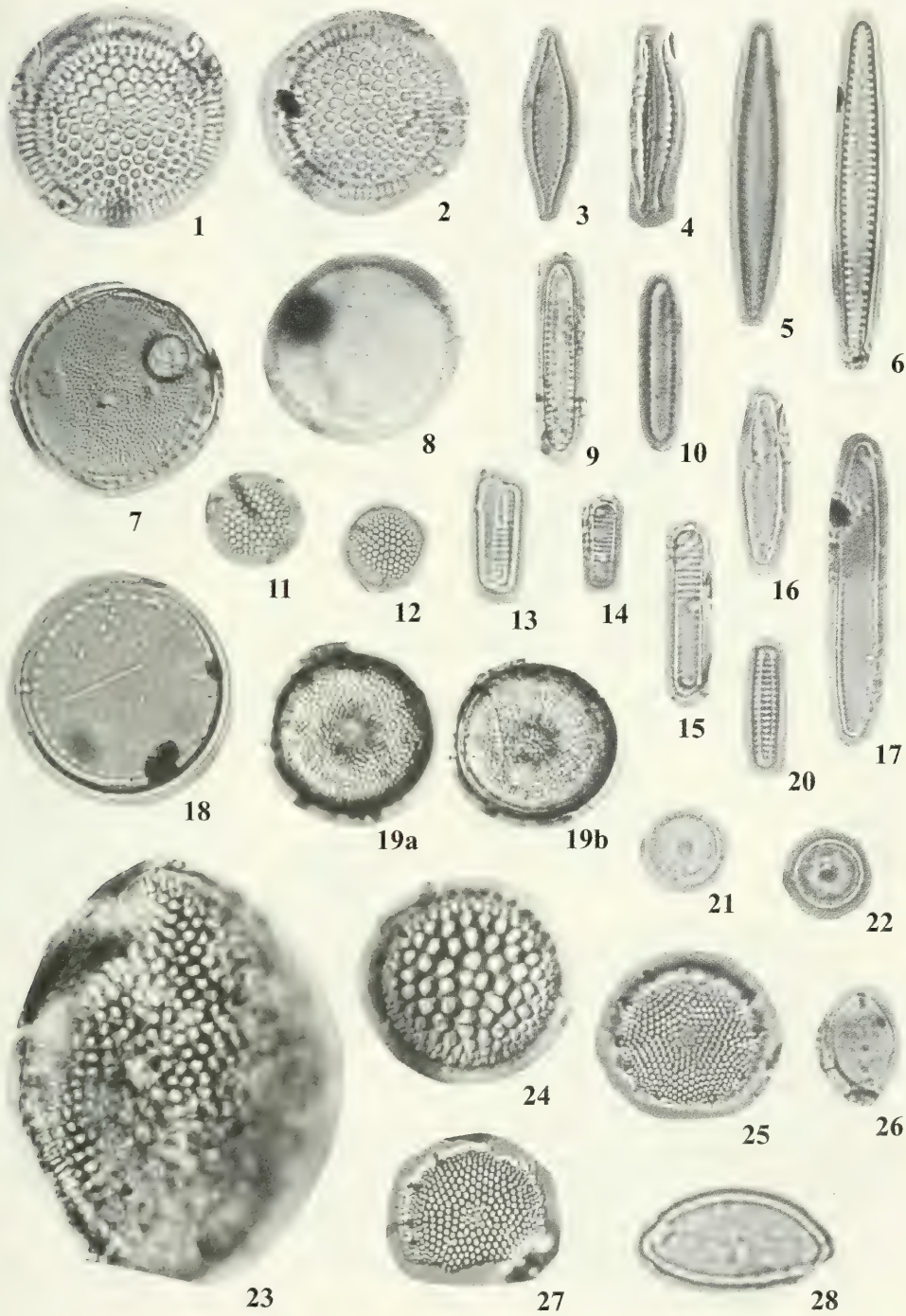


Plate 4

Figs. 1–2, 7: *Rhaphoneis angularis*. Figs. 3–6, 10–11: *Delphineis angustata* group. Fig. 8: *Cymatosira debyi*. Fig. 9: *Thalassiothrix robusta*. Fig. 12: *Rhizosolenia hebetata* group. Fig. 13: *Delphineis sachalinensis*. Fig. 14: *Thalassiosira eccentrica*. Fig. 15: *Thalassiosira* sp. cf. *T. convexa*. Fig. 16: *Cosmiodiscus insignis*. Fig. 17: *Thalassiosira leptopus*. Fig. 18: *Bacterosira fragilis*. Fig. 19: *Thalassiosira undulosa*.

LM. Magnification $\times 1000$.

Figs. 1–2: CAS 617358. Figs. 3–6: CAS 608379. Figs. 7, 9–13, 16: CAS 608382. Figs. 14, 8, 19: CAS 608376. Fig. 15: CAS 608378. Fig. 17: CAS 608370. Fig. 18: CAS 608371.

PLATE 4

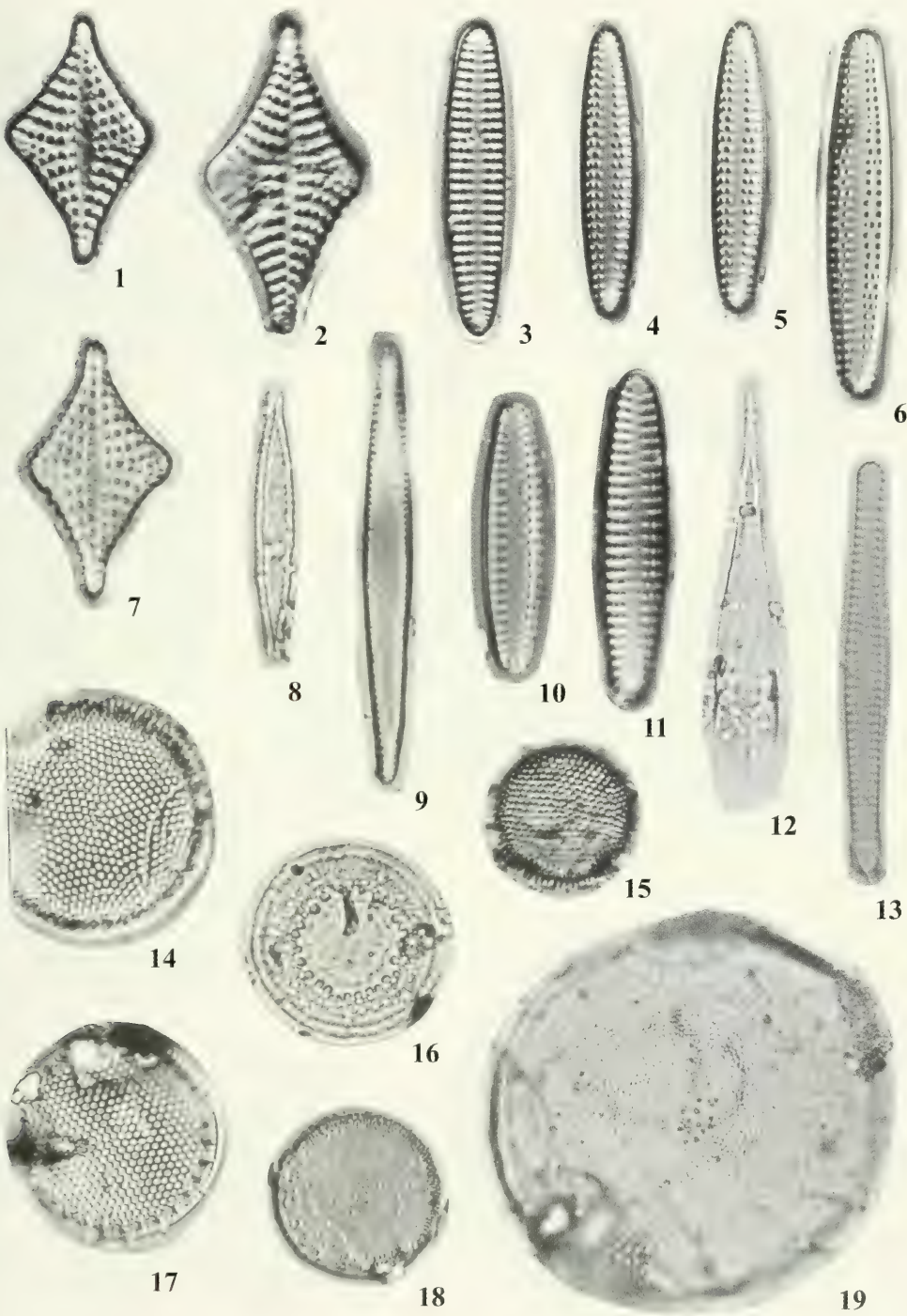


Plate 5

Fig. 1: *Actinoptychus splendens*. Figs. 2–4: *Neodenticula kamtschatica*. Fig. 5: *Actinocyclus octonarius*. Figs. 6–7: *Delphineis simonsenii*. Fig. 8: *Actinoptychus senarius* (a–b: valve in different focus). Fig. 9: *Actinocyclus ochotensis*. Fig. 10: *Detonula confervacea*. Fig. 11–12: *Actinocyclus curvatulus*.

LM. Magnification $\times 1000$.

Figs. 1, 3–4, 6–7, 9, 12: CAS 608382. Fig. 2: CAS 608376. Fig. 5: CAS 608400. Fig. 8: CAS 608378. Fig. 10: CAS 617358. Fig. 11: CAS 608392.

PLATE 5

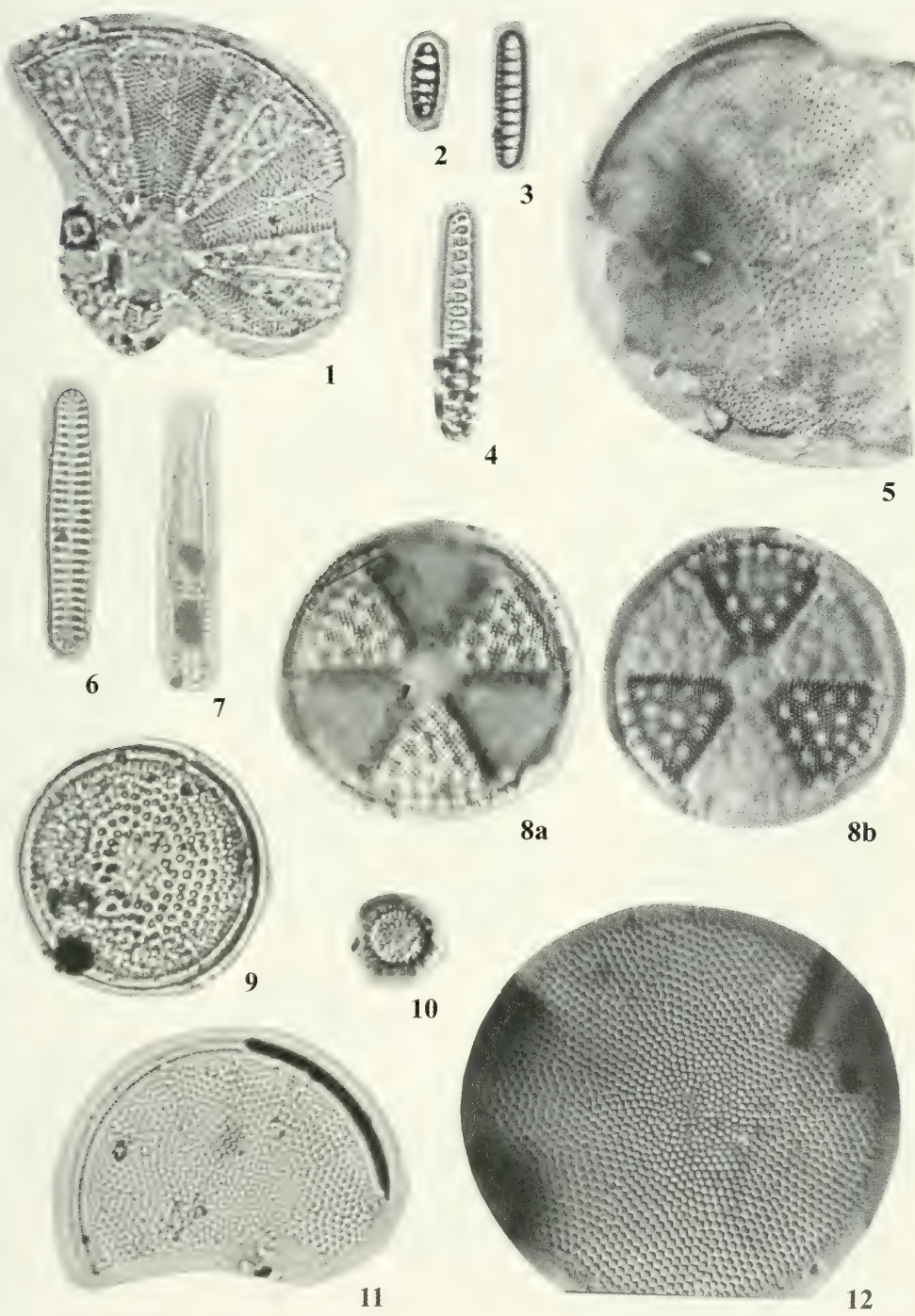


Plate 6

Fig. 1: *Thalassiosira latimarginata*. Figs. 2–3, 5: *Cosmiodiscus insignis*. Fig. 4: *Neodenticula kamtschatica*. Figs. 6, 10: *Rhaphoneis angularis*. Figs. 7–8: *Thalassiosira jacksonii* (a–b: valve in different focus). Fig. 9: *Thalassiosira eccentrica*. Figs. 11, 13–17: *Thalassiosira* sp. cf. *T. convexa* (a–b: valve in different focus). Fig. 12: *Porosira punctata*.

LM. Magnification $\times 1000$.

Figs. 1: CAS 608408. Figs. 2, 6: CAS 617358. Figs. 3, 5, 9, 11: CAS 608382. Figs. 4, 7–8, 14–17: CAS 608376. Fig. 10: CAS 608379. Fig. 12: CAS 608378. Fig. 13: CAS 60269–s.

PLATE 6

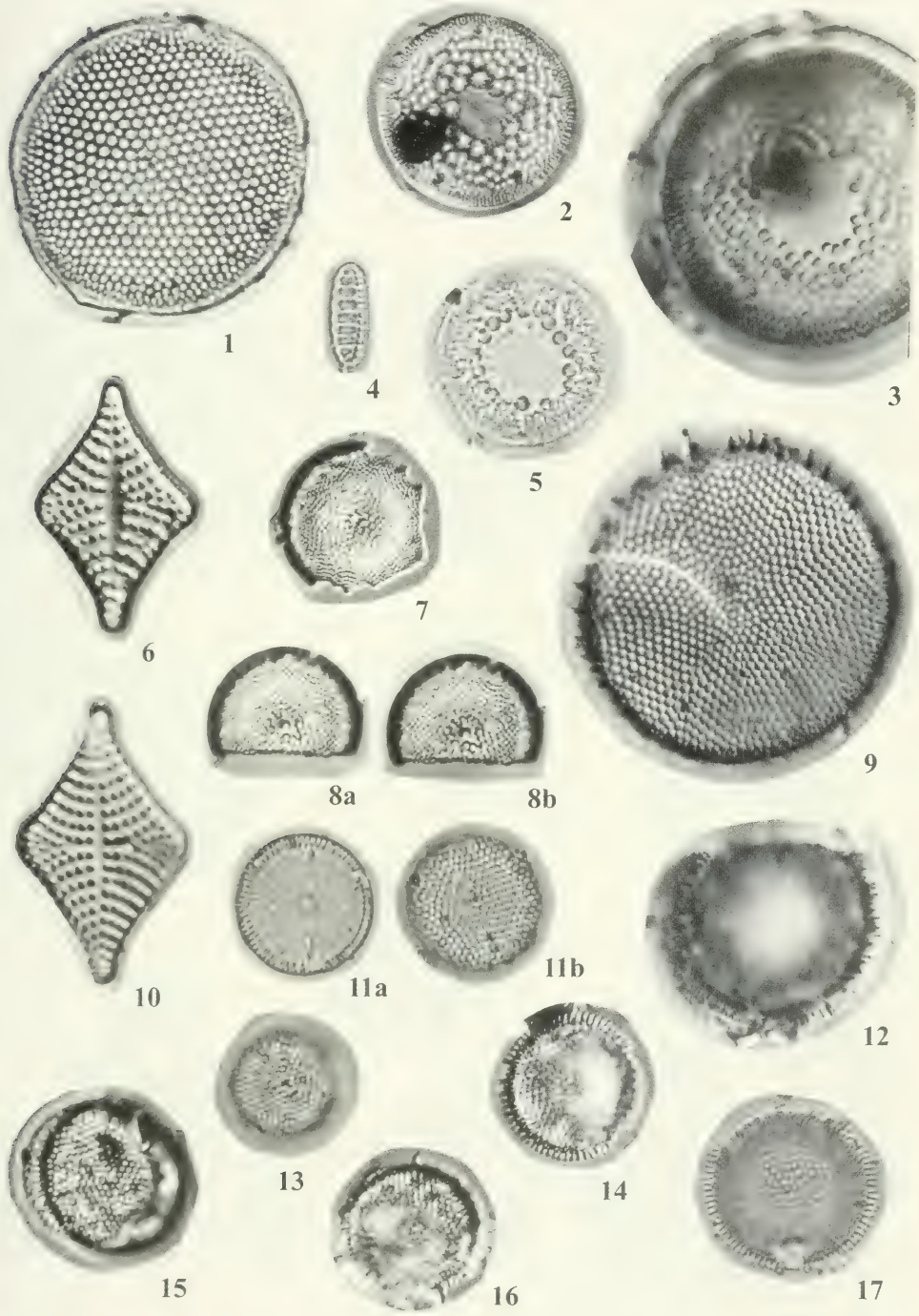


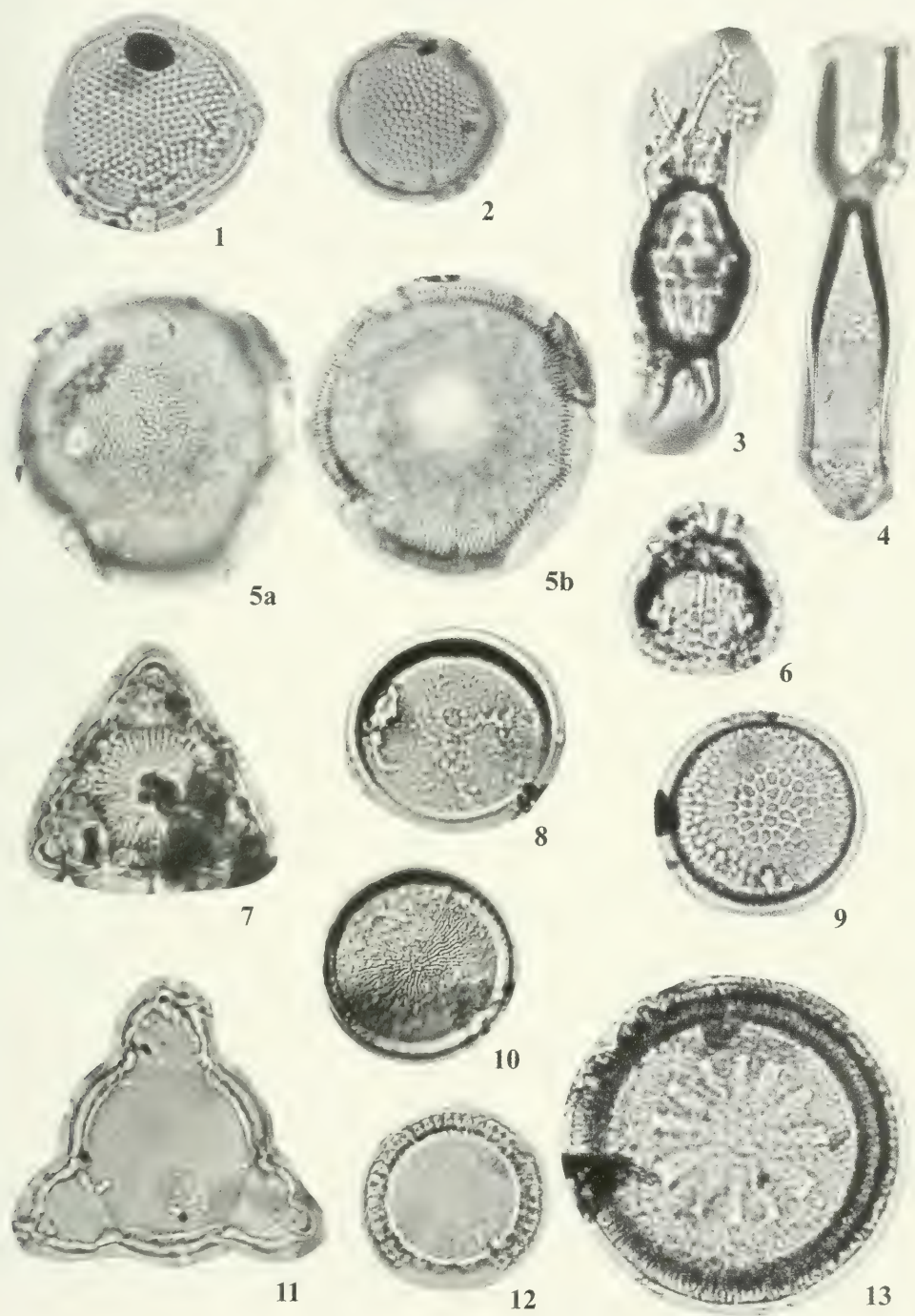
Plate 7

Figs. 1–2: *Thalassiosira praeoestrupii*. Figs. 3, 6: *Cladogramma dubium*. Fig. 4: *Pseudopyxilla americana*. Fig. 5: *Porosira glacialis* (a–b: valve in different focus). Figs. 7, 11: *Lithodesmium minusculum*. Figs. 8, 10: *Thalassiosira manifesta*. Fig. 9: *Thalassiosira orientalis*. Figs. 12–13: *Paralia sulcata*.

LM. Magnification $\times 1000$.

Figs. 1–2: CAS 60269–s. Figs. 3–4, 8–9, 11–12: CAS 608382. Figs. 5, 7: CAS 608376. Fig. 6: CAS 608408. Fig. 10: CAS 617358. Fig. 13: CAS 608392.

PLATE 7



Caryophyllidia-bearing Dorid Nudibranchs (Mollusca, Nudibranchia, Doridacea) from Costa Rica

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The tropical eastern Pacific dorid nudibranch *Taringa aivica* Ev. Marcus and Er. Marcus, 1967 is redescribed based on the examination of specimens collected from the Pacific coast of Costa Rica. The differences between *Taringa aivica timia* Ev. Marcus and Er. Marcus, 1967 and *Taringa aivica aivica* Ev. Marcus and Er. Marcus, 1967 are not consistent and do not justify the existence of two subspecies of *Taringa aivica*. Examination of the type material of *Peltodoris nayarita* Ortea and Llera 1981, another eastern Pacific species, confirmed that it is a synonym of *Peltodoris greeleyi* MacFarland, 1909, originally described from Brazil. The study of *Discodoris aurila* Marcus, 1976 from Panama and Costa Rica, shows that this species is characterized by the absence of jaw elements, the presence of hamate and smooth radular lateral teeth, and the innermost teeth hamate, elongated, and lacking denticles.

Peltodoris greeleyi and *Discodoris aurila* are transferred to the genus *Diaulula* based on the presence of caryophyllidia, low rhinophoral and branchial sheaths, a flattened prostate divided into two portions, penis and vagina unarmed, hamate radular teeth and smooth labial cuticle. The geographic range of *Diaulula greeleyi* is extended to Punta Uvita, Costa Rica and the geographic range of *Diaulula aurila* is extended from Mexico to Panama.

RESUMEN

La especie de dórido nudibranquio del Pacífico Este tropical *Taringa aivica* Ev. Marcus y Er. Marcus, 1967 es redescrita en base al estudio de especímenes recolectados en la costa Pacífica de Costa Rica. Las diferencias entre *Taringa aivica timia* Ev. Marcus y Er. Marcus, 1967 y *Taringa aivica aivica* Ev. Marcus y Er. Marcus, 1967 no son consistentes y no justifican la existencia de dos subespecies diferentes de *Taringa aivica*. El estudio del material tipo de *Peltodoris nayarita* Ortea y Llera, 1981, otra especie del Pacífico Este, ha confirmado que ésta es un sinónimo de *Peltodoris greeleyi* MacFarland, 1909, que fue originalmente descrita de Brasil. El estudio de *Discodoris aurila* Marcus, 1976 de Panamá y Costa Rica, muestra que esta especie se caracterizada por la ausencia de uncinos, y la presencia de dientes laterales de la rádula ganchudos y lisos, dientes centrales ganchudos, alargados y sin denticulos. *Peltodoris greeleyi* y *Discodoris aurila* son transferidas al género *Diaulula* en base a la presencia de cariofilídeos, vainas rinofóricas y branquiales no elevadas, una próstata aplanada dividida en dos regiones, pene y vagina lisos, dientes de la rádula en forma de gancho y cutícula labial lisa. La distribución geográfica de *Diaulula greeleyi* es extendida hasta Punta Uvita, Costa Rica y la distribución geográfica de *Diaulula aurila* es extendida desde México hasta Panamá.

Intensive field work along the Pacific coast of Costa Rica has revealed the presence of three species of caryophyllidia-bearing dorids. The species, *Taringa aivica* Ev. Marcus and Er. Marcus, 1967, *Peltodoris nayarita* Ortea and Llera, 1981 and *Discodoris aurila* Marcus, 1976 have already been reported from other areas in the eastern Pacific, but their anatomy was poorly described and the presence of caryophyllidia had been overlooked.

Valdés and Gosliner (2001) recently studied the phylogenetic relationships of the caryophyllidia-bearing dorids, which according to these authors are a monophyletic group. They also synonymized several genera previously considered as valid or regarded as uncertain. Therefore, the caryophyllidia-bearing dorid species from Costa Rica need to be re-examined in light of the new evidence.

The objective of the present paper is to re-examine the three described species of the caryophyllidia-bearing dorids present in Costa Rica.

The material examined is deposited at the Department of Invertebrate Zoology and Geology, California Academy of Sciences, San Francisco (CASIZ), Instituto Nacional de Biodiversidad, Costa Rica (INBio), the Natural History Museum of Los Angeles County (LACM), Muséum National d'Histoire Naturelle, Paris (MNHN), and the National Museum of Natural History (USNM).

SPECIES DESCRIPTION

Genus *Taringa* Er. Marcus, 1955

Type species: *Taringa telopia* Er. Marcus, 1955

Taringa aivica Ev. Marcus and Er. Marcus, 1967

(Figs 1A–B, 2A–D, 3A–E)

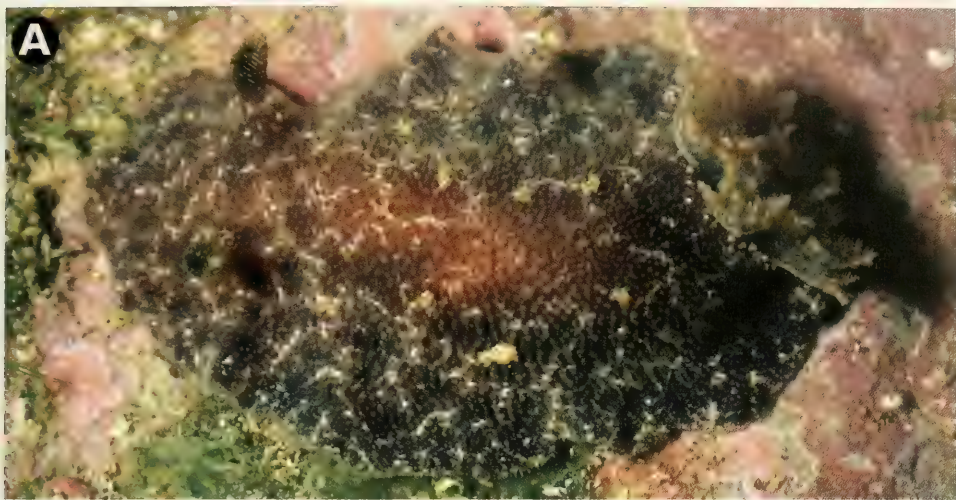
Taringa aivica Marcus and Marcus, 1967:89–92, figs. 115–119.

Taringa aivica timia Marcus and Marcus, 1967:189–191, figs. 47–51; Behrens and Henderson, 1982:197–199, figs.1–4.

MATERIAL EXAMINED

San Miguel, Cabo Blanco, Costa Rica, May 16, 1998, 1 specimen, 12 mm preserved length, 2 m depth, leg. A. Berrocal (INB0001496644); San Miguel Station, Cabo Blanco, Costa Rica, January 28, 1999, 2 specimens, 30–31 mm preserved length, intertidal, leg. F. Alvarado (INB0001496686); San Miguel Station, Cabo Blanco, Costa Rica, January 28, 1999, 11 specimens, 10–20 mm preserved length, intertidal, leg. F. Alvarado (INB0001496491); San Miguel Station, Cabo Blanco, Costa Rica, January 22, 1999, 18 specimens, 9–23 mm preserved length, intertidal, leg. F. Alvarado (INB0001496522); San Miguel Station, Cabo Blanco, Costa Rica, May 17, 1999, 1 specimen, 4 mm preserved length, 2 m depth, leg. S. Ávila (INB0001496524); Playa Coralito, Peñón del Coral, Puntarenas, Costa Rica, January 29, 1999, 1 specimen, 12 mm preserved length, intertidal, leg. F. Alvarado (INB0001496675); Punta Uvita, Puntarenas, Costa Rica, January 15, 2000, 9 specimens, 4–12 mm preserved length, intertidal, leg. M. Calderón (INB0001496174); San Pedrillo, Osa Peninsula, Costa Rica, January 19, 2000, 1 specimen, 6 mm preserved length, intertidal, leg. A. Berrocal (INB0001496548); San Pedrillo, Osa Peninsula, Costa Rica, January 15, 2000, 1 specimen, 16 mm preserved length, intertidal, leg. M. Calderón (INB0001495952); San Pedrillo, Osa Peninsula, Costa Rica, February 27, 1998, 3 specimens, 9–10 mm preserved length,

FIGURE 1. Living animals. A–B. *Taringa aivica* (INB0001496491); C. *Diaulula greeleyi* (INB0001496508); D. *Diaulula aurila* (INB0001495896).



intertidal, leg. A. Berrocal (INB000146490); San Pedrillo, Osa Peninsula, Costa Rica, February 27, 1998, 1 specimen, 9 mm preserved length, intertidal, leg. A. Berrocal (INB0001496489); Playa Gallardo, Golfo Dulce, Costa Rica, February 12, 1997, 1 specimen, 16 mm preserved length, intertidal, leg. S. Ávila (INB0001496523); Punta Larga, Golfo Dulce, Costa Rica, November 29, 1997, 6 specimens, 5–16 mm preserved length, intertidal, leg. M. Madrigal (INB0001496484); Punta Larga, Golfo Dulce, Costa Rica, November 27, 1997, 2 specimens, 14–18 mm preserved length, intertidal, leg. A. Berrocal (INB0001496525).

GEOGRAPHIC RANGE

From Palos Verdes, California (Behrens and Henderson, 1982) to Sonora, Mexico and the Canal Zone, Panama (Marcus and Marcus, 1967).

EXTERNAL MORPHOLOGY

The body is oval to elongate (Fig. 1A–B). The dorsum is covered with caryophyllidia about 0.15 mm long (Fig. 2D). There are some larger, conical tubercles arranged in two rows on both sides of the visceral hump. The dorsal color is variable ranging from pale yellow to dark brown. There is no correlation between the size of the animal and the dorsal color. Normally specimens have irregularly distributed darker patches on the dorsum; patches may be more densely arranged on the center of the dorsum. The larger tubercles are white or cream white in most specimens. There is a row of white patches on both sides of the dorsal hump, around the larger tubercles, that may be absent in some specimens and may be larger in others, almost occupying the entire mantle margin. The rhinophores are dark gray or black with numerous white or cream white spots on the club. The rhinophores have 17 lamellae. Occasionally there are white spots surrounding the rhinophoral sheath. The rhinophoral apex is white or cream-white. The gill is composed of six tripinnate branchial leaves. The leaves are yellowish or cream-white with minute dark spots. Ventrally, the anterior border of the foot is grooved and notched (Fig. 3E).

ANATOMY

The labial cuticle is smooth. The radular formula is $32 \times (39.0.39)$ in a 26 mm preserved length specimen (INB0001496522). Rachidian teeth are absent (Fig. 2A). The innermost teeth are hamate with a wide base and denticles. The lateral teeth are hamate, having a narrow base and a very conspicuous prolongation on the upper side (Fig. 2B). There are four to nine denticles on each lateral tooth. These denticles decrease in number towards the central part of the radula. The lateral teeth increase in size gradually towards the medial portion of the half-row. There are three or four pectinate outermost teeth (Fig. 2C). The stomach is oval and connects distally to the long intestine that forms a loop and runs to the anal opening (Fig. 3A).

The ampulla is very long and convoluted in the middle portion (Fig. 3C). It enters the female glands near their nidamental opening. The deferent duct is long and convoluted, and enters the flattened prostate. The proximal end of the deferent duct opens into a common atrium with the vagina. The vagina is long and tubular in shape and almost as thick as the deferent duct. At its distal end, the vagina connects to the large and oval bursa copulatrix. Both, the duct that leads from the seminal receptacle to the bursa copulatrix and the vaginal duct, are joined. The pear-shaped seminal receptacle is smaller than the bursa copulatrix (Fig. 3D). It is connected to the bursa copulatrix by a long and coiled duct. The penial cuticle is conical or bell-shaped (Fig. 3B).

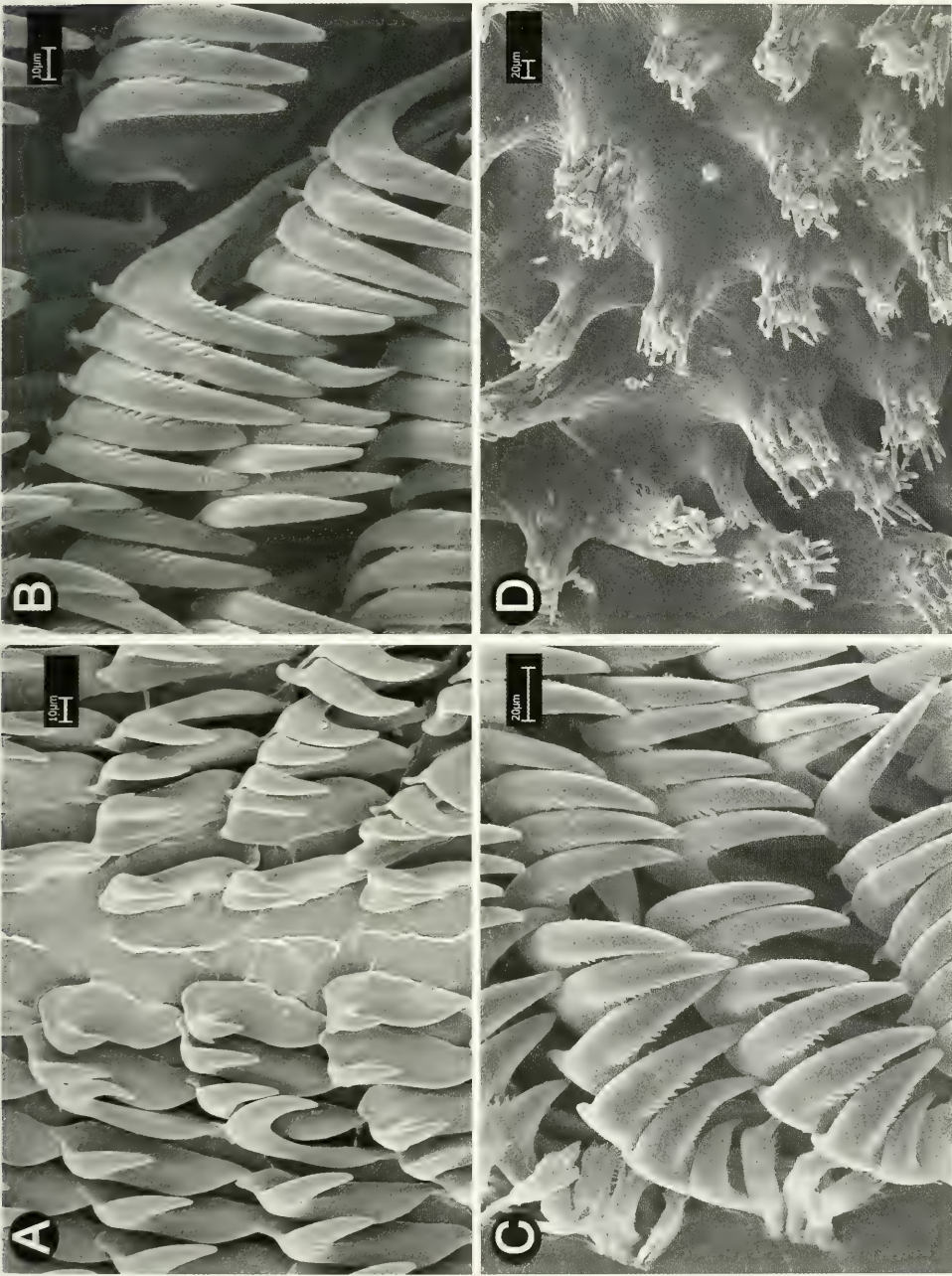


FIGURE 2. *Taringa aiivica* (INB0001496522), SEM photographs. A. Inner lateral teeth, scale bar= 10µm. C. Outer lateral teeth, scale bar=20 µm. D. Caryophyllidia, scale bar= 20µm.

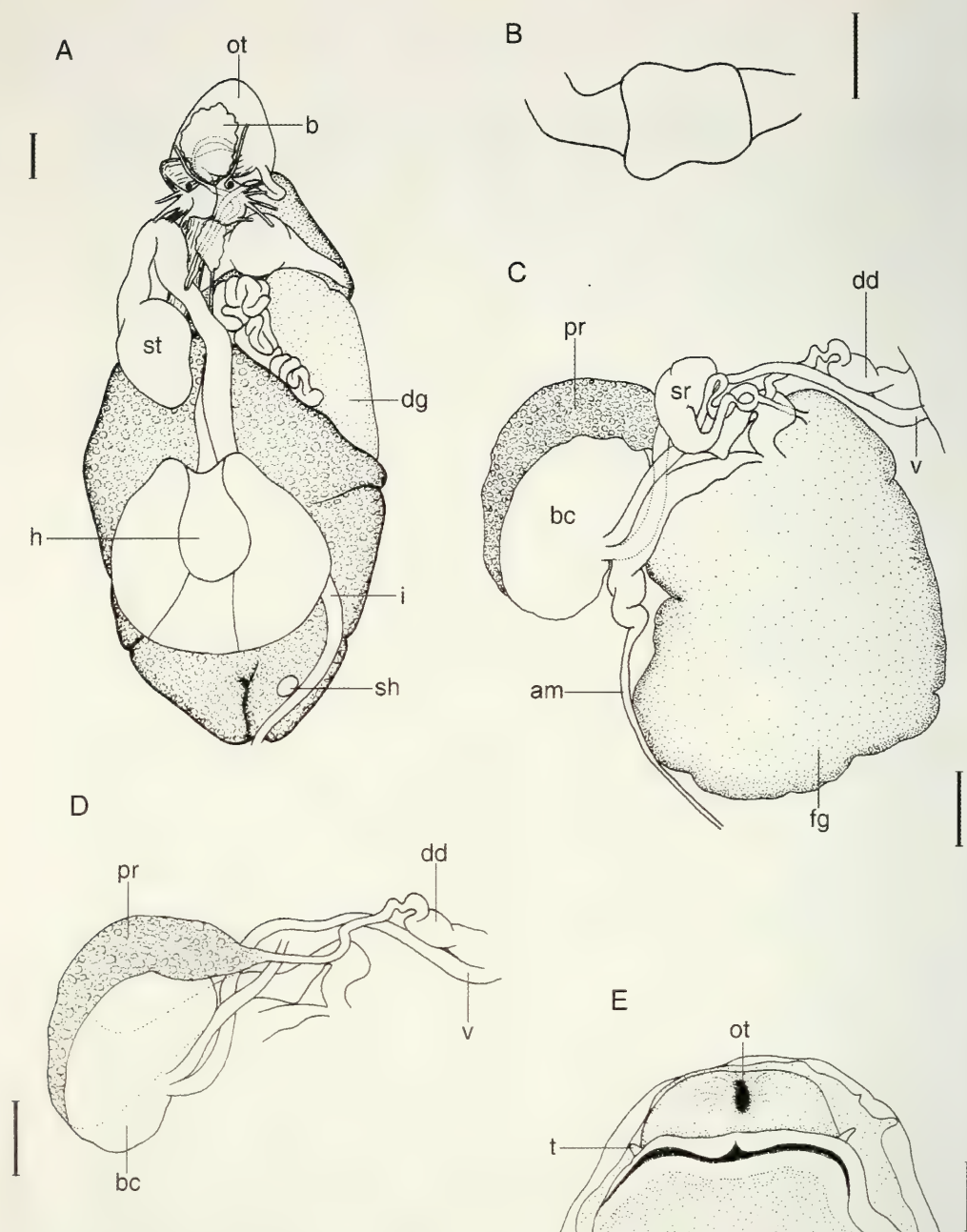


FIGURE 3. Anatomy of *Taringa aivica* (INB0001496522). A. Dorsal view of the internal organs, scale bar= 1mm; B. Penis, scale bar= 0.25 mm; C. Reproductive system, scale bar= 1mm; D. Detail of the reproductive system, scale bar=1mm; E. Ventral view of the mouth area, scale bar= 1mm. Abbreviations: am=ampulla; b=blood gland; bc=bursa copulatrix; dd=deferent duct; dg=digestive gland; fg=female gland; h=heart; i=intestine; ot=oral tube; pr=prostate; sh=syrinx; sr=seminal receptacle; st=stomach; t=oral tentacle; v=vagina.

REMARKS

The study of several specimens and the review of the original description confirms that the external and internal features of this species fit with those of the genus *Taringa*. The presence of a flattened prostate with two portions, an unarmed vagina, a penis armed with a cuticular structure, inner and mid-lateral hamate radular teeth and pectinated outermost teeth are characteristics of this genus (Valdés and Gosliner 2001).

According to Marcus and Marcus (1967) the differences between *Taringa aivica aivica* and *Taringa aivica timia* are the presence of an outermost pectinated tooth with a broad spine in *Taringa aivica timia* that is not present in *T. aivica aivica* and the strong denticles of the lateral teeth in *T. aivica aivica*. Also, they found uniformly distributed caryophyllidia and sometimes bicuspid papillae in *Taringa aivica timia*, and very small caryophyllidia and conical papillae in *Taringa aivica*.

Behrens and Henderson (1982) reported *Taringa aivica timia* from Palos Verdes, California, and provided additional anatomical details. In this study Behrens and Henderson found a bell-shaped papilla in the penial cuticle and 5 to 10 pointed denticles on the outer side of their cusp, but apparently the broad spine mentioned by Marcus and Marcus (1967) is missing.

In the present study, we have found great variability in dorsal coloration as well as in the arrangement of the caryophyllidia and papillae (Figs. 1A–B). A spine on the outermost pectinated teeth was not found in the material study and is also absent in the specimens assigned to *Taringa aivica timia* by Behrens and Henderson (1982). The presence or absence of this spine as well as the shape of the penial cuticle are most likely due to intraspecific variation. We consider that the features mentioned by Marcus and Marcus (1967) are not enough to justify the existence of two different subspecies and *Taringa aivica timia* and *Taringa aivica aivica* should be synonymized.

Genus *Diaulula* Bergh, 1878

Type species: *Doris sandiegensis* Cooper, 1863

***Diaulula greeleyi* (MacFarland, 1909)**

(Figs. 1C, 4A–D, 5A–D)

Peltodoris greeleyi MacFarland, 1909:84–88, pl.15, figs. 77–82; Marcus, 1955; Marcus and Marcus, 1967; Eyster, 1980:588.

Peltodoris nayarita Ortea and Llera, 1981:47–51, figs. 1–4 (also cited as *Anisodoris*).

MATERIAL EXAMINED

HOLOTYPE of *Peltodoris greeleyi*: Alagoas, Riacho Doce, Brazil, July 28, 1899, 1 specimen, 9 mm preserved length, leg. A.W. Greeley. (CASIZ 21021).

HOLOTYPE of *Peltodoris nayarita*: Isabel Island, Nayarit, Mexico (21°52' N, 105°54' W), 1 specimen, 22 mm preserved length, contracted and dissected (MNHN).

ADDITIONAL MATERIAL EXAMINED

San Miguel Station, Cabo Blanco, Costa Rica, May 17, 1998, 1 specimen, 10 mm preserved length, 2 m depth, leg S. Ávila (INB0001500647); San Miguel Station, Cabo Blanco, Costa Rica, January 26, 1999, 22 specimens, 3–13 mm preserved length, intertidal, leg. F. Alvarado (INB0001496509); San Miguel Station, Cabo Blanco, Costa Rica, January 22, 1999, 39 specimens, 2–16 mm preserved length, intertidal, leg. F. Alvarado (INB0001496508); Ballena Island, Uvita,

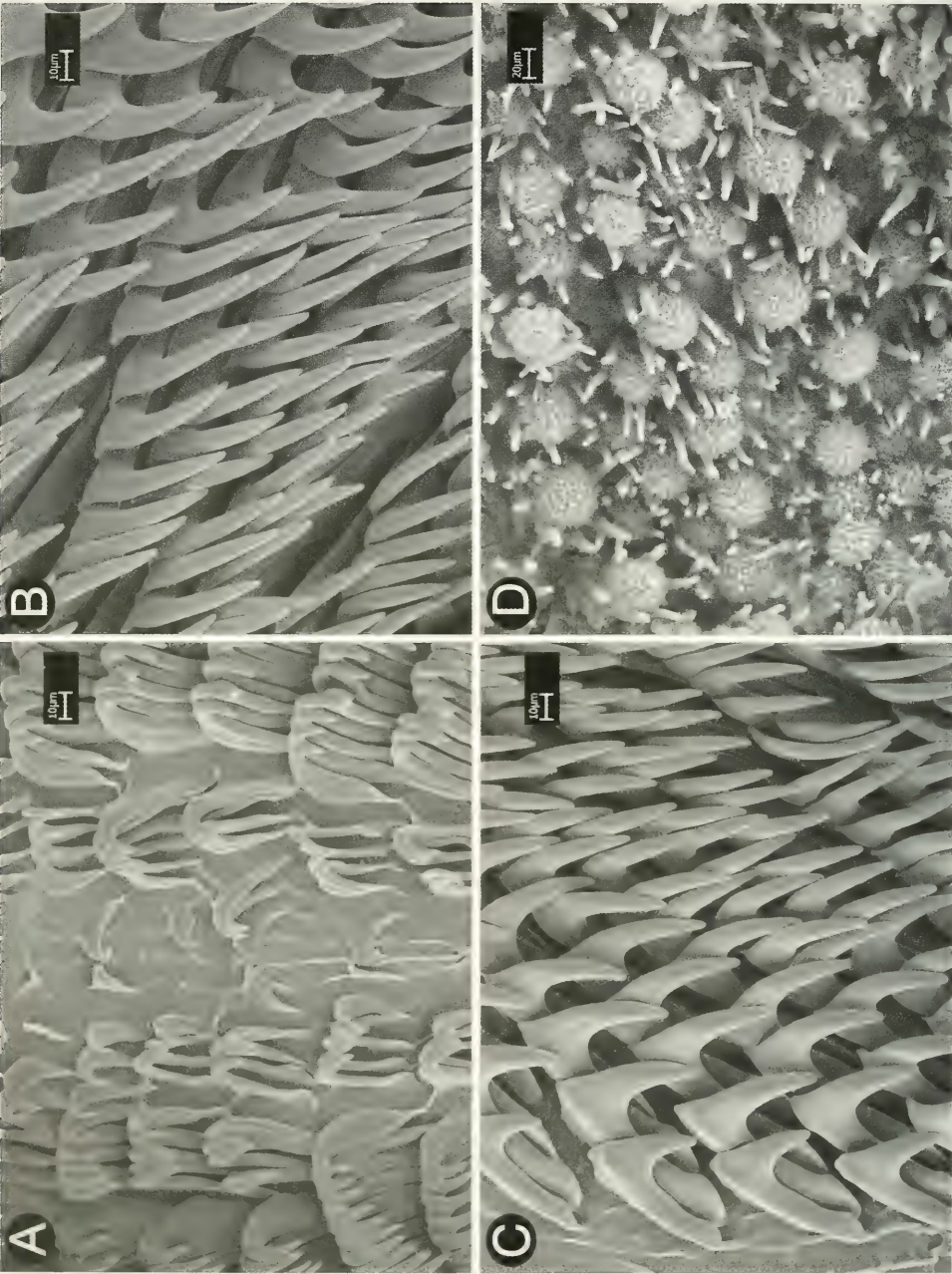


FIGURE 4. *Diatula greeleyi* (INB0001496508). A. Inner lateral teeth, scale bar= 10 μm; B. Lateral teeth, scale bar= 10μm. C. Outer lateral teeth, scale bar= 10μm. D. Caryophyllidia, scale bar= 20μm.

Puntarenas, Costa Rica, January 16, 2000, 3 specimens, 2–6 mm preserved length, 6 m depth, leg. M. Calderón (INB0001496530); Punta Uvita, Puntarenas, Costa Rica, January 15, 2000, 7 specimens, 5–9 mm preserved length, intertidal, leg. M. Calderón (INB0001496515); Playa Ventanas, Puntarenas, Costa Rica, January 17, 2000, 5 specimens, 5–6 mm preserved length, intertidal, leg. M. Calderón (INB0001496529); San Pedrillo, Osa Peninsula, January 27, 1998, 1 specimen, 11 mm preserved length, intertidal, leg. A. Berrocal (INB0001496507); San Pedrillo, Osa Peninsula, Costa Rica, January 20, 2000, 2 specimens, 2–10 mm preserved length, intertidal, leg. M. Calderón (INB0001496521); San Pedrillo, Osa Peninsula, Costa Rica, January 19, 2000, 2 specimens, 10–11 mm preserved length, intertidal, leg. A. Berrocal (INB0001496516).

GEOGRAPHIC RANGE

This species is found in Florida (Marcus and Marcus 1967), Brazil (Marcus 1955), South Carolina (Eyster 1980), Nayarit, Mexico (Ortea and Llera 1981), Punta Eugenia, Baja California, México (Bertsch et al. 2000) and the Pacific coast of Costa Rica.

EXTERNAL MORPHOLOGY

The body is oval to elongate (Fig. 1C). The dorsum is covered with long caryophyllidia, about 100 mm long (Fig. 4D). The body is pale yellow to orange. The dorsum is covered with a number of brown patches that may be darker in some specimens. These patches are more densely arranged near the mantle edge. On the mantle edge there are some large, opaque white patches. The rhinophoral sheaths are very inflated and pale cream white or white in color. The gill sheath is also pale or white and in some specimens it is edged by a thin brown line. The rhinophores are pale yellow, with the club brown and the apex opaque white or pale yellow. There are 13 lamellae present in the rhinophores. The gill is composed of 12 unipinnate branchial leaves. They are yellow to dark brown. In the living animal the branchial leaves are oriented inwards. Ventrally the anterior border of the foot is grooved and notched. The oral tentacles are short and conical (Fig. 5D).

ANATOMY

The labial cuticle is smooth. The radular formula is $37 \times (55.0.55)$ in a 10 mm preserved length specimen (INB0001496508). Rachidian teeth are absent (Fig. 4A). The lateral teeth are hamate, having a single cusp and lacking denticles (Fig. 4B). The teeth increase in size gradually towards the medial portion of the half-row. The outermost teeth are very small and elongate, also lacking denticles (Fig. 4C). The esophagus is long and connects directly to the stomach (Fig. 5A).

The ampulla is very long (Fig. 5B). It enters the female glands near their nidamental opening. The prostate is flattened and granular. It is divided into two different portions that are clearly distinguishable by their different texture and coloration. The deferent duct is long, and expands into the wide ejaculatory portion. The deferent duct opens into a common atrium with the vagina. There are no penial hooks. The vagina is long and wide. At its distal end, the vagina connects to the large and rounded bursa copulatrix. Another duct, which connects to the seminal receptacle and the uterine duct, leads from the bursa copulatrix. The bursa copulatrix is about ten times larger than the seminal receptacle (Fig. 5B–C).

REMARKS

MacFarland (1909) described *Peltodoris greeleyi* from Brazil. Later, Marcus (1955) and Marcus (1967) redescribed this species from the same locality. According to these authors, the main

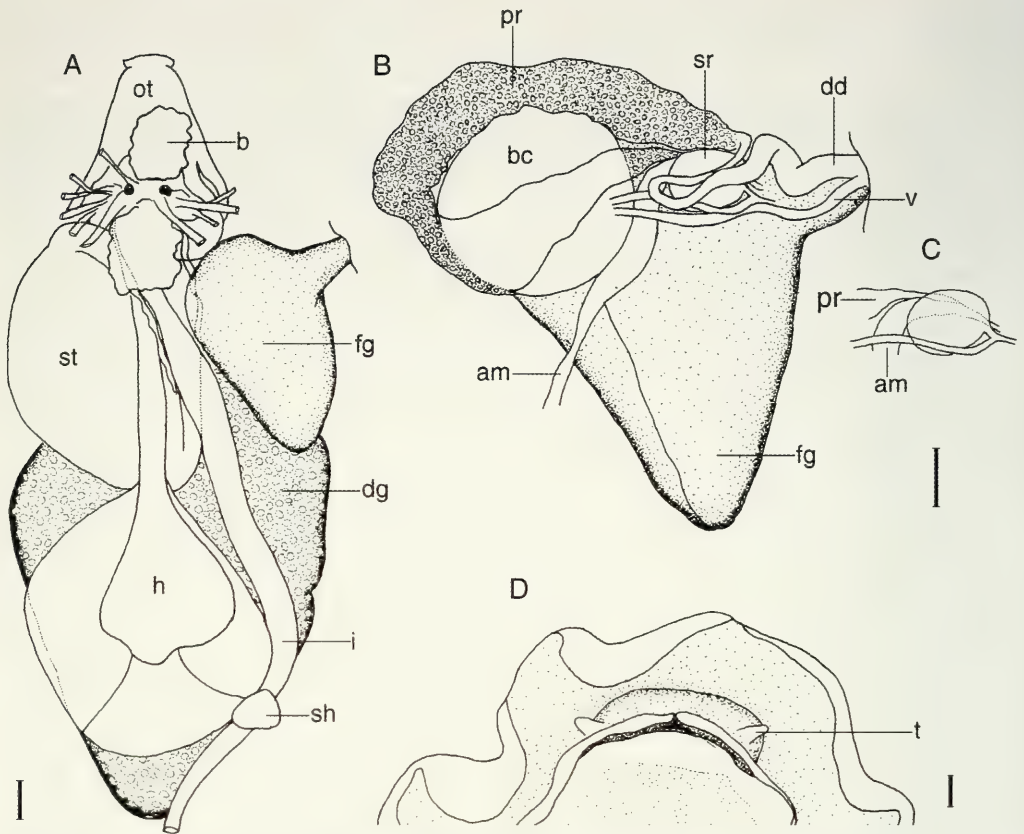


FIGURE 5. Anatomy of *Diaulula greeleyi* (INB0001496508). A. Dorsal view of the internal organs, scale bar= 1mm; B. Reproductive system, scale bar= 1 mm; C. Detail of the reproductive system, scale bar= 1 mm; D. Ventral view of the mouth area, scale bar= 1mm. Abbreviations: am=ampulla; b=blood gland; bc=bursa copulatrix; dd=deferent duct; dg=digestive gland; fg=female gland; h=heart; i=intestine; ot=oral tube; pr=prostate; sh=syrinx; sr=seminal receptacle; st=stomach; t=oral tentacle; v=vagina.

distinctive features of this species are the yellowish to orange color of the living animals with some small brown spots on the center and sides, the prominent branchial and rhinophoral sheaths, the smooth labial cuticle, the absence of rachidian teeth, the unipinnate gills, the outermost tooth smaller than the remaining teeth, the absence of denticles and the outermost, and midlateral teeth with cusps.

Ortea and Llera (1981) described the species *Peltodoris nayarita* from Nayarit, Mexico. *Peltodoris nayarita* is characterized by having a yellow mantle with small brown spots all over the dorsum and sometimes concentrated in the middle portion, high branchial and rhinophoral sheaths, smooth labial cuticle, unipinnate branchial leaves, outermost teeth smaller and outermost midlateral teeth with a cusp. Ortea and Llera (1981) placed this species in the genera *Peltodoris* and *Anisodoris* at the same time with no clear explanation. They also considered that *Peltodoris* and *Anisodoris* are synonyms.

By studying the type material of *Peltodoris greeleyi* and *Peltodoris nayarita*, we found that both species share the presence of a smaller outermost tooth with a single cusp and no denticles, hamate lateral teeth with no denticles and a single cusp, and outermost teeth smaller than the

remaining ones. There are several other features shared by the type specimens of these two taxa. The coloration of the living animals is orange to light brown with small brown spots covering the mantle, the gills are unipinnate, the labial cuticle is smooth and the rhinophores and branchial sheaths high (MacFarland 1909; Marcus 1955; Marcus and Marcus 1967; Ortea and Llera 1981).

In the reproductive system drawn by MacFarland (1909), Marcus and Marcus (1967) and our material from Costa Rica, the deferent duct has a loop and is longer than the slender vagina, the bursa copulatrix is larger than the seminal receptacle and both are rounded in shape. However, all of these features are difficult to observe in the incomplete drawing by Ortea and Llera (1981, fig 4).

When comparing all these features with the type material of *P. greeleyi*, *P. nayarita*, and the material studied from Costa Rica, we concluded that these two species are synonyms.

This species is transferred to the genus *Diaulula* due to a unique combination of features: the presence of caryophyllidia, the low rhinophoral and branchial sheaths, the penis and vagina unarmed, the labial cuticle smooth, and the radular teeth hamate and smooth (see Valdés and Gosliner 2001). *Diaulula greeleyi* is also different from *D. aurila* in radular morphology, external coloration, the presence of high rhinophoral and branchial sheaths and unipinnate branchial leaves.

***Diaulula aurila* (Marcus, 1976)**

(Figs 1D, 6A–D, 7A–D)

Discodoris aurila Marcus, 1976: 85–87; figs 108–111

MATERIAL EXAMINED

SYNTYPES of *Discodoris aurila*: Deale Beach (Ft. Kobbe Beach), Canal Zone, Panama, December 1962, 2 specimens 15–20 mm preserved length, leg. F. Bayer and R. Bayer (USNM 576268). Two microslides: F–814 (USNM 576268) and F–185 (USNM 576268).

ADDITIONAL MATERIAL EXAMINED

San Miguel Station, Cabo Blanco, Costa Rica, January 28, 1999, 3 specimens, 6–14 mm preserved length, intertidal, leg. F. Alvarado (INB0001482472); San Miguel Station, Cabo Blanco, Costa Rica, January 26, 1999, 1 specimen, 12 mm preserved length, intertidal, leg. F. Alvarado (INB0001496506). San Miguel Station, Cabo Blanco, Costa Rica, January 26, 1999, 1 specimen, 9 mm preserved length, intertidal, leg. F. Alvarado (CASIZ 159788); San Miguel Station, Cabo Blanco, Costa Rica, January 26, 1999, 1 specimen, 7 mm preserved length, intertidal, leg. F. Alvarado (INB0001496505); Playa Ventanas, Puntarenas, Costa Rica, January 17, 2000, 1 specimen, 12 mm preserved length, intertidal, leg. M. Calderón (LACM 2922); Ballena Island, Uvita, Puntarenas, Costa Rica, January 16, 2000, 13 specimens, 6–10 mm preserved length, 6 m depth, leg. M. Calderón (INB0001495896); Punta Uvita, Puntarenas, Costa Rica, January 15, 2000, 1 specimen, 8 mm preserved length, intertidal, leg. M. Calderón (INB0001496574); Playa Coralito, Peñón del Coral, Costa Rica, January 29, 1999, 1 specimen, 14 mm preserved length, intertidal, leg. F. Alvarado (INB0001496280); Punta Voladera, Golfo Dulce, Costa Rica, February 12, 1997, 2 specimens, 8 mm preserved length, 6 m depth, leg. M. Calderón (INB0001496510); Punta Voladera, Golfo Dulce, Costa Rica, February 11, 1997, 2 specimens, 7–9 mm preserved length, intertidal, leg. Manuel Lobo (INB0001487296); San Pedrillo, Osa Peninsula, Costa Rica, January 21, 2000, 1 specimen, 10 mm preserved length, intertidal, leg. M. Calderón (INB0001495947).

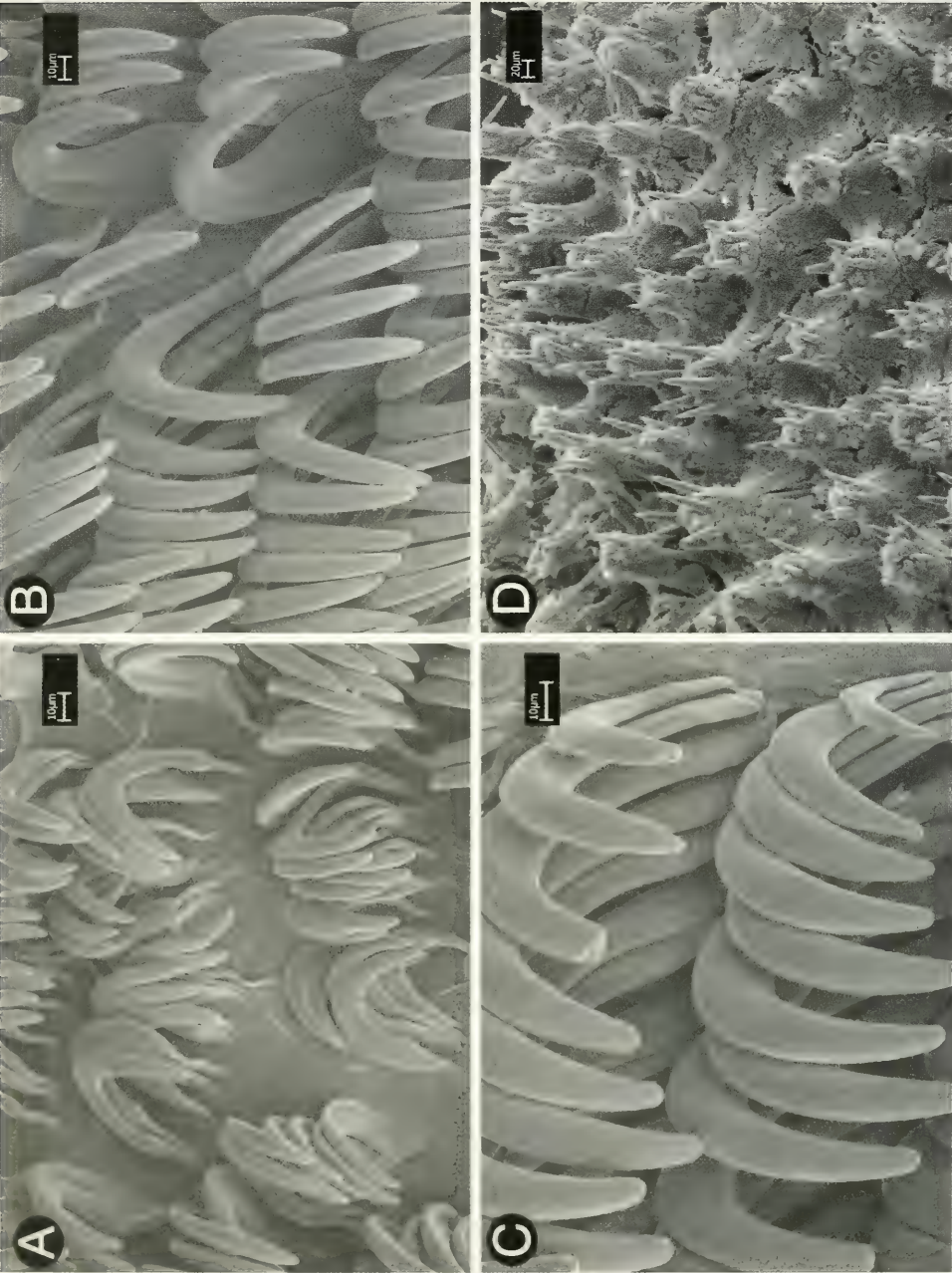


FIGURE 6. *Diadula aurita* (INB0001482472), SEM photographs. A. Outer lateral teeth, scale bar=20µm B. Inner lateral teeth, scale bar=10µm C. Caryophyllidia, scale bar=10µm D. Lateral teeth, scale bar=10µm.

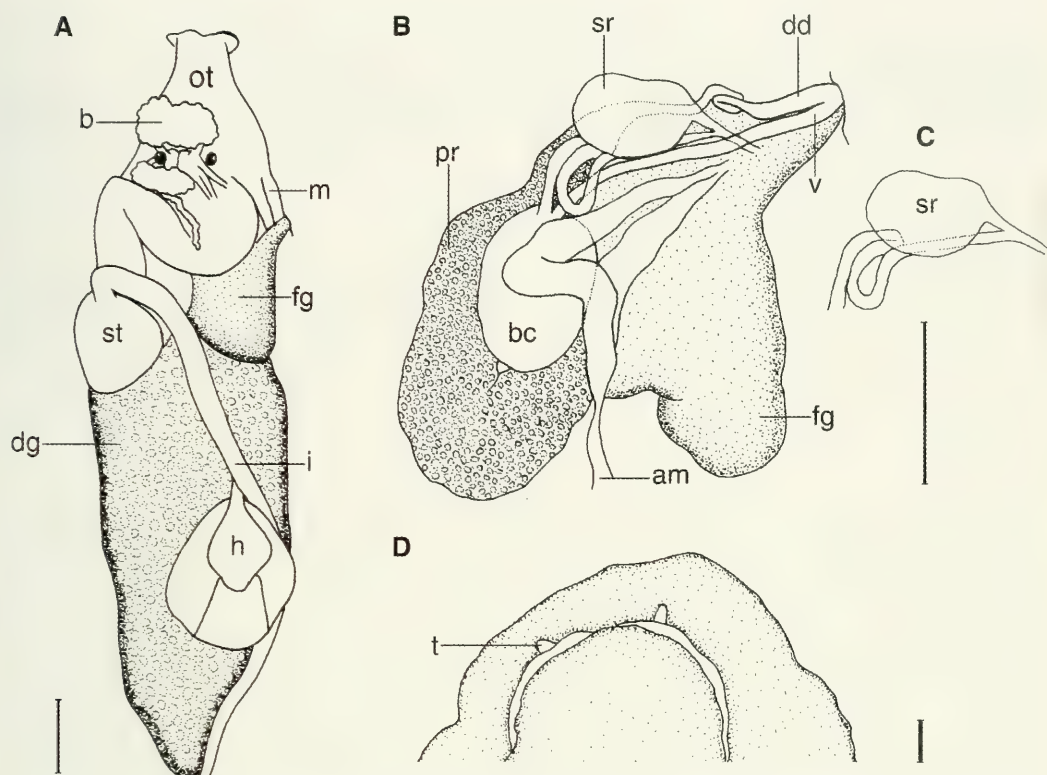


FIGURE 7. Anatomy of *Diaulula aurila* (INB0001482472). A. Dorsal view of the internal organs, scale bar= 1mm; B. Reproductive system, scale bar= 1mm; C. Detail of the reproductive system, scale bar= 1mm; D. Ventral view of the mouth area, scale bar= 1mm. Abbreviations: am=ampulla; b=blood gland; bc=bursa copulatrix; dd=deferent duct; dg=digestive gland; fg=female gland; h=heart; i=intestine; m=retractor muscle; ot=oral tube; pr=prostate; sh=syrinx; sr=seminal receptacle; st=stomach; t=oral tentacle; v=vagina.

GEOGRAPHIC RANGE

This species is known from the Pacific coast of Costa Rica (present study) and Panama (Marcus, 1976).

EXTERNAL MORPHOLOGY

The body is oval (Fig. 1D). The dorsum is covered with long caryophyllidia, about 190 μ m long (Fig. 6D). The body is pale gray, with a diffuse, thick, black line in the middle of the dorsum, running from the rhinophores to the gill. This line is composed of a number of small black dots. The viscera are visible as a pale brown patch in the center of the dorsum. There are some black dots and numerous white dots on the mantle margin. In some specimens the black dots may line up to form longitudinal, diffuse lines. The rhinophores have 17 lamellae. They are translucent white with the club dark yellow and the apex and rachis opaque white. The gill is composed of 6 tripinnate branchial leaves. They are gray to dirty yellow with some orange, apparently glandular spots. Ventrally the anterior border of the foot is grooved and notched. The oral tentacles are short and slender (Fig. 7D).

ANATOMY

The labial cuticle is smooth. The radular formula is $20 \times (39.0.30)$ in a 15 mm preserved length specimen (INB000148247). The radula has no rachidian teeth (Fig. 6A). The lateral teeth are hamate and smooth (Fig. 6B). The innermost teeth are also hamate and very elongated, lacking denticles. The outermost teeth are small, elongated and smooth. However, sometimes the tooth has up to 5 denticles (Fig. 6C). The esophagus is long and connects directly to the stomach (Fig. 7A).

The ampulla is very long and convoluted in the middle portion and divides into the short oviduct and prostate (Fig. 7B). It enters the female glands near the middle of the mass. The prostate is large, flattened and granular. It narrows into the short and coiled deferent duct, which expands again into the muscular and wide ejaculatory portion. The deferent duct opens into a common atrium with the vagina. The vagina is long and tubular. The penis is unarmed. The uterine duct is short and thin, and opens near the center of the female gland mass. The seminal receptacle is slightly oval, almost as large as the pyriform bursa copulatrix (Fig. 7C).

REMARKS

The anatomical examinations indicate that this species should be placed in the genus *Diaulula*, which is characterized by the presence of a dorsum covered with elongated caryophyllidia, low rhinophoral and branchial sheaths, a flattened prostate divided into two portions, penis and vagina unarmed, radular teeth hamate and smooth, and a labial cuticle smooth (see Valdés and Gosliner 2001). Marcus (1967) described *Discodoris aurila* as having jaw elements; however in the specimens studied here from Costa Rica and the microslide of the syntype (F-184) mounted by Marcus herself, the labial cuticle is smooth.

Other species of *Diaulula* from the eastern Pacific are *Diaulula punctuolata* (D'Orbigny 1837, *Diaulula sandiegensis* (Cooper 1863) and *Diaulula greeleyi* (MacFarland 1909). *Diaulula aurila* is different from *D. punctuolata* and *D. sandiegensis* in the external coloration. The general color of the body of *Diaulula aurila* is pale gray, with a line in the middle of the dorsum composed of a number of small black dots as well as black or white dots on the mantle margin. In *Diaulula punctuolata* the dorsum is white to yellowish and has two rows of small dots between the rhinophores and gill. These small dots can be light or dark in color (Schrödl 1996). In *Diaulula sandiegensis*, the general color of the living animals varies from white to pale brown. The dorsum has several dark brown or dark rings of various sizes often aligned in two longitudinal rows, one on either side of the body (Valdés and Gosliner 2001). According to Behrens and Valdés (2001) *Diaulula sandiegensis* sometimes has denticles on the two outermost lateral teeth, a feature that is not always present. As in *D. sandiegensis*, we have found some denticles on the outermost teeth in some specimens of *D. aurila*. *Diaulula aurila* is also different from *D. greeleyi* in radular morphology, external coloration, presence of low rhinophoral and branchial sheaths and tripinnate branchial leaves.

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available the holotype of *Peltodoris nayarita* and the syntypes of *Discodoris aurila* respectively. Benoit Dayrat made constructive comments to this manuscript.

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Systematics and Osteology of Leptoglaninae a New Subfamily of the African Catfish Family Amphiliidae, with Descriptions of Three New Genera and Six New Species

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Leptoglaninae (type species *Leptoglanis xenognathus* Boulenger, 1902) is proposed as a new subfamily of the African catfish family Amphiliidae. It is characterized by an encapsulated swim bladder with a transverse bony intercapsular bridge between the two lateral capsules as well as by distinctive coloration and behavior. In contrast to other amphiliids, all or most of which are rheophilic or even torrenticolous, typically living in rocky or stony habitats, leptoglanins are arenicolous (sand-dwelling). Several taxa have been observed buried in sand with just the eyes exposed or diving into sand. Four of the five genera and 14 of the 16 known species are endemic to the Congo basin. The Congolese genus *Leptoglanis* comprises a single species, *L. xenognathus*. It differs from all other amphiliids in its highly specialized mouth and jaws and soft digitiform pharyngeal processes and from all other leptoglanins except *Zaireichthys rotundiceps* in having the relatively primitive principal caudal fin ray count of 7+8.

The Congolese species formerly known as *Leptoglanis bouilloni*, although it superficially looks like a short-bodied relative of *L. xenognathus*, does not have an encapsulated swim bladder and is not a leptoglanin or even an amphiliid, but rather a bagrid or claroteid. The species previously known as *Leptoglanis camerunensis*, *L. mandevillei*, and *L. rotundiceps* are placed in the formerly monotypic leptoglanin genus *Zaireichthys* (type species *Z. zonatus* Roberts, 1967). *Zaireichthys* differ from all other leptoglanins and amphiliids in having dorsal and pectoral fins with stout spines and locking mechanisms, thus forming the classical “defensive tripod” of primitive and generalized catfishes. *Zaireichthys* is the only amphiliid with stout serrae on the pectoral fin spine. The leptoglanin *Tetracamphilius pectinatus* also has pectoral fin serrae, but they are much smaller and the pectoral spine does not have a locking mechanism. *Leptoglanis brevis* is placed as a junior synonym of *Z. rotundiceps*. The *Zaireichthys rotundiceps* species complex is characterized by having the pectoral girdle with a large humeral process more or less extensively covered with sharp conical denticulations. These arise indistinguishably from the bony surface of the humeral process and are not true teeth. The only other leptoglanin in which such denticulations have been observed is *Z. zonatus*, which has a few small ones on the humeral process of its pectoral girdle.

Tetracamphilius new genus, comprising the species formerly known as *Amphilius angustifrons* and *A. notatus* and two new species *T. pectinatus* and *T. clandestinus*, is distinguished from all other amphiliid genera by tiny fan-shaped jaw teeth with up to four cusps rather than jaw teeth conical or absent. The species of *Tetracamphilius* all have 6+7 principal caudal fin rays. The exceptionally elongate and otherwise distinctive leptoglanin formerly known as *Leptoglanis brieni* is designated type species

of a new genus, *Dolichamphilius*. A new species that might be its closest relative is placed tentatively in *Dolichamphilius*, *D. longiceps*. These two species also have 6+7 principal caudal fin rays. The new genus *Psammophiletria*, comprising two new species, *P. nasuta* and *P. delicata*, differs from all other leptoglanins in having the dorsal fin remote from the cranium and in the extreme reduction of its caudal fin rays, with fewer procurent rays than in any other leptoglanin and only 5+6 principal caudal fin rays, the lowest count known in Amphiliidae.

Leptoglanis xenognathus Boulenger, 1902, type species of *Leptoglanis* Boulenger, 1902, is a highly distinctive catfish found only in the Congo basin with specializations not found in other known taxa. *Leptoglanis* has had a long history as a "catch-all" genus. This began with the assignment of *Gephyroglanis rotundiceps* Hilgendorf, 1905 to *Leptoglanis* by Boulenger (1911). Several more highly distinctive species subsequently were described in *Leptoglanis* by Pellegrin (1926); and by Poll (1959, 1967). Most of these are amphiliids, but "*Leptoglanis*" *bouilloni* Poll (1959) belongs in Bagridae or Claroteidae.

Previous failure to recognize the heterogeneous nature of *Leptoglanis* (*sensu lato*) can be attributed to lack of osteological information. Osteological study was impeded until very recently by scarcity of material, and before that by inadequate methods of preparing small fish specimens for osteological study. This is now somewhat less of a problem, and it has been possible to study cleared and stained osteological preparations of almost all of the leptoglanin taxa. This study treats all taxa that are closely related to *Leptoglanis*. These are recognized herein as forming the subfamily Leptoglaninae of Amphiliidae. Included are *Zaireichthys zonatus*, the species formerly known as *Amphilius angustifrons*, and *Amphilius notatus*, and several previously undescribed species.

The leptoglanin genera *Leptoglanis* and *Zaireichthys* were described originally as Bagridae. A significant advance in their classification came when it was recognized that they are Amphiliidae (Bailey and Stewart 1984:9). These authors based their conclusion on examination of the type species of *Leptoglanis* and *Zaireichthys*. A similar conclusion, utilizing more osteology, was reached by Mo (1991:68–73) but was based on species that are not congeneric with *Leptoglanis* and *Zaireichthys*. For his concept of the genus *Leptoglanis* Mo examined "*Leptoglanis*" (now *Zaireichthys*) *rotundiceps*; for *Zaireichthys* he examined "*Zaireichthys rhodesiensis*," an unpublished taxon that is either a junior synonym or a very close relative of *Z. rotundiceps*. Not surprisingly, his observations indicated that the two taxa are sister species. Nevertheless, Mo looked at leptoglanin osteology in greater detail than previous authors and reported several distinctive characters, notably the posteriorly triradiate palatine bone characteristic of all Amphiliidae.

Many of African Bagridae have numerous large, fleshy fingerlike ("digitiform") processes in the pharynx and especially on the branchial arches; Asian Bagridae generally lack such structures (pers. obser.). I shared this information with Mo, who published it without acknowledgment as part of his evidence for non-monophyly of the Bagridae and for a sister-group relationship of the subfamilies Claroteinae and Auchenoglanidinae of the African family Claroteidae (Mo 1991:62). What I also pointed out to him, but what he failed to report, is that apparently identical structures are found in the amphiliid genus *Leptoglanis*. If these structures (which are generally distributed on the pharynx and not just on the gill arches as indicated by Mo) are homologous and occur only in the taxa in which they have been found thus far, they may be evidence (a synapomorphy) indicating that Amphiliidae are related to (presumably derived from) the African Bagridae or Claroteidae. This would lessen, although it would not eliminate, the possibility that Amphiliidae are most closely related to other Old World (i.e., Asian) catfish groups such as Sisoridae (see He and Meunier 1998; He et al., 1999), Akysidae, and Parakysidae, which share with Amphiliidae the character

complex of a bilaterally compartmented swim bladder enclosed in auditory bulla, or capsules, modified from parapophyses of vertebrae 4 and 5. Whether such a character complex is diagnostic of an ancient monophyletic group of catfishes found in Africa, Asia, and South America or has evolved independently at least three times is one of the major unresolved issues in siluroid higher classification. In Africa it occurs only in the family Amphiliidae (Chardon 1968; Mo 1991; He et al. 1999). Recognition of this character complex in *Leptoglanis* and *Zaireichthys* led to the transfer of these genera from Bagridae to Amphiliidae by Bailey and Stewart (1984:9).

A ventral bony bridge (here named "intercapsular bridge") linking the ossified swim bladder capsules was found in *Leptoglanis xenognathus*, *Zaireichthys zonatus*, *Z. rotundiceps*, and *Amphilius notatus* by Bailey and Stewart (1984:9) (Fig. 1). They did not find a similar bridge in other amphiliids, and predicted that the taxa with the bridge represented a monophyletic assemblage. This monophyletic grouping, as they envisioned it, corresponds to the Leptoglaninae as recognized herein. An intercapsular bridge is present in all of the leptoglanin species for which osteological study material has been available. However, a well-developed intercapsular bridge also is present in the doumein amphiliid *Andersonia leptura* (pers. obser.; He et al. 1999:133, fig. 7), so it is not a character unique to Leptoglaninae. The presence of the intercapsular bridge in *Andersonia* and leptoglanins has led to the hypothesis that Doumeinae is the sister-group of *Leptoglanis* and the leptoglanins (here Leptoglaninae) (*op cit.* 117,142). Their concept of *Leptoglanis* and leptoglanins is based upon study of a single species, *Leptoglanis camerunensis* (here *Zaireichthys camerunensis*).

Most catfish families probably have ribs with a single head and relatively simple articulation. In Leptoglaninae, however, the proximal end of each rib is "bicipital" or two-headed. The ribs articulate with a lateral process or an anteroventral process arising from the corresponding vertebral centrum. In addition, at least in *Leptoglanis xenognathus*, each rib is attached to an anterodorsal process of the corresponding vertebra by a ligament arising just below its bicipital head (Fig. 2).

Amphiliidae are bottom-dwelling catfishes ranging in size from 20 to 150 mm. Eleven genera and about 64 species (including those described herein) are known. The better-known species live in the parts of swift-flowing streams with rocky bottom including mountain streams and rapids of large lowland rivers. These belong to the subfamilies Amphiliinae (comprising the genera *Amphilius* and *Paramphilius*, with some 25 species) and Doumeinae (*Andersonia*, *Belonoglanis*, *Doumea*, *Phractura*, and *Trachyglanis*, with some 23 species). These two subfamilies (especially Amphiliinae) are very widely distributed in tropical Africa. The third subfamily, Leptoglaninae, with 5 genera and at least 16 species, occurs mainly in the Congo basin. Its species live mainly in rivers with extensive stretches of sandy bottom. Amphiliinae and Doumeinae frequently occur together, but are seldom (almost never) found together with Leptoglaninae. Synonymies and information on distribution of Amphiliidae are provided by Skelton and Teugels (1986). For an illustrated key to the genera see Poll and Gosse (1994:186–190).

Due to their small size, near restriction to the Congo basin, and tendency to inhabit large stretches of open sandy habitat with low fish species diversity, Leptoglaninae are among the least known fishes of the African ichthyofauna. When this study began, only two genera (*Leptoglanis* and *Zaireichthys*) and about 10 valid species had been described. The present account adds three new genera and six new species, and more taxa surely remain to be discovered. All of the leptoglanin genera are present in the Congo basin, as are 15 of the total of 16 species recognized here (Fig. 3). Fourteen of the species are known only from the Congo basin and presumably are endemic to it. The only known leptoglanin species not present in the Congo basin is *Zaireichthys camerunensis*, known only from the Niger basin..

Knowledge of the biology of Leptoglaninae is virtually non-existent. Their feeding and reproductive behavior have not been observed. *Zaireichthys rotundiceps* (as *Leptoglanis rotundiceps*) and *Zaireichthys* cf. *dorae* (as *Leptoglanis* cf. *dorae*) were reported as occurring over fine sand, "lying buried with only the eyes protruding" by Skelton (1993:218, 220). The actual sand-diving behavior has not been previously recorded. At Banda (on the Ubangui River upstream from Bangui) I placed several leptoglanins about one inch long in a small bowl with sand on the bottom. When undisturbed the fish rested quietly on top of the sand. If mildly disturbed, they darted about on the sand with incredible rapidity. When badly disturbed, they instantly disappeared below the sand and stayed there for several minutes. While buried in the sand their eyes did not project. Although the species thus observed were not identified in the field at Banda, they were at least two and possibly three species, probably *Zaireichthys mandevillei*, *Tetracamphilus angustifrons* or *T. clandestinus*, and perhaps *Psammophiletria nasuta*. On this and other occasions I noted the extraordinarily copious mucus secretion exuding from the pectoral gland. When handling live specimens at Banda, two of the fish slipped out of my fingers and were suspended by a long transparent strand of mucus 10–12 inches long. The mucus strand was nearly equal in thickness to the body diameter of the fish, and its origin from just above the pectoral fin (i.e., from the axillary pore of the pectoral gland) was observed quite clearly. *Zaireichthys heterurus* was observed diving into the sand, apparently as an escape reaction, in the rivière Lulindi. I have observed in several species that the eyes of live species have pupils with slit-like horizontal openings, at least in fish caught in bright daylight. This is perhaps an adaptation related to their sand-diving behavior. Upon preservation the slit-like shape of the pupils fairly rapidly disappears and they appear to be round. From superficial observation of gut contents of cleared and stained specimens, leptoglanins appear to be mainly carnivores, preying on very small arthropods (insects and crustaceans).

This paper takes into consideration literature on *Leptoglanis* and *Zaireichthys* recorded in Eschmeyer's "On Line Fish Species Catalogue" up to 9 September 2002.

MATERIALS AND METHODS

MATERIAL EXAMINED.— Specimens used in this study are deposited in the following institutions: AMNH, American Museum of Natural History, New York; BMNH, The Natural History Museum, London; CAS, California Academy of Sciences, San Francisco; MNHN, Muséum National d'Histoire Naturelle, Paris; MRAC, Musée Royale pour l'Afrique Centrale, Tervuren; and UMMZ, University of Michigan Museum of Zoology.

Specimen lengths given throughout this paper are standard length, SL (from tip of snout to end of hypural plate). Specimens for osteological study were macerated with KOH and stained with alizarin, or macerated with trypsin and stained with alcian blue and alizarin. Radiographs were prepared in dorsal as well as lateral view.

LOCALITIES.— Locality data presented in this paper represents nearly all known samples of every species of Leptoglaninae except for the species or species complex *Zaireichthys rotundiceps*. This is the only species with an extensive range outside as well as inside the Congo basin, and it is by far the most frequently collected leptoglanin. It is likely that *Z. rotundiceps* represents several closely related species (pers. obser.; Skelton 1993; Seegers 1996). In presenting the localities, the type locality or localities of the species is given first, generally followed by other localities approximately grouped from N to S and from W to E. The locality dated are presented in the language and wording of the original collector(s). My own original locality records for specimens collected in the Congo basin are a mixture of English and French. Localities of leptoglanin specimens examined from the Congo basin are indicated in Fig. 3 (in some cases two or more localities very close

together for the same species are indicated by a single symbol).

SYNONYMY.—Synonymies include primary synonymy (original descriptions and name proposals) and secondary synonymy (name changes). Additional references may be included in a synonymy if they have direct bearing on systematics and identification has been confirmed by examination of voucher specimens or can be determined from the reference itself. In secondary synonymies and misidentifications the name is followed by a comma.

COUNTS.—Counts of gill rakers and vertebrae, previously unused by catfish workers, have proved to be extremely useful in distinguishing species in group after group of catfishes: *Akysis* (Roberts 1989a, table 9); *Bagarius* (Roberts 1983); *Chiloglanis* (Roberts 1989b); *Gagata* (Roberts and Ferraris 1998); *Kryptopterus* (Roberts 1989a, table 10); *Leiocassis* (Roberts 1989a, table 5); Pangasiidae (Roberts and Vidhayanon 1991); *Malapterurus* (Roberts, 2000) *Mystus* (Roberts 1989a, tables 7–8; Roberts 1992; Roberts 1994); *Nangra* (Roberts and Ferraris 1998); *Ompok* (Roberts, 1989a, table 11); and *Silurichthys* (Roberts 1989a, table 12).

GILL RAKERS.—Counts of gill rakers are extremely useful in distinguishing catfish species. In most catfishes, as is usual in teleosts, the number of gill rakers becomes fixed at a fairly early stage, but in some groups (e.g., *Clarias*, *Mystus*) there are species in which the number of gill rakers increases throughout life. In Leptoglaninae, however, gill raker counts do not seem to be very useful. Due to the small size of the specimens and the small size of the gill rakers, it is difficult or impossible to obtain counts from whole specimens. Counts can be obtained only after the gill arches have been removed from cleared and stained specimens. But the main reason gill raker counts are not useful in Leptoglaninae is because the rakers are few in number as well as very small.

VERTEBRAE.—As in other catfishes, vertebral counts are useful for distinguishing species and recognizing evolutionary trends in Leptoglaninae. It is informative to give counts of abdominal and postabdominal (or “caudal”) as well as total vertebrae. Counts given in this paper were all obtained from cleared and stained specimens. They include four anteriormost vertebrae incorporated into the Weberian apparatus. The hypural fan is counted as one vertebra. In amphiliids as in most catfishes the first rib-bearing vertebra is almost invariably vertebra 6. Only one specimen of Leptoglaninae has been noted in which vertebra 5 had ribs (the holotype of *Dolichamphilius longiceps*), and they were much smaller than the ribs on vertebra 6.

In practice, whether counting vertebrae from cleared and stained specimens or from radiographs, the count begins from the first vertebra bearing ribs, i.e. vertebra 6. Abdominal and postabdominal vertebrae are distinguished by the relationship of their hemal spines to the anal fin pterygiophores. Abdominal vertebrae are all those with hemal spines lying anterior to the anal fin pterygiophore that extends furthest anteriorly. If a vertebra has its hemal spine with the tip exactly meeting the anterior tip of the first anal fin pterygiophore, it is included in the count of abdominal vertebrae. In practice the abdominal and postabdominal vertebrae are readily distinguished in amphiliids by this method, whether in cleared and stained specimens or in radiographs. Vertebrae in the caudal peduncle or peduncular vertebrae are those lying posterior to a vertical line through the posteriormost anal fin pterygiophore. The terms used here and in other papers by me, abdominal and postabdominal, are anatomically correct and easily understood. The definitions are such that they apply to all catfish groups and to nearly all groups of teleosts. One major advantage of these simple definitions is that they can be readily used to obtain vertebral counts from radiographs. Another is that they can be used to obtain counts from fossils of most teleosts, including catfishes (Roberts and Jumnonghai 2000). Total vertebral counts of incomplete fossil fish specimens, although often reported, are almost worthless. When part of a fossil is missing, exact counts often can be obtained for either the abdominal or postabdominal vertebrae.

Counts of abdominal and postabdominal vertebrae are particularly useful in distinguishing cat-

fish species. In many instances related catfish species have the same total number of vertebrae composed of quite different numbers of abdominal and postabdominal vertebrae.

FIN RAYS.— All of the rayed fins of amphiliids provide valuable meristic data for systematic study except the pelvic fins, which usually have 6 rays on both sides in all species of Amphiliidae (I have observed a few specimens with 7 rays on one side or the other, and one with only 5 rays on one side). In Amphiliidae, and especially Leptoglaninae, the most useful fin ray counts are those of the caudal fin. None of the amphiliids exhibit the most primitive count of principal caudal fin rays known in catfishes, 9+9, reported only in the primitive Neotropical catfish family Diplomystidae. But the family includes species with nearly all of the principal caudal fin ray counts otherwise known in catfishes (see Lundberg and Baskin, 1969), from 8+9 to 5+6. Leptoglaninae have counts ranging from 7+8 to 5+6. In several taxa the upper principal rays are more numerous than the lower; the new species *Zaireichthys heterurus* has 7+5. Although caudal fin ray counts differ considerably within the family Amphiliidae, and also within some leptoglanin genera (cf. *Zaireichthys*), they usually are constant within a species and in several instances within a genus. The leptoglanin genus *Tetracamphilus* has five species, all with 6+7.

In the dorsal and anal fins, as in most teleosts, sometimes the last ray only and sometimes the last two rays articulate with the posteriormost pterygiophore. The latter condition is usually (but incorrectly) described as “last ray divided to base.” Depending upon the author the last ray divided to base may be included or excluded from the total count fin rays. The last ray, when separately notated, is referred to as “ $\frac{1}{2}$ ” (also incorrect, because it is in itself a complete ray). Here the convention is followed of indicating the additional last ray, when it is present, by “ $\frac{1}{2}$ ”.

Principal caudal fin rays may be defined as all of the branched rays articulating with the upper and lower halves of the hypural fan, plus one upper and one lower unbranched ray. Principal rays of the upper and lower caudal fin lobes are readily distinguished in Amphiliidae, since they articulate with either the upper or the lower half of the hypural fan and there is invariably a distinct gap between them. All of the rays anterior to the uppermost and lowermost principal caudal rays are the procurent caudal fin rays. A caudal fin ray count given as 10–12,6/7,11–13 indicates 6 upper and 7 lower principal rays, and 10–12 upper and 11–13 lower procurent rays.

SCOPE.— This work represents a thorough revision of the subfamily Leptoglaninae to the species level with the exception of the species complex *Zaireichthys rotundiceps*. The latter group is found in eastern and southern Africa including Angola and also in the eastern part of the Congo basin (Seegers, 1989; Skelton, 1993; Seegers, 1996; some new locality records for eastern part of Congo basin herein). BMNH and MRAC have many samples that I have examined only superficially, mainly to verify that they have an elongate denticulated humeral process. Several institutions in eastern and southern Africa have samples that I have not examined. The only other leptoglanin with an extra-Congolese distribution is *Zaireichthys camerunensis* in the Niger basin in West Africa. Its distribution is thus widely disjunct from the rest of the known Leptoglaninae. Leptoglanins are unknown from the Ogooué and other West African coastal basins.

My original intention was to publish a more extensively illustrated osteological account of the leptoglanin taxa together with the systematic revision. Due to difficulties in completing observations on some of the taxa and other commitments the osteological work has been curtailed. Enough has been done, however, to provide evidence for monotypy of the Leptoglaninae, reassign “*Leptoglanis*” *bouilloni* to Bagridae or Claroteidae, and contribute to diagnoses of leptoglanin genera and species.

ORDER OF TAXONOMIC PRESENTATION.— The taxa are presented in the following order: *Leptoglanis*, type genus and earliest described genus of Leptoglaninae is given first, followed by *Zaireichthys*, the only other previously described leptoglanin genus. After *Zaireichthys* the three

new genera *Dolichamphilius*, *Psammphiletria*, and *Tetracamphilius* are given in alphabetical order. Within each genus the generic type species is treated first, followed by the other species (including new species) in alphabetical order.

SUBFAMILY NAMES.— In this as in my other papers, the subfamily termination is given as “-in” (rather than “-ine preferred by some authors), i.e. “leptoglanin,” rather than “leptoglanine”. This might not be classically correct Latin, but since “-id” is now universally used instead of the more classically correct “-ide” for families, it is consistent to use -in for subfamilies.

ILLUSTRATIONS.— For ease of use, the figures are grouped together in a separate section following the bibliography.

SYSTEMATIC ACCOUNT

LEPTOGLANINAE Roberts, new subfamily

Type species: *Leptoglanis xenognathus* Boulenger, 1911

DIAGNOSIS.— Amphiliid catfishes with the left and right osseous swim bladder capsules connected ventrally by a transverse intercapsular bony bridge. Cranium narrow anteriorly. Anterior fontanelle either small or absent; posterior cranial fontanelle absent. Branchiostegal rays 3–8. Gill rakers poorly developed, a maximum of 10 rakers on leading edge of lower element of first gill arch. Upper elements of gill arch without gill rakers (present in Amphiliinae). Outermost pectoral and pelvic fin rays without elaborate lepidotrichia and unculiferous pads (both highly developed in all Amphiliinae and most Doumeinae). Pectoral fin with only one rod- or plate-like ossified radial element (most other amphiliids and other catfishes with two). Adipose fin invariably elongate. Ribs relatively few, from 3 to 6 pairs (ribs also few in Doumeinae, more numerous in Amphiliinae). Caudal fin, variable in form, from deeply forked to truncate. Principal caudal fin rays 7+8, 7+7, 6+7, 7+5, 6+5, or 5+6 (not 8+9). Principal caudal fin ray counts of Leptoglaninae and other Amphiliidae are presented in Table 1.

COMMENTS.— Leptoglaninae comprises arenicolous or sand-dwelling amphiliids occurring mainly in the Congo basin. They are all relatively small species. *Leptoglanis xenognathus*, the

TABLE 1. Principal caudal fin ray counts in Leptoglaninae and other amphiliids (data from Lundberg and Baskin 1969; Skelton 1986, 1989, 1993; and pers. obser.)

n/n+1:	
8+9=17	<i>Amphilius baudoni</i> , <i>A. cryptobullatus</i> , <i>A. kivuensis</i> , <i>A. uranoscopus</i> , <i>A. zairensis</i> , <i>Doumea alua</i> , <i>Paramphilius teugelsi</i> , <i>Phractura</i> sp.
7+8=15	<i>Amphilius longirostris</i> , <i>A. opisthophthalmus</i> , <i>Belonoglanis</i> sp, <i>Doumea thysi</i> , <i>Leptoglanis xenognathus</i> , <i>Paramphilius trichomycteroides</i> , <i>Zaireichthys rotundiceps</i>
6+7=13	<i>Amphilius atesuensis</i> , <i>A. brevis</i> , <i>A. lentiginosus</i> , <i>A. maesii</i> , <i>A. pictus</i> , <i>Dolichamphilius brienii</i> , <i>D. longiceps</i> , <i>Paramphilius firestonei</i> , <i>Tetracamphilius angustifrons</i> , <i>T. notatus</i> , <i>T. pectinatus</i> , <i>Zaireichthys zonatus</i>
5+6=11	<i>Psammphiletria delicata</i> , <i>P. nasuta</i>
n/n:	
7+7=14	<i>Andersonia leptura</i> , <i>Zaireichthys camerunensis</i>
n/n?1:	
6+5=11	<i>Zaireichthys mandevillei</i>
n/n?2:	
7+5=12	<i>Zaireichthys heterurus</i>

largest, attains only slightly over 60 mm in standard length. The smallest species, *Psammphyletria nasuta*, *P. delicata*, and *Tetracamphilius clandestinus*, are only 20 mm or a bit longer. The largest *Zaireichthys* are only 40 mm. At least some species dive completely into the sand (behavior observed for several species collected by me in the Ubangui and elsewhere), an activity unknown in other amphiliids. All or many of them have a large humeral or axial pectoral gland producing mucus. Amphiliinae and the “naked” (plateless) doumein genus *Doumea*, on the other hand, are known for their ability to inhabit torrential streams and to cling to rock substrates by means of their paired fins. The armored (plate-bearing) genera of Doumeinae cling to submerged grassy vegetation in swift current. Such clinging is facilitated by thickened epidermal pads on the ventral surface of the paired fins. When the pads are observed with scanning electron microscopy they are found to be composed of thousands of unculi, or unicellular keratinous hooklets (Roberts 1982). In Amphiliinae and in most Doumeinae (*Andersonia* an exception), these pads are supported by greatly enlarged outer pectoral and pelvic fin rays with numerous expanded lepidotrichia. The pads are either absent or very feebly developed in Leptoglaninae, in which the lepidotrichia of the outer pectoral and pelvic fin rays are simple and relatively few. Unculiferous pads were not observed in specimens of *Tetracamphilius pectinatus*, *T. clandestinus* and *Psammphyletria nasuta* examined with SEM.

With the exception of some of the species of *Zaireichthys*, nearly all of the Leptoglaninae have very narrow heads. The crania of all Leptoglaninae (including *Zaireichthys*) are characterized by narrow frontal bones (or frontal bones narrowed at least anteriorly) and no anterior or posterior fontanels. Most Amphiliinae and Doumeinae have anterior and posterior fontanels; *Andersonia* has the anterior fontanel only. Leptoglaninae have milky white, opaque or translucent (but not glasslike or transparent) bodies with delicately banded or spotted color patterns; some species have very little coloration. As is typical of small sand-dwelling catfishes in South America and Asia, the body sometimes has a faint yellowish tinge and the spotting or banding tend to be yellowish, brownish, or even orangish. Amphiliinae and Doumeinae have darkly opaque bodies with variously mottled cryptic color patterns typical of catfishes inhabiting rocky streams. As in many other sand-dwelling catfishes, leptoglanins are capable of modifying the openings of their pupils, reducing them to small horizontal slits in bright light. Similar pupillary modification has not been observed in Amphiliinae or Doumeinae.

Structure of the dorsal and pectoral fins and their supporting elements differ so much among leptoglanin genera that it might easily be supposed they belong in different subfamilies or in different families. *Zaireichthys* was described as a genus of Bagridae (Roberts 1967a) because it has a stout dorsal fin spine with a locking mechanism and a strong, serrated pectoral fin spine. But *Zaireichthys* is very similar osteologically to other genera of leptoglanins and especially to *Tetracamphilius*, one species of which has a weakly serrate pectoral fin spine but no pectoral locking mechanism (*T. pectinatus*).

KEY TO GENERA OF THE SUBFAMILY LEPTOGLANINAE

- 1 Dorsal and pectoral fins without locking mechanisms; dorsal fin with single elongate flexible spine; pectoral fin spine flexible, without serrae or with small serrae in one species 2
- Dorsal and pectoral fins with locking mechanisms; dorsal fin with two stout spines, anterior one small; pectoral fin spine stout, with large serrae *Zaireichthys*
- 2 Jaw teeth conical 3
- Jaw teeth multicuspid *Tetracamphilius*

- 3 Upper jaw without fleshy lobes; entire premaxillary with teeth; lower jaw with teeth 4
Upper jaw with fleshy lobes or fimbriae; anterior portion of premaxillary and lower jaw
without teeth *Leptoglanis*
- 4 Insertion of dorsal fin near head; upper caudal fin lobe with 6 principal rays; snout without
rhinal lobe *Dolichamphilius*
Insertion of dorsal fin nearer mid-body, over vertebra 11–13; upper caudal fin lobe with
5 principal rays; snout prolonged by a discrete rhinal lobe *Psammophiletria*

Genus *Leptoglanis* Boulenger 1902

Leptoglanis Boulenger, 1902:42 (type species *Leptoglanis xenognathus* Boulenger, 1902, by monotypy).

DIAGNOSIS.— *Leptoglanis*, here regarded as a monotypic genus, is in several respects the most highly modified member of the Leptoglaninae. It has the following specialized characters unique within Amphiliidae: (1) anterior margin of mouth with a single large medial fleshy lobe or fimbria and several lateral fleshy lobes or fimbriae of variable size (Fig. 4b); (2) premaxillary with toothless anterior portion, posterior portion with slender conical teeth (Figs. 4–6); (3) lower jaw toothless and exceptionally elongate (Figs. 4–6); (4) coronomeckelian bone exceptionally large and well defined, immovably articulated to Meckel’s cartilage and lower jaw, and with a distinct posterior process for ligamentous attachment to basicranium (Fig. 7b); (5) hyomandibular and quadrate joined by a complex joint consisting of a cartilaginous ball partially enclosed by bony sockets formed in the hyomandibular and quadrate (Fig. 7a); (6) an exceptionally short braincase (Figs. 4–6); (7) pharynx and gill arches with numerous soft fleshy fingerlike or digitiform structures; and (8) pectoral and pelvic fin rays excessively branched (Fig. 9a). Principal caudal fin rays 7+8 (the only other Leptoglaninae with 7+8 principal caudal fin rays is *Zaireichthys rotundiceps*). Vertebrae 20–23+17–19=38–41.

COMMENTS.— The oral fimbriae and digitiform pharyngeal structures of *Leptoglanis*, possibly homologous to each other, may be adaptations to feeding on organisms living in the sand. Comparable structures have not been found in any other species of Leptoglaninae or Amphiliidae. Structures comparable to the pharyngeal digitiform structures of *Leptoglanis* occur in many species of the African bagrid catfish subfamilies Claroteinae and Auchenoglanidinae. Structures comparable to the oral fimbriae have not been found in any other African catfish. In other amphiliids virtually the entire oral surface of the premaxilla bears teeth. No other amphiliids are known with a toothless lower jaw. The excessive branching of the pectoral and pelvic fin rays results in terminal branches that are exceptionally long and fine (Fig. 9a), and quite unlike those present in other leptoglanins (Figs. 9b–f). Thus, the paired fins of *Leptoglanis* are exceptionally flexible. The membranes connecting the fin rays of the paired fins are very thin. There is no sign of the large unculiferous pads present on the ventral surface of the pectoral and pelvic fin rays in species of *Amphilius*. *Leptoglanis xenognathus*, *Zaireichthys camerunensis*, and *Z. doriae* are the only leptoglanins with abdominal vertebrae notably more numerous than postabdominal vertebrae. *Zaireichthys camerunensis* and *Z. doriae* usually have fewer total vertebrae than *Leptoglanis*, only 34–39. In other leptoglanins except *Dolichamphilius brienii* the ratio of abdominal to caudal vertebrae is more nearly 1:1. In *D. brienii* (formerly placed in *Leptoglanis*) number of total vertebrae is slightly more (43–44) than in *Leptoglanis*, and caudal vertebrae considerably outnumber abdominal vertebrae. Vertebral counts of Leptoglaninae are presented in Table 2.

TABLE 2. Leptoglaninae vertebral counts.

	Abdominal								Postabdominal								Total													
	16	17	18	19	20	21	22	23	16	17	18	19	20	21	22	23	24	25	33	34	35	36	37	38	39	40	41	42	43	44
<i>Leptoglanis xenognathus</i>																														
Ubangui (holotype)							1				1																	1		
Stanley Pool					4	11	3				7	10	1												7	11				
Lualaba, Wagenias						1						1																1		
Lualaba, Panga							1					1																1		
<i>Zaireichthys zonatus</i>																														
Kinshasa (paratypes)	1										1										1									
<i>Zaireichthys camerunensis</i>																														
Benoué (syntypes)				1	2	3					2	4									1	4	1							
Guinea, Upper Niger					5	2					2	4	1											1	5	1				
<i>Zaireichthys doriae</i>																														
Luachimo (holotype)						?					?														1					
<i>Zaireichthys flavomaculatus</i>																														
Kamaiemby (holotype)						?					1																?			
<i>Zaireichthys heterurus</i>																														
Lulindi	1	3									4										1	3								
Avokoko (types)		2									2											2								
<i>Zaireichthys mandevillei</i>																														
Stanley Pool (holotype)	?											?										1								
Ubangui	2	5									2	3	2								3	3	1							
<i>Zaireichthys rotundiceps</i>																														
Bubu (syntypes)			2	2							1	1	2									1	1	1	1					
Luwoyeye				1							1												1							
<i>Dolicamphilius brieni</i>																														
Stanley Pool (types)					2														1	1								1	1	
<i>Dolicamphilius longiceps</i>																														
Lualaba (holotype)						1						1															1			
<i>Psammphyletria nasuta</i>																														
Ubangui (types)				3							1	2										1	2							
<i>Psammphyletria delicatus</i>																														
Stanley Pool (paratype)	1										1										1									
<i>Tetracamphilius pectinatus</i>																														
Lulua (types)	2	5	3								3	6	1								1		9							
Ubangui (types)					1	1					1	1														2				
<i>Tetracamphilius angustifrons</i>																														
Ubangui (syntypes)			2								1		1									1			1					
Ubangui				2	4						5	1										1		5						
Lualaba, Wagenias	1											1												1						
<i>Tetracamphilius cladestinus</i>																														
Ubangui (types)		5									5											5								
<i>Tetracamphilius notatus</i>																														
Faradje (holotype)			1								1											1								
Chinko			1									1													1					

***Leptoglanis xenognathus* Boulenger, 1902**

(Figs. 1–2, 4–9)

Leptoglanis xenognathus Boulenger, 1902:42, pl. 14, fig. 1 (type locality “Ubangi à Banzyville [=Mobaye]).**DIAGNOSIS.**— Same as diagnosis of monotypic genus *Leptoglanis*.**COMMENTS.**— Specimens from Ubangui and from Stanley Pool usually have 4–9 large dermal lobes or fimbriae (together with several very small fimbriae) on anterior margin of the mouth. The only two specimens known from the upper Congo (57.4 and 47.7 mm) have only 3 large lobes. In other features examined, these specimens are similar to *L. xenognathus* from Ubangui and Stanley Pool, but their status should be reconsidered when more material becomes available. It should be noted that these very soft structures are highly susceptible to drying, after which they can be difficult to detect.**COLORATION.**— The freshly collected 35.8-mm specimen from Ubangui at Bawili had the body milk-white (opaque, not translucent) in life. The most noticeable color features were on the fins: two broad oblique bands on the dorsal fin, two broad vertical bands on the caudal fin, and a single broad band in the middle of the pectoral fin, all composed of brownish melanophores lying superficially on the fin rays (not in the interradial membranes). Anal fin with a few fine melanophores on some rays, otherwise colorless. Adipose and pelvic fins without notable color features, almost devoid of melanophores. Dorsal part of head especially snout, basal portion of barbels, and cheeks with fine, faint melanophores; occiput (over hindbrain) with large, brownish melanophores; distal portion of barbels and ventral surface of head without melanophores. Body with fine, faint melanophores concentrated just above and below lateral line canal and in dorsal portions of myoseptal troughs. Three faint oval spots composed of fine melanophores at beginning, middle and end of adipose fin base. Two faint mid-dorsal oval spots between dorsal and adipose fins. Ventrolateral and ventral surfaces of body almost entirely without melanophores. A thin, sharply demarcated black line in midventral myopsepta from vent about half-way to anal fin origin.**GILL RAKERS AND DIGITIFORM PHARYNGEAL STRUCTURES.**— Gill rakers numerous for a leptoglanin, with soft fleshy covering and slender axial core staining faintly blue in alcian-alizarin preparations. The 53.4-mm cleared and stained specimen from Stanley Pool has the following counts of gill rakers on leading/trailing edge of gill arches 1–5: (1) 8/0; (2) 10/0; (3) 0/8; (4) 5/3; and (5) 0. The leading edge of arch 4 lacks rakers with an axial core, but its distal portion bears a close-set series of 4 fleshy digitiform structures (Fig. 8b).

Gill rakers and especially digitiform structures are much more numerous in the 62.2-mm specimen (not cleared and stained) from Stanley Pool. It has the following counts of gill rakers of the leading/trailing edge of gill arches 1–5: (1) 12/4; (2) 12/5; (3) 4/8; (4) 2+8/4; and (5) 1. Digitiform structures, mostly much larger than the gill rakers, are as follows: roof of pharynx near posterior margin of hyoid arch with 7 irregularly scattered or clustered; gill arch 1 with 3 on trailing edge of lower part of arch and a row of 6 on upper part of arch and continuing onto roof of mouth; gill arch 2 with 2 on trailing edge of lower limb and 10 irregularly scattered on upper limb and extending onto roof of mouth; gill arch 3 with 5 on dorsomedian part of lower limb; arch 4 and arch 5 without digitiform structures.

VERTEBRAL COUNTS (Table 2).— Specimens from the lower Congo mainstream (Malebo Pool or Stanley Pool) have consistently fewer vertebrae (38–39) than those from the upper Congo at Panga (40) and from the Ubangui River (41). This might indicate that they represent different species. The problem should be investigated when more material becomes available.

MATERIAL EXAMINED

REPUBLIQUE CENTRAFRICAINE: CAS 92614, 35.8 mm, R. Ubangui near Bawili, 68–69 km upriver from Bangui, 5 March 1988, T.R. Roberts; REPUBLIQUE DU CONGO (KINSHASA): MRAC 118463–118488, 22:29.9–64.8 mm, Stanley Pool [=Malebo Pool at KINSHASA], passe devant la refuge Jipo, 17 Oct. 1957, P. Brien, M. Poll, J. Bouillon; UMMZ 196084, 4:41.4–60.5 mm, Stanley Pool, passe devant la refuge Jipo, 17 Oct. 1957, P. Brien, M. Poll, J. Bouillon; MRAC 118458–118461, 3:29.3–62.2 mm, Stanley Pool, le long de l'île Funa, 7 Oct. 1957, P. Brien, M. Poll, J. Bouillon; MRAC 118453–118456, 2:33.3–36.3 mm, Stanley Pool, 27 Oct. 1957, P. Brien, M. Poll, J. Bouillon; MRAC 29644, 57.4 mm, Panga [=Lualaba?], Bock; MRAC 90–29–P–123, 47.7 mm, Chutes Wagenia near Kisangani, 1989, V. Nyangombe.

SKELETAL STUDY MATERIAL.—MRAC 118463–118489, 2:42.9–47.4 mm and UMMZ 196084, 2:41.4–47.4 mm, Stanley Pool, passe devant le refuge Jipo, 17 Oct. 1957, P. Brien, M. Poll, J. Bouillon (cleared and stained with alizarin); MRAC 118463–118489, 53.4 mm, Stanley Pool, passe devant le refuge Jipo, 17 Oct. 1957, P. Brien, M. Poll, J. Bouillon (cleared and stained with alcian and alizarin).

Genus *Zaireichthys* Roberts, 1967

Zaireichthys Roberts, 1967b:124 (type species *Zaireichthys zonatus*, by original designation and monotypy).

DIAGNOSIS.—*Zaireichthys* differs from all other Amphiliidae in having “a defensive tripod” consisting of stout dorsal and pectoral fin spines with mechanisms for locking them into erect position. First dorsal fin spine (part of locking mechanism) short, second large, non-serrate; dorsal fin branched rays 6. Pectoral fin spine with 4–10 strong serrae on its inner margin; pectoral fin branched rays 7–8. Humeral process of pectoral girdle variably developed, from very short and smooth (non-denticulate) to elongate and extensively covered with small denticulations (the species *Z. zonatus* exhibits an intermediate condition, with a short humeral process bearing a few small but well-defined denticulations). Caudal fin shape highly variable from deeply forked (as in other leptoglanins) to rounded or truncate. Principal caudal fin ray counts highly variable (albeit nearly invariable within each species): 7+8, 7+7, 7+5, 6+7, or 6+5.

CRANIUM.—Compared to that of *Leptoglanis*, the cranium of *Zaireichthys* is generalized. The drawing of the dorsal surface of the cranium of *Z. zonatus* (Fig. 11) is not entirely satisfactory, mainly because the single specimen available for clearing and staining did not stain very well and was damaged. Thus it was not possible to distinguish clearly between the pterotic and supracleithrum in the dorsal view, and no attempt was made to draw the cranium in ventral view. The dorsal view (Fig. 11) indicates the striking difference between the skull of a generalized leptoglanin (*Zaireichthys*) and that of one of the most specialized forms, *Leptoglanis xenognathus* (Fig. 5).

COMMENTS.—A small first dorsal fin spine is lacking in all other members of the family Amphiliidae, none of which have a stout elongate dorsal fin spine or can lock the dorsal fin into erect position. The pectoral fin spine is non-serrate in all other amphiliids except *Tetracamphilius pectinatus*, which has small serrations on its pectoral fin spine. No other amphiliids can lock the pectoral fin into erect position.

KEY TO SPECIES OF *ZAIREICHTHYS*

This key should work for all of the species included in *Zaireichthys* except for *Z. flavomaculatus* and *Z. dorae* which are too poorly known to be adequately characterized. Specimens of these two species should key out under *Z. rotundiceps*. Some meristic and other characters distinguishing the species of *Zaireichthys* (except *Z. dorae* and *Z. flavimaculatus*) are presented in Table 3.

- 1. Head not bulbous; eyes visible from the side; adipose fin ending well before caudal fin; body spotted 2
Head bulbous due to greatly enlarged mandibular muscles; eyes visible from above only; adipose fin connected posteriorly to caudal fin; body banded. *Z. zonatus*
- 2. Humeral process short, without denticulations; principal caudal fin rays fewer than 7+8 3
Humeral process long and spinelike, more or less extensively covered with denticulations; principal caudal fin rays 7+8 *Z. rotundiceps*
- 3. Abdominal and postabdominal vertebrae nearly equal in number; 3–5 pairs of ribs; principal caudal fin rays not 7+7 4
Abdominal vertebrae always more numerous than caudal; 6 pairs of ribs; principal caudal fin rays 7+7 *Z. camerunensis*
- 4. Principal caudal fin rays 7+5; head broad, without dermal ridges *Z. heterurus*
Principal caudal fin rays 6+5; head narrow, usually with dermal ridges *Z. mandevillei*

TABLE 3. Comparison of the species of *Zaireichthys* (excepting *Z. dorae* and *Z. flavomaculatus*)

	<i>zonatus</i>	<i>camerunensis</i>	<i>heterurus</i>	<i>mandevillei</i>	<i>rotundiceps</i>
head shape	bulbous	narrow	broad	narrow	rounded or blunt
branchiostegal rays	7	6-7	7	6-7	6-7
pectoral spine serrae	3-4	3-5	6-9	7-8	8
pectoral fin rays	8	7	6-7	7-8	8
humeral denticulations	few	-	-	-	many
dorsal fin rays	5-6	4-6	5-6	6	6
anal fin rays	10	9	8-10	9-11	10
caudal fin shape	rounded	emarginate	forked	forked	truncate
principal caudal fin rays	6/7	7/7	7/5	6/5	7/8
procurrent caudal fin rays	10/11	11-13/10-13	13-17/13-15	13-18/12-14	14/12
ribs	5	6	3-5	3-5	5-6
vertebrae	34	35-38	33-34	34-36	36-38
coloration	banded	spotted	spotted	spotted	spotted
collar	-	-	+	+	-
largest specimen (mm SL)	24.5	33.3	34.6	26.2	37.9

Zaireichthys zonatus Roberts, 1967

(Figs. 9b; 10; 11; 12a)

Zaireichthys zonatus Roberts, 1967b:124, figs. 3–4 (type-locality lower rapids of Congo River, just below Stanley Pool, at Kinsuka village, within Leopoldville city limits).

DIAGNOSIS.— *Zaireichthys zonatus* is immediately distinguished from all other leptoglanins by greatly expanded oral musculature, giving the head a characteristically bulbous appearance (Fig. 10a), and greatly enlarged jaw teeth (Fig. 12a). In the holotype, which has the oral musculature much better developed than in the paratype, the eyes are only visible when the head is viewed from above (Fig. 10a). In all other *Zaireichthys* the eyes are also visible when viewed from the side. Eyes small. eye diameter 11–12 times in head length. Snout broadly rounded. Body with vertical bands having darkened margins (similar coloration in *Tetracamphilius pectinatus* but not in other amphiliids). Dorsal fin spine and pectoral fin spines very stout and short. Pectoral spine with only 4 serrae. Humeral process short, with a few fine denticulations on ventral margin of its tip. Adipose

fin very long, low, with gently rounded (not triangular) margin, confluent posteriorly with procurrent rays of upper caudal fin lobe (adipose fin entirely separate from caudal fin in all other leptoglanins). Gill rakers on leading/trailing edges of gill arches 1–5: 1) 3/0; 2) 3/0; 3) 0/4; 4) 3/3; and 5) 3/0 (from cleared and stained 18.1-mm paratype). Caudal fin rays 11,6+7,11. Vertebrae 16+18 = 34.

COMMENTS.— Placement of the nominal species of *Leptoglanis* with stout dorsal fin spine and serrate pectoral fin spines in *Zaireichthys* was proposed by Mo (1991:12). Reservations have been voiced by Seegers (1996:199) who retained the species in *Leptoglanis*, where they clearly do not belong. Presence of minute serrations on the humeral spine of *Z. zonatus*, a character unknown to Seegers, is an additional reason for following the placement proposed by Mo. The alternative is to designate a new genus for *L. rotundiceps* and related forms with denticulated humeral process. This procedure, however, would leave *L. camerounensis*, *L. heterurus*, and *L. mandevillei* without generic placement. The solution adopted here, retaining the species in *Zaireichthys*, seems best at least until further study has been done.

DISTRIBUTION.— *Zaireichthys zonatus* is known only from the two type specimens collected in the mainstream rapids of the River Congo just below Stanley (or Malebo) Pool. Although the habitat was predominantly rocky, the specimens were collected on the edge of a sandy area within a meter or so of each other.

MATERIAL EXAMINED

TYPE MATERIAL.— REPUBLIQUE DU CONGO (KINSHASA): CAS(SU) 64126, 24.5 mm, lower rapids of Congo River at Kinsuka village, just below Stanley Pool, 21 July 1964, T.R. Roberts (holotype); CAS(SU) 64127, 18.1 mm, collected with the holotype (paratype; cleared and stained with alizarin).

ADDITIONAL MATERIAL EXAMINED

None; species known only from the two type specimens.

Zaireichthys camerunensis (Daget and Stauch, 1963), new comb.

(Figs. 8d, 12b, 13)

Leptoglanis camerunensis Daget and Stauch, 1963:94–95, fig. 1 (type locality R. Benoué à Lakdo, Cameroun).

DIAGNOSIS.— *Zaireichthys camerunensis* differs from all other *Zaireichthys* and all other leptoglanins in having 7+7 principal caudal fin rays, and from all except *Dolicamphilius longiceps* in having 6 pairs of ribs rather than only 3–5. First pair of ribs on vertebra 6 (first pair on vertebra 5 in *D. longiceps*). Neural and hemal spines tend to be simple and slender rather than complexly laminate (Fig. 13). Branchiostegal rays 6/6 or 7/7. Pectoral fin spine with 3 to 5 serrae. Humeral process of pectoral girdle short, without denticulations. No broad black collar just behind head. Gill rakers on leading/trailing edges of gill arches 1–5 moderately large: (1) 7/0; (2) 7/0; (3) 0/6; (4) 3/3; (5) 0/0 (from cleared and stained specimen). Two proximal gill rakers on the leading edge of the first gill arch lie on the leading edge itself; four medial rakers lie on top of the flattened portion of the arch; and one distal raker lies on or nearly on the trailing edge of the arch. On the other arches gill rakers are more clearly located on leading and trailing edges (Fig. 8d). Procurrent caudal fin rays 11–13/10–13. Vertebrae 18–21+16–18 = 34–39. Largest known specimen 33.3 mm.

COMMENTS.— The only other amphiliid observed with 7+7 principal caudal fin rays is the armored doumein *Andersonia leptura* (Table 1).

DISTRIBUTION.— *Zaireichthys camerunensis* is the only species of leptoglanin known from

north of the Congo basin. It has been found only in the Niger basin, in the Upper Benue in Cameroun, and in the Upper Niger in Guinea (for map of distribution map see Risch, 1992:418).

MATERIAL EXAMINED

NIGER BASIN, CAMEROUN: MNHN 1962-1272, 6:17.0-21.7 mm, R. Benoué à Lakdo, May 1960, Stauch (syntypes); NIGER BASIN, GUINEA: MNHN 1988-1151, 3:20.7-23.8 mm, R. Milo à Boussolé, 10 Dec. 1986, D. Paugy; MNHN 1988-1150, 15:23.4-31.7 mm, and CAS 92615, 9:22.4-31.3 mm (3:24.1, 27.2, and 30.0 mm cleared and stained), R. Dele, tributary of R. Niandan, on road from Firawa to Kissidougou, March 1988, B. Hugueny; MNHN 1988-1152, 6:27.4-31.4 mm, R. Bouyé at Bouye (Niandan watershed, Niger basin), 30 April 1987, B. Hugueny; MNHN 1988-1167, 3:29.4-31.4 mm, R. Niandan at Fermessoudou, B. Hugueny; MNHN 1988-1168, 3:28.3-33.3 mm, R. Niandan at Sougounbaya, March 1988, B. Hugueny.

Zaireichthys doraе (Poll, 1967), new comb.

Leptoglanis doraе Poll, 1967:211, fig. 95 (type locality "rapides de la Luachimo, dans les flaques d'eau résiduelles"[Congo basin], Angola).

COMMENTS.— The 27-mm holotype and only known specimen of *Zaireichthys doraе* probably is immature. Pectoral fin spine with 4 or 5 large serrae. Humeral process moderately long, denticulations poorly developed. Neural and hemal processes relatively slender (not laminate). Vertebrae $20?+17?=37$. The species should be redescribed from more material.

Note that "*Leptoglanis* cf. *doraе* (non Poll 1967)" briefly described and figured reported from the "Okavango, Kwando, Chobe, and Zambesi systems) by Skelton (1993:220) is not conspecific with *L. doraе* Poll (1967).

DISTRIBUTION.— Known only from the rio Luachimo, Congo basin, Angola.

MATERIAL EXAMINED

TYPE MATERIAL.— MRAC 161646, 27 mm, rapides du rio Luachimo, aval du barrage, [Congo basin], Angola, 10 Feb. 1957, D. Machado (holotype *L. doraе*).

ADDITIONAL MATERIAL EXAMINED

None; species known only from holotype.

Zaireichthys flavomaculatus (Pellegrin, 1926), new comb.

Leptoglanis flavomaculatus Pellegrin, 1926:204 (type locality "Kamaiembi" [=Sankuru, Kamaiembi, rivière Lulua, Congo basin]; Pellegrin, 1928:29, fig. 17).

COMMENTS.— The holotype and only known specimen is in poor condition. Humeral process long and denticulate (as in *Z. rotundiceps*). Radiographs show caudal fin with 15,7+8,15 rays; vertebrae $18?+18=36?$ The species should be redescribed from more material.

A single specimen has been reported as *L. flavomaculatus* from the rio Lufume, a tributary of the rivière Luele (in Angola) by Poll (1967:211, fig. 94). It differs markedly from the holotype of *Z. flavomaculatus* in having a finely spotted coloration overall and a truncate caudal fin, and evidently represents an undescribed species.

DISTRIBUTION.— *Zaireichthys flavomarginatus* is known only from the rivière Lulua in southern Congo (Kasai).

MATERIAL EXAMINED

TYPE MATERIAL.— MRAC 19721, 39.3 mm, Kamaiembi, H. Schouteden (holotype *L. flavo-maculatus*).

ADDITIONAL MATERIAL EXAMINED

None; species known only from holotype.

***Zaireichthys heterurus* Roberts, new species**

(Fig. 14)

HOLOTYPE.— REPUBLIC DU CONGO (KINSHASA): MRAC 87-42-P-1140, 31.4 mm, R. Avokoko, affluent rive droit fleuve Zaïre, km 21 route Kisangani-Wanie Rukula, 29 March 1987, L. De Vos and A. Kimbembé.

DIAGNOSIS.— *Zaireichthys heterurus* differs from all other amphiliids in having 7+5 principal caudal fin rays. Humeral process moderately long and stout but not denticulated. Barbels attenuate, maxillary barbel extending posteriorly almost to end of pectoral fin spine. Head broadly rounded. Eyes small. Color pattern spotted, with a broad dark collar (as in *Z. mandevillei*) immediately posterior to head. Caudal peduncle moderately slender; caudal fin deeply forked, upper lobe much shorter and smaller, and falcate, lower lobe rounded; fin rays in lower lobe noticeably thicker than those in upper lobe. Largest known specimen 34.6 mm. With growth, individual fish become increasingly stouter, more perhaps than any other leptoglanin species (compare Fig. 14b of the stout 31.4-mm holotype with Fig. 14c of a cleared and stained and much more slender 23.0-mm specimen). Vertebrae 16-17+17=33-34.

COMMENTS.— The two non-type specimens from the Lufira both have 7+5 principal caudal fin rays, but the caudal peduncle seems more slender than in other *Z. heterurus*.

DISTRIBUTION.— *Zaireichthys heterurus* is widely distributed in the eastern sector of the Congo basin. It occurs in clear, swift flowing tributaries lying to the east of the Congo River mainstream.

ETYMOLOGY.— The name *heterurus* is from the Greek *heteros*, different, and *oura*, tail.

MATERIAL EXAMINED

HOLOTYPE.— REPUBLIC DU CONGO (KINSHASA): MRAC 87-42-P-1140, 31.4 mm, R. Avokoko, affluent rive droit fleuve Zaïre, km 21 route Kisangani-Wanie Rukula, 29 March 1987, L. De Vos and A. Kimbembé.

PARATYPES.— REPUBLIC DU CONGO (KINSHASA): MRAC 87-42-P-1140-43, 3:23.2-26.6 mm, MRAC 90-47-P-538-549, 12:23.4-30.1 mm, R. Avokoko, 27 Dec. 1987, L. De Vos; MRAC 88-24-P-1-8, 8:22.4-32.5 mm, R. Avokoko, same collection data as holotype (2:26.0-30.4 mm cleared and stained with alcian and alizarin); CAS 92617, 84:17.6-31.5 mm, R. Lulindi, 21 km by road N of Lusangi (route Kongolo-Kasongo), 28 Aug. 1986, T.R. Roberts (4:22.4-23.2 mm cleared and stained with alcian and alizarin); CAS 92618, 24.7 mm, R. Lukuga just downstream from Niemba, 20-21 Aug. 1986, T.R. Roberts; MRAC 90-47-P-524-537, 6:24.9-29.9 mm, R. Avokoko, km 22 route Kisangani-Wanie Rukula, 17 Dec. 1989, L. De Vos, Kambasu; MRAC 90-47-P-564-580, 8:20.7-27.3 mm, R. Avokoko, 19 Jan. 1990, L. De Vos, Kambasu; MRAC 90-30-P-1198-256, 2:24.4-32.3 mm, Chutes Wagénia, Kisangani, 7 Feb. 1990, L. De Vos.

ADDITIONAL MATERIAL EXAMINED

REPUBLIC DU CONGO (KINSHASA): MRAC 87-61-P-1-2, 2:24.3-26.3 mm, R. Lufira, Oct. 1947, G. F. de Witte.

***Zaireichthys mandevillei* (Poll, 1957), new comb.**

(Figs. 8e, 12c; 15a)

Leptoglanis mandevillei Poll, 1959:98, pl. 25 fig. 2 (type locality Stanley Pool [Congo R. near Kinshasa]).

DIAGNOSIS.—*Zaireichthys mandevillei* is the most slender-bodied and perhaps the smallest species of *Zaireichthys*. Largest known specimen 26.3 mm. Snout more pointed than in other *Zaireichthys*. Eyes small. Barbels attenuate, maxillary barbel extending posteriorly to middle of pectoral fin spine. Most specimens have entire dorsal surface of head with longitudinally oriented, interrupted ridges (presumably keratinous) not observed in other leptoglanins (small, scattered ridges, presumably keratinous, present in some specimens of *Z. heterurus* and *Z. rotundiceps*). Pectoral fin spine elongate, with 7-9 strong serrae. Humeral process very short, without denticulations. Color spotted, with a prominent dark collar just behind head (as in *Z. heterurus*). Caudal peduncle very slender; caudal fin forked, lower lobe larger and longer than upper lobe; principal caudal fin rays 6+5.

COMMENTS.—Ridges similar those of *Z. mandevillei* occur on the dorsal surface of the head of an African mochokid catfish, *Chiloglanis reticulatus* (Roberts 1989:159, 169, fig. 5). *Zaireichthys mandevillei* has perhaps the most reduced gill rakers of any leptoglanin. Gill rakers (very small) on leading/trailing edge of gill arches 1-5: (1) 1/0; (2) 1/0; (3) 1/2; (4) 2/1; and (5) 0 (in 22.3-mm cleared and stained specimen) (Fig. 8e).

DISTRIBUTION.—Previously known only from Stanley Pool in the Congo River (type locality). *Z. mandevillei* is now reported from the Ubangui and Lualaba. So far as known, it is confined to sandy reaches of the mainstream of the Congo River and its largest tributaries.

MATERIAL EXAMINED

TYPE MATERIAL.—REPUBLIC DU CONGO (KINSHASA): MRAC 118533-536, 4:19.9-22.8 mm, Stanley Pool, entrée de la passe de Limbili, 19 Sept. 1957, P. Brien, M. Poll, J. Bouillon (paratypes).

ADDITIONAL MATERIAL EXAMINED

REPUBLIC DU CONGO (KINSHASA): MRAC 1313, 19.8 mm, R. Ubangui at Banzyville, 1901, Royaux (poor condition; originally identified as *Amphilius angustifrons*); MRAC 90-30-P-1192, 26.2 mm, Chutes Wagenia, Kisangani, 23 Jan. 1990, L. De Vos; MRAC 90-30-P-1193-1197, 2:22.6-24.8 mm, Chutes Wagenia, Kisangani, 25 Jan. 1990, L. De Vos; MRAC 90-30-P-1198-256, 23:21.2-26.3 mm, Chutes Wagenia, Kisangani, 7 Feb. 1990, L. De Vos; MRAC 90-47-P-581-632, 21:21.9-24.9 mm, Chutes Wagenia near Kisangani, 3-8 June 1990, L. De Vos; MRAC 90-47-P-633-651, 8:22.1-23.3 mm, Chutes Wagenia, Kisangani, 24 June 1990, L. De Vos.

REPUBLIQUE CENTRAFRICAINE: CAS 92619, 22:16.3-24.2 mm, R. Ubangui at Isle Molenge 82 km upriver from Bangui, 27 Feb. and 7 March 1988, T.R. Roberts; CAS 92620, 19.4 mm, R. Ubangui near Isle Baskiki, 75 km upstream from Bangui, 6 March 1988, T.R. Roberts; CAS 92621, 49:13.6-23.9 mm, Ubangui R. near Banda, 72 km upriver from Bangui, 5 March 1988, T.R. Roberts (7:17.0-23.5 mm cleared and stained with alcian and alizarin); CAS 92622, 11:15.3-21.3 mm, R. Ubangui near Bawili, 68-69 km upstream from Bangui, 5 March 1988, T.R. Roberts.

***Zaireichthys rotundiceps* (Hilgendorf, 1905), new comb.**

(Fig. 15b)

Gephyroglanis rotundiceps Hilgendorf, 1905:412 (type locality "Im Bubu bei Irangi" [Rufiji basin, Tanganyika])

Leptoglanis rotundiceps, Boulenger, 1911:352, fig. 273.

Leptoglanis brevis Boulenger, 1915:169 (type locality riv. Lumumbashi à Elisabethville).

?*Leptoglanis wamiensis* Seegers, 1989:285, fig. 1 (type locality Kisangata-Bach bei Mvumi, 32 kilometer SW Kidete, am Wege nach Kimamba/Kilosa im Wami-Einzug NW Morogoro, Tanzania).

?*Leptoglanis* sp Seegers, 1989:284 (see Seegers 1996:196)

DIAGNOSIS.— *Zaireichthys rotundiceps* of this account, which probably represents several species, has humeral process of shoulder girdle well developed, elongate, with its ventral margin and sometimes entire surface covered with fine denticulations. Pectoral fin spine stout with strong serrae (7 or more in larger specimens). Dorsal fin spine stout, with a well-developed locking mechanism. Caudal fin shape variable, from slightly forked through, emarginate, truncate, or even slightly rounded, but not deeply forked. Principal caudal fin rays 7/8 (only checked in a few specimens). Head broad, snout rounded or blunt, body relatively stout. Adipose fin elongate, its margin rounded. Coloration highly variable, from abundant dark spots in several rows to light pale spotting pattern (never banded). Marks often present on head and fins as well as body.

Gill rakers moderately well developed, leading/trailing edges of gill arches 1–5 with 1) 6/0; 2) 6/0; 3) 0/5; 4) 5/5; and 5) 5 rakers; rakers on leading edge of gill arch 5 (lower pharyngeal) not stained with alizarin or alcian, but clearly discernible (24.1-mm cleared and stained specimen from Luwoyeye). Coloration of the *Zaireichthys rotundiceps* species complex is highly variable, involving more or less numerous spots of variable size and distribution over most of the body. There is no humeral collar or band of dark pigmentation just behind the hind.

COMMENTS.—A large denticulate humeral process was observed in all of the type and non-type specimens listed as material examined of *Z. rotundiceps*. Detailed study of all of this material has not been attempted, but some preliminary comments are in order. I have examined the humeral denticulations in a 24.1-mm specimen of *Z. rotundiceps* from rivière Luwoyeye, CAS 92623. Superficially resembling sharp conical teeth, the denticulations are concentrated along the lower margin of the humeral process. Apparently they are not true teeth. They arise directly from the bony humeral process; there are no tooth sockets; and, although the denticulations are numerous and differ in size, there is no sign of any stages of tooth formation or of tooth replacement. Direct comparison of the BMNH syntypes of *L. rotundiceps* and *L. brevis* reveals that they are closely similar, possibly conspecific. For further discussion of *L. rotundiceps* and *L. brevis* see Seegers (1996).

A large denticulated humeral process also occurs in *Z. dorae* and *Z. flavomaculatus*, two poorly characterized species known only from the holotypes, that clearly are not conspecific with *Z. rotundiceps*. A smaller humeral process bearing relatively few denticulations is present in *Z. zonatus*. Similar denticulations have not been reported in any other members of the family Amphiliidae.

Leptoglanis wamiensis Seegers, 1996 undoubtedly is a *Zaireichthys*. It may be tentatively regarded as a junior synonym of *Z. rotundiceps*. Seegers emphasized its small size and unique color pattern as species characters. Size and color are highly variable in the samples of *Zaireichthys* identified here as *Z. rotundiceps*. Problems with such characters as body size and number and size of spots in the color pattern (and their intensity) are 1) they are continuously variable and difficult to describe and record, let alone compare; 2) they are probably influenced by non-genetic factors such as water clarity, food availability, and physiological condition; and 3) they differ in virtually every

population sample. Characters that might prove more useful in distinguishing the different species include shape and width of premaxillary tooth patch, length of lateral line canal; and numbers of branched dorsal and caudal fin rays (D. H. Eccles, in lit., 23 Oct. 1979).

Two species of *Zaireichthys* are reported (as *Leptoglanis rotundiceps* and *L. cf. dorae*) from the Zambesi and other southern African localities by Skelton (1993:218–220). The behavior of lying buried in fine sand with only the eyes protruding is recorded for both species by Skelton. *Zaireichthys cf. rotundiceps* in Lake Malawi lives in shells of the snail *Lanistes* (D. J. Stewart, in litt., 18 June 1979).

MATERIAL EXAMINED

TYPE MATERIAL.—EASTERN AFRICA: BMNH 1905.7.25. 43–46, 4: 20.7–30.1 mm, and MRAC 76–50–P–1, 26.1 mm, Bubu River near Irangi, Rufiji basin, July 1897, O. Neumann (syntypes *G. rotundiceps*); REPUBLIC DU CONGO (KINSHASA) BMNH 1920.5.26.93, 25.1 mm, R. Lubumbashi, Elizabethville, Congo basin, 9 June 1911, L. Stappers (syntype *L. brevis*).

ADDITIONAL MATERIAL EXAMINED

REPUBLIC DU CONGO (KINSHASA): CAS 92623, 3:24.1–33.3 mm, riv. Luwoyeye, a tributary of rivière Lukuga, about 10 km by road S of Nyunzu, 22 Aug. 1986, T.R. Roberts (24.1-mm specimen cleared and stained); MRAC 89–43–P–2242, riv. Kawe II, affl. riv. Lubutu, km 260 route Kisangani-Bukavu, & July 1989, L. De Vos; MRAC 182734, 25.4 mm, vallee riv. Lupweshi, affluent de la riv. Lufira, 8 June 1958, N. Magis; MRAC 183297–340, 44:18.8–34.8 mm, au pont route de la riv. Lubumbashi, camp forestier de la Kipopo, 1 and 8 May 1960, T. van den Audenaerde; MRAC 18341–342, 2:22.4–25.2 mm, étang de la station de la Kipopo, June 1960, D.F. Thys van den Audenaerde; MRAC 183343–44, 2:28.7–31.1 mm, Kiubo, dans les rapides au-dessus des chutes des riv. Lufira et Luwilombo, 8 Aug. 1960, T. van den Audenaerde; MRAC 79–1–P–4382, 30.2 mm, riv. Bowa, affl. droit de la Kalule Nord et 1/ affl. droit du Lualaba, pres de Kiamalwa, 2–3 March 1949, G.F. de Witte; MRAC 83416, 35.3 mm, Elizabethville, Parc Heenen, 7 Jan. 1947, Mission Pisc. Katanga; MRAC 90262–90263, 2:34.4–36.3 mm, riv. Koki, entre Mulenge et Kamulenge, 28 Sept.–1 Oct. 1947, M. Poll; MRAC 90264, 37.4 mm, riv. Kitwe, affluent de la Lukuga à Kokompwa; MRAC 93050, 28.9 mm, riv. Luvubu, 9 Sept. 1952, G. Marlier; MRAC 152631–33, 3:24.0–26.4 mm, riv. Kilobelobe, Katanga, 21 June 1963, M. Lips.

OUTSIDE CONGO BASIN.—BMNH 1987.7.13.77, 25.7 mm, Cubango (Okavango) R. at Nkurunkuru, M. J. Penrith; BMNH 1979.12.6.6–10, 5:22.3–25.9 mm, Kunene R. one mile E of Epupa Falls, Oct. 1971, M. J. Penrith; BMNH 1979.12.6.2–5, 4:20.3–25.4 mm, Kwando R. at Choyi near Kongolo, Caprivi, 3 June 1975; BMNH 1979.12.6.30, 30.0 mm, Impalilay Stream near confluence of Zambesi and Chobe, E Caprivi, 7 Aug. 1975, B. van der Waal; BMNH 1979.12.6.1, 23.2 mm, Kafue R., Zambesi system, 16 Dec. 1963; BMNH 1976.12.6.11–13, 3:18.0–19.5 mm, Mazinzi Bay, Lake Malawi (trawled in shells at 11–13 m), Oct. 1974, D. H. Eccles; BMNH 1979.12.6.17–21, 5:20.3–31.7 mm, western affluent streams of Lake Malawi, Oct. 1978, D. Tweddle and N. J. Willoughby; BMNH 1979.12.6.22–25, 4:27.0–33.1 mm, Sabi R., eastern Rhodesia, 4 Dec. 1960; MRAC 90–46–P–1–6, 3:29.9–37.9 mm, Rwimi R., road between Portal and Kasese, Uganda, 13 June 1990, R. Wildekamp.

***Dolichamphilius* Roberts, new genus**Type species: *Leptoglanis brieni* Poll, 1959

DIAGNOSIS.— *Dolichamphilius* was placed in *Leptoglanis*, but differs in numerous respects from the generic type-species *L. xenognathus*: (1) body and especially caudal peduncle extremely elongate; (2) pectoral fin with 9–11 instead of only 8 branched rays; (3) pectoral- and pelvic-fin branched rays with long simple branches medially and extremely foreshortened compound branches distally (this character is shared with *Psammphyletria*); (4) outermost branched ray of pectoral and pelvic fins more elongate, so these fins have a falcate shape; (5) principal caudal fin rays 6+7 instead of 7+8; (6) upper and lower jaws with teeth (vs. lower jaw toothless); and (7) premaxillary bone of generalized usual shape for amphiliids, with entire ventral surface dentigerous (vs. premaxillary with an extensive non-dentigerous area anteriorly).

ETYMOLOGY.—From the Greek *dolichos*, long or elongate; *ammos*, sand; and *philos*, beloved, dear. Gender masculine.

***Dolichamphilius brieni* (Poll, 1959), new comb.**

(Figs. 9e, 16a)

Leptoglanis brieni Poll, 1959:96, pl. 24 fig. 2 (type locality “Stanley Pool, passe devant le refuge Jipo”).

DIAGNOSIS.— *Dolichamphilius brieni* is readily distinguished from all other leptoglanins by its extremely slender body and elongate caudal peduncle; pectoral fin with a flexible spine and 11 rays; first branched ray of pectoral and pelvic fins distinctly longer than other rays; both jaws with conical teeth; lower jaw with only a single short row of 8–10 fine sharp conical teeth; caudal vertebrae more numerous than abdominal, vertebrae 19+24–25=43–44; peduncular vertebrae 17.

DISTRIBUTION.— *Dolichamphilius brieni* is known only from the type locality, Stanley Pool [Congo River at Kinshasa].

MATERIAL EXAMINED

TYPE MATERIAL.— REPUBLIC DU CONGO (KINSHASA): MRAC 118504–118506, 26.9 mm, Stanley Pool, extérieur des îles de l’archipel N’Djili vers l’île de Cristal, 7 Oct. 1957, P. Brien, M. Poll, J. Bouillon (paratype); MRAC 118504, 31.2 mm, Stanley Pool, passe devant le refuge Jipo, 7 Oct. 1957, P. Brien, M. Poll, J. Bouillon (paratype; cleared and stained with alcian and alizarin).

ADDITIONAL MATERIAL EXAMINED

None; species known only from type specimens.

***“Dolichamphilius” longiceps* Roberts, new species**

(Fig. 16c)

HOLOTYPE.—REPUBLIC DU CONGO (KINSHASA): MRAC 90–47–P–704–708, 42.2 mm, Chutes Wagania, Kisangani, 24 June 1991, L. De Vos.

DIAGNOSIS.— Dorsal fin rays i5½; anal fin rays iii7; pectoral fin rays i9. Caudal fin rays 10.6+7.12. Vertebrae 20+20=40; 6 pairs of ribs. First pair of ribs, on vertebra 5, smaller than ribs on vertebra 6 (in all other leptoglanins, first pair of ribs are largest and occur on vertebra 6). Caudal peduncle elongate, but much less so than in *D. brieni*, with only 12 vertebrae. Body with four or five elongate oval spots centered on midline; spot nearest middle of body considerably enlarged on

both sides of body in holotype would be a diagnostic feature if characteristic of the species.

COMMENTS.— This distinctive species is unfortunately known only from the holotype, which has been radiographed but not cleared and stained for osteology. It resembles in some ways the species of *Tetracamphilius* but differs from them in having simple conical jaw teeth and more numerous vertebrae. It is provisionally assigned to *Dolichamphilius*, even though it differs in several respects from the generic type species. Because of doubt that this species belongs to *Dolichamphilius*, its characters have not been taken into account in the diagnosis of *Dolichamphilius*.

DISTRIBUTION.— *Dolichamphilius longiceps* is known only from the type locality, Chutes Wagania on the R. Lualaba near Kisangani.

ETYMOLOGY.— The name *longiceps* is from the Latin, *longus*, long; and *-ceps*, derived from *caput*, head.

***Psammphiletria* Roberts, new genus**

Type species: *Psammphiletria nasuta* Roberts, new species.

DIAGNOSIS.— Small, sand-dwelling amphiliid catfishes (largest known specimen 23.7 mm) with a prominent fleshy rhinal lobe; basal half of maxillary barbel included in maxillary membrane; branchiostegal rays 4–5; tubiferous portion of lateral line incomplete, ending above anal fin; dorsal and pectoral fins without locking mechanisms, their fin rays all slender and flexible; dorsal fin origin very far behind head and pectoral fin, over vertebra 11–13; adipose fin triangular, moderately elongate, its origin over base of third anal fin ray; 3–4 pairs of ribs; pectoral- and pelvic-fin branched rays with long simple branches medially and extremely foreshortened compound branches distally (this character is shared with *Dolichamphilius*); pelvic fin origin below vertebra 10–11; principal caudal fin rays 5/6; lower lobe of caudal fin distinctly prolonged; vertebrae 17–18+16–18=33–36; neural and hemal spines expanded distally (lamellar).

COLORATION.— Head and body overall white, translucent but not transparent. There is an almost continuous median row of brown spots or marks on the dorsal surface of the body. Head, fins, and side of body without markings except for a diamond-shaped peduncular spot and some smaller indistinct markings just anterior to it.

COMMENTS.— *Psammphiletria* looks superficially like the young of *Amphilius*, but there are numerous differences. *Amphilius* differs from *Psammphiletria* in having no rhinal lobe; anterior and posterior cranial fontanelles present; branchiostegal rays 6–8; gill rakers present on upper portion of gill arches (absent in *Psammphiletria*); 10 or more pairs of ribs; pelvic fin origin very much farther posterior; pectoral girdle with two ossified radials instead of only one; principal caudal fin rays 6+7 or more; lower caudal fin lobe not prolonged.

Zaireichthys differs in having very stout dorsal and pectoral fin spines with well-developed locking mechanisms; serrate pectoral fin spine; principal caudal fin rays always more than 5+6; and procurrent caudal fin rays much more numerous. *Dolichamphilius* differs in having a more elongate body, more numerous vertebrae, dorsal fin origin immediately behind cranium; pectoral fin with 11–12 rays; first branched ray of pectoral and pelvic fins prolonged.

ETYMOLOGY.— From the Greek *psammo* “sand” and *philetria* “lover of”. Gender feminine.

***Psammphiletria nasuta* Roberts, new species**

(Figs. 8f, 9d, 17a–d)

HOLOTYPE.— REPUBLIQUE CENTRAFRICAINE: CAS 92624, 23.5 mm, Central African Republic,

sandy riffle in R. Ubangui near Banda, 72 km upriver from Bangui, 5 March 1988, T.R. Roberts.

DIAGNOSIS.—A species of *Psammphyletria* with 4–6 unbranched anal fin rays. Dorsal fin with only 5 rays; dorsal fin pterygiophores 4. Rhinal lobe very large. Gill rakers on first gill arch 3–4. Vertebrae 18+17–18=34–36.

DISTRIBUTION.—*Psammphyletria nasuta* is known only from the Ubangui River upstream from Bangui.

ETYMOLOGY.—The name *nasuta* is from the Latin *nasutus*, long-nosed.

MATERIAL EXAMINED

HOLOTYPE.—REPUBLIQUE CENTRAFRICAINE: CAS 92624, 23.5 mm, Central African Republic, sandy riffle in R. Ubangui near Banda, 72 km upriver from Bangui, 5 March 1988, T.R. Roberts.

PARATYPES.—REPUBLIQUE CENTRAFRICAINE: CAS 92625, 11:14.8–22.7 mm, same data as holotype (3:16.1–23.7 mm cleared and stained with alcian and alizarin); CAS 92626, 16.5 mm, R. Ubangui at Isle Basiki, 75 km upriver from Bangui, 6 March 1988, T. R. Roberts.

Psammphyletria delicata Roberts, new species

(Fig. 17e)

HOLOTYPE.—MRAC 118455, 20.5 mm, Stanley Pool, 27 Sept. 1957, P. Brien, M. Poll, J. Bouillon.

DIAGNOSIS.—*Psammphyletria delicata* is distinguished from *P. nasuta*, its only congener, by slight differences in counts of dorsal and anal fin rays, and in having dorsal and anal fin pterygiophores and laminar portions of neural and hemal spines more expanded. Dorsal fin rays 7 (5 in *P. nasuta*). Dorsal fin pterygiophores 7 (4 in *P. nasuta*). All three type specimens have anal fin with three simple rays, three branched rays, and a simple ray (last simple ray only ray on last anal fin pterygiophore). Rhinal lobe large, but not so large as in *P. nasutus*; this may be partly due to differences in preservation and condition of the specimens, those of *P. delicata* being in less good condition. Vertebral count of the single cleared and stained paratype 17+16=33.

DISTRIBUTION.—*Psammphyletria delicata* is known only from Stanley Pool (Malebo Pool).

ETYMOLOGY.—The trivial name *delicata* is Latin for dainty or delicate.

MATERIAL EXAMINED

HOLOTYPE.—MRAC 118455, 20.5 mm, Stanley Pool, 27 Sept. 1957, P. Brien, M. Poll, J. Bouillon.

PARATYPES.—MRAC 118456, 19.5 mm, same data as holotype (cleared and stained with alcian and alizarin); MRAC 118489, 18.6 mm, Stanley Pool, passe devant la refuge Jipo, 17 Oct. 1957, P. Brien, M. Poll, J. Bouillon.

Tetracamphilius Roberts, new genus

Type species: *Tetracamphilius pectinatus* Roberts, new species.

DIAGNOSIS.—*Tetracamphilius* differs from all other leptoglanins and from all other amphiliids in having pedicellate jaw teeth with a fan-shaped distal end typically armed with two to six tiny flattened triangular cusps (Fig. 19). All other amphiliids have simple conical jaw teeth or jaw teeth absent. Adipose fin triangulate, its origin well in advance of a vertical line through anal fin origin. Caudal peduncle slender, peduncular vertebrae 9–12. Caudal fin deeply forked, lower lobe slightly larger than upper, principal caudal fin rays 6+7.

COMMENTS.— The cusps on the jaw teeth of *Tetracamphilius* are possibly unique not only in catfishes but perhaps also in Ostariophysi. I do not know of any other catfishes with comparable cusps. Multicuspid characoid jaw teeth are superficially similar but are much larger, and usually formed by combination of individual conical elements (Roberts 1967b), which does not appear to be so in *Tetracamphilius*. Scanning electron microscopic observations of the jaw teeth in a specimen of *T. pectinatus* reveals that the cusps are flattened, not really conical, and that they are frequently broken off, so that it is difficult to find a tooth with more than one or two intact cusps; many of the teeth have all of the cusps broken off, so that they are squared off distally or peg-like in shape. The number of cusps increases with growth. The largest cleared and stained specimen examined, a 37.2 mm *T. angustifrons*, had jaw teeth with as many as six cusps. When the cusps of such a tooth are broken off, the crown has a discoid shape. The multicuspid teeth of *Tetracamphilius* are present on the upper as well as lower jaw, but not in the pharynx (upper and lower pharyngeal teeth in all leptoglanins including *Tetracamphilius* are simple conical teeth).

ETYMOLOGY.—From the Greek *tetra*, four, and *akis*, point, in reference to the multicuspid teeth, and *Amphilius*, a generical name for this group of catfishes.

KEY TO SPECIES OF *TETRACAMPHILIUS*

Some meristic and other characters distinguishing the species of *Tetracamphilius*, presented in Table 4, should be used in conjunction with this key.

- 1. Pectoral fin spine without serrae; body spotted 2
Pectoral fin spine with fine serrae on inner margin; body with dark-margined, pale-centered bands *T. pectinatus*
- 2. Lamellar portion of olfactory organ large, its length nearly equal to eye diameter; posterior nares much larger than anterior nares 3
Lamellar portion of olfactory organ not enlarged, its length less than half eye diameter; anterior and posterior nares equal in size *T. notatus*
- 3. Dorsal fin rays 8–9; anal fin rays 9–10; pectoral fin rays 8–9 *T. angustifrons*
Dorsal fin rays 6–7; anal fin rays 8; pectoral fin rays 7–8 *T. clandestinus*

TABLE 4. Comparison of the species of *Tetracamphilius*

	<i>pectinatus</i>	<i>angustifrons</i>	<i>clandestinus</i>	<i>notatus</i>
pectoral spine serrae	6-7	-	-	-
pectoral fin rays	8-9	9	7-8	8
dorsal fin rays	8-9	6-7	6-7	8
anal fin rays	8-10	9-10	8	10
procurrent caudal fin rays	13-14/13-14	9-11/10-12	9-12/9-10	13/11
branchiostegal rays	7-8	6-7	6-7	6-7
ribs	4	4-5	3-4	5
total vertebrae	34-38	36-38	35	35-37
largest specimen (mm SL)	33.7	39.4	19.5	32.5

Tetracamphilius pectinatus, Roberts, new species

(Figs. 18)

HOLOTYPE.— REPUBLIC DU CONGO (KINSHASA): CAS 92627, 33.7 mm gravid female, Congo basin, tributary of R. Luala 26 km N of Kibunzi (8 km S of turnoff to Kibunzi, Luozi dist.), 45°6.5' S, 13°48' E, 24 July and 17 Aug. 1973, T.R. Roberts and D.J. Stewart.

DIAGNOSIS.— *Tetracamphilius pectinatus* differs from the other species of the genus and from all other amphiliids except *Zaireichthys* in having a serrated pectoral fin spine. Unlike *Zaireichthys*, which has very large pectoral spine serrae, the serrae are very small, and the pectoral fin spine does not possess a locking mechanism. It differs from all other leptoglanins (and all other amphiliids) except *Z. zonatus* in having color pattern with a series of bands with paler inner part and darkened margins.

COLORATION IN LIFE.— *Tetracamphilius pectinatus* is the most colorful known leptoglanin. In life, the dark narrow bands are a dark chocolate brown, the dorsum of the head and areas between the narrow bands tan or orangish tan, and the abdomen and other pale areas cream-colored.

HABITAT NOTES.— The tributary of the rivière Luala in Bas-Congo where adult *T. pectinatus* were collected in breeding condition was clear, moderately swift flowing, with sand, gravel, and rock rubble bottom, 6–8 m wide and 1 m deep, in rolling or hilly savannah. On 24 July 1973 collecting was done with a square frame net, by pushing it into the sandy or other bottom, or by holding it in place and kicking rocky rubble and gravel 1–3 m upstream from it. Some 8 specimens of *T. pectinatus* were collected together with ornately banded mochokid catfish, *Chiloglanis reticulatus* Roberts, 1989, along the interface of sand and gravel. A second mochokid species, the mottled *C. batesii* Boulenger, 1904, was collected only in rocky rubble and riffles along with a species of the rheophilic cyprinid genus *Garra*. No other catfishes were collected at this locality. On 17 August 1973 a larger collection was made at the same spot using toxaphene.

DISTRIBUTION.— *Tetracamphilius pectinatus* is known from the mainstream of the Ubangui upstream from Bangui, from a small tributary of the rivière Luala in the Lower Congo basin (Bas-Congo), and from the Luala in southern Congo (Kasai).

ETYMOLOGY.— The trivial name *pectinatus* is Latin for comb-like, in reference to the small serrations on the pectoral fin.

MATERIAL EXAMINED

HOLOTYPE.— REPUBLIC DU CONGO (KINSHASA): CAS 92627, 33.7 mm gravid female, Congo basin, tributary of R. Luala 26 km N of Kibunzi (8 km S of turnoff to Kibunzi, Luozi dist.), 45°6.5' S, 13°48' E, 24 July and 17 Aug. 1973, T. R. Roberts and D. J. Stewart.

PARATYPES.— REPUBLIQUE CENTRAFRICAINE: CAS 92628, 31:26.3–33.7 mm, collected with the holotype (3:27.4–29.2 mm cleared and stained with alcian and alizarin; 7:26.3–29.6 mm, cleared and stained with alizarin); CAS 92629, 2:23.4–24.5 mm, R. Ubangui, riffles in sand bar at Isle Basiki, 75 km upstream from Bangui, 6 March 1988, T. R. Roberts; CAS 92630, 5:21.2–26.3 mm, R. Ubangui, riffles in shallow sandy area near Banda, 72 km upstream from Bangui, 5 March 1988, T. R. Roberts (2:21.9–24.0 mm cleared and stained with alcian and alizarin); CAS 92631, 23.3 mm, R. Ubangui upstream from Bangui, 1 March 1988. REPUBLIC DU CONGO (KINSHASA): T. R. Roberts; CAS 92632, 28.6 mm, R. Lulua just below Chutes de Mbombo, near Luluaburg [=Kananga], 7 Sept. 1986, T. R. Roberts.

***Tetracamphilius angustifrons* (Boulenger, 1902), new comb.**

(Figs. 19, 20a)

Anoplopterus angustifrons Boulenger, 1902:42, pl. 10 fig. 4 (type locality "Banzyville" [=Mobaye on the rivière Ubangui]).

Amphilius angustifrons Boulenger, 1911:362, fig. 282.

DIAGNOSIS.—A *Tetracamphilius* differing from all other species except *T. clandestinus* in having a relatively elongate snout with an enlarged olfactory organ; length of lamellar portion of olfactory organ nearly equal to eye diameter; and anterior and posterior nostrils widely separated, posterior much larger than anterior. From *T. clandestinus* it differs in having more dorsal fin rays (8–9 vs. 6–7; more anal fin rays (9–10 vs 7–8); and more pectoral fin rays (9 vs 7–8).

NOTES ON SYNTYPES.—BMNH and MRAC syntypes are all in very poor condition. Probably they were accidentally dried when the species was being described, because the drawing of the whole specimen evidently was based on a specimen in very good condition, while the drawing of the dorsal view of the head evidently was based on a specimen that had dried. This apparently led to the erroneous illustration of the posterior nostrils and the statement "posterior nostril midway between eye and end of snout" (Boulenger 1911:362). On the MRAC syntype I did not find posterior nasal openings in the position indicated by Boulenger. I found the large posterior nostril only after careful searching with fine forceps. The openings were tightly pressed to the dorsal surface of the lateral ethmoids, only slightly in advance of the eyes, and were very difficult to see until gently lifted.

Amphilius angustifrons was known only from the original series of 5 syntypes, from the Ubangui River near Banzyville (near Bangui), all of them now in very poor condition (Skelton, 1986: 266; present observations). Judging from the original figure, at least one of the specimens was in good condition when studied by Boulenger (1902; 1911).

One of the two BMNH syntypes was cleared and stained for this study. The preparation was not satisfactory, however. Bone and cartilage stained well, but soft tissues were stained deep blackish blue. The specimen broke into pieces, and some bits were lost. The caudal fin skeleton and most of the fins rays disintegrated. The head has been dissected and sketches and observations made on the jaws, vomer, gill arches, branchiostegal rays, and auditory capsules. The multicupid jaw teeth (most fallen out) were observed and drawn. In this specimen, the multicupid jaw teeth included individual teeth with up to 6 cusps; teeth with the cusps all broken off are left with broadly rounded distal ends. Vertebral counts were obtained from radiographs of three syntypes.

REMARKS ON IDENTIFICATION OF SPECIMENS.— Identification of freshly collected material from Ubangui as *T. angustifrons* is based mainly on direct comparison with one of the syntypes, a larger specimen in very poor condition. Identification of the specimens from the Chutes Wagonia is problematic. The head is narrow anteriorly, as in *T. angustifrons*, but the color pattern is somewhat more like that of specimens identified as *T. notatus*. The eyes are smaller than in specimens identified as *T. angustifrons* or *T. notatus*. If correctly identified, these are the only specimens of *T. angustifrons* known from a locality other than the Ubangui.

DISTRIBUTION.—*Tetracamphilius angustifrons* is known only from the Ubangui mainstream above Bangui, with the exception of one lot of specimens tentatively identified as *T. angustifrons* from the Chutes Wagonia, Lualaba.

MATERIAL EXAMINED

TYPE MATERIAL.—REPUBLIC DU CONGO (KINSHASA): MRAC 1313, 39.4 mm, Banzyville, 1901, Royaux (syntype; the other specimen from this lot, 19.8 mm, has been reidentified as

Zaireichthys mandevillei); BMNH 1901.12.27.40, 37.2 mm, Banzyville, 1901, Royaux (syntype; cleared and stained with alcian and alizarin, but specimen did not clear and disintegrated, see below).

ADDITIONAL MATERIAL EXAMINED

REPUBLIQUE CENTRAFRICAINE: CAS 92633, 9:17.4–31.7 mm, R. Ubangui at Isle Molinge, 82 km upstream from Bangui, 27 Feb. and 7 March 1988, T.R. Roberts; CAS 92634, 6:17.4–27.3 mm, R. Ubangui at Isle Basiki, 75 km upstream from Bangui, 6 March 1988, T.R. Roberts; CAS 92652, 6:18.0–24.8 mm, sandy riffle in R. Ubangui near Banda, 72 km upriver from Bangui, 5 March 1988, T.R. Roberts (cleared and stained with alcian and alizarin); CAS 92635, 15:15.2–26.6 mm, R. Ubangui in shallow sandy area at Bawili, 68–69 km upstream from Bangui, 5 March 1988, T.R. Roberts. REPUBLIC DU CONGO (KINSHASA): MRAC 90–47–P–704–708, 4:26.0–29.3 mm, Congo River in Chutes Wagania near Kisangani, 24 June 1990, L. De Vos.

Tetracamphilius clandestinus Roberts, new species

(Fig. 20b)

HOLOTYPE.— REPUBLIQUE CENTRAFRICAINE: CAS 92653, 17.8 mm, riffles in shallow sandy area of Ubangui near Banda, 72 km upstream from Bangui, 5 March 1988, T. R. Roberts.

DIAGNOSIS.— *Tetracamphilius clandestinus*, with largest known specimen 19.5 mm, is perhaps the smallest leptoglanin species. It is very similar to *T. angustifrons* but has slightly fewer vertebrae, ribs, dorsal and pectoral fin rays, and differently shaped auditory capsules. Dorsal branched fin rays 5 or 5½ (6½ or 7½ in *T. angustifrons*). Pectoral fin branched fin rays 6 or 7 (usually 8, very rarely 7 or 9 in *T. angustifrons*). Usually 3 pairs of ribs, sometimes 4 (usually 5 pairs of ribs, sometimes 4 in *T. angustifrons*). In *T. clandestinus* and *T. angustifrons* of the same size, the fleshy rostrum usually is more pronounced in *T. clandestinus*. Total vertebrae 17+18=35 in five cleared and stained paratypes (*T. angustifrons* and other species of *Tetracamphilius* usually with 36 or more vertebrae; Table 1). Consult diagnosis of *T. angustifrons*.

DISTRIBUTION.— *Tetracamphilius clandestinus* is known only from the Ubangui mainstream above Bangui.

ETYMOLOGY.— The trivial name *clandestinus* is Latin, meaning secret or hidden.

MATERIAL EXAMINED

HOLOTYPE.— REPUBLIQUE CENTRAFRICAINE: CAS 92653, 17.8 mm, riffles in shallow sandy area of Ubangui near Banda, 72 km upstream from Bangui, 5 March 1988, T.R. Roberts.

PARATYPES.— REPUBLIQUE CENTRAFRICAINE: CAS 92654, 22:14.4–19.5 mm, collected with the holotype (5:17.3–19.2 mm cleared and stained with alcian and alizarin); CAS 92655, 2:15.2–15.7 mm, R. Ubangui near Bawili, 68–69 km upstream from Bangui, 5 March 1988, T.R. Roberts.

Tetracamphilius notatus (Nichols & Griscom, 1917), new comb.

(Fig. 20c)

Amphilius notatus Nichols & Griscom, 1917:715, fig. 24 (type locality Faradje [=R. Uele, a large tributary of the Ubangui]).

DIAGNOSIS.— A *Tetracamphilius* species with non-serrate pectoral fin spines, spots instead of bands on the body, and olfactory organ not greatly enlarged.

REMARKS ON IDENTIFICATION OF SPECIMENS.— This species was known only from the holotype. Specimens from the Chinko and the Mbomou were identified as *T. notatus* by comparing them directly with the holotype. Holotype has dorsal fin rays $i6\frac{1}{2}$, anal $ii7\frac{1}{2}$, pectoral $i8/i7$, caudal $14.6/7.13$. Color pattern evidently has faded somewhat, but melanophores are still visible and the original color pattern is therefore discernible. All features of color pattern identical with those in freshly preserved specimens.

DISTRIBUTION.— *Tetracamphilius notatus* is known from the mainstream of the Ubangui, from several of its larger and smaller tributaries, and from the R. Lufira in eastern Congo.

MATERIAL EXAMINED

TYPE MATERIAL.— REPUBLIC DU CONGO (KINSHASA): AMNH 6711, 28.5 mm, Faradje, Jan. 1913, Lang and Chapin (holotype).

ADDITIONAL MATERIAL EXAMINED

REPUBLIQUE CENTRAFRICAINE: CAS 92656, 2:24.9–26.7 mm, R. Chinko at Rafai, Republique Centrafricaine, 30 Jan. 1987, T.R. Roberts (25.9 mm cleared and stained); CAS 92657, 25.2 mm, rapids in R. Mbomou about 10 km SW of Rafai, Republique Centrafricaine, 1 Feb. 1987, T.R. Roberts; CAS 92658, 19.1 mm, R. Ubangui, riffles in sand bar at Isle Basiki, 75 km upstream from Bangui, 6 March 1988, T.R. Roberts; CAS 92659, 4:15.8–24.2 mm, R. Ubangui, riffles in sandy shallow area near Banda, 72 km upstream from Bangui, 5 March 1988, T.R. Roberts; CAS 92650, 23.9 mm, R. Ngougoufon near where it flows into R. Topia, about 120 km due E of Berberati, 23 March 1988, T.R. Roberts. REPUBLIC DU CONGO (KINSHASA): MRAC 87–61–P–3, 32.5 mm, Kilwezi, affluent droit, de la rivière Lufira, alt. 800 m, 30 Aug. 1948, G.F. de Witte.

OSTEOLOGY

This is a summary account of leptoglanin osteology. Adequate drawings for a reasonably full osteological account of even a single species have not been completed. This is due to the inordinate amount of time and effort involved. A comprehensive osteological account of just the cranium of one species should include four drawings: dorsal, ventral, lateral, and occipital view. A full set of osteological drawings for one species would involve 15 or more figures. A comprehensive osteological account of Leptoglaninae, including descriptions, comparisons, and analysis of relationships just within Leptoglaninae and Amphiliidae, could easily run to 100 pages.

Enough leptoglanin osteology is presented here to introduce the topic. It is intended to permit discussion of morphological trends within Leptoglaninae. It may also be useful in discussions of relationships within Amphiliidae. Ichthyologists primarily interested in the catfishes of Asia and South America recently have investigated the possible relationships of Amphiliidae and Leptoglaninae to various South American and Asian catfish families, in particular to the Asian family Sisoridae (Pinna 1996; He and Meunier 1998; He et al. 1999). This is beyond the scope of this paper.

The osteological features of Leptoglaninae showing the greatest diversity and specialization are the cranium, jaws and dentition, pectoral fin girdle, and axial skeleton. The jaws of *Leptoglanis xenognathus* are perhaps most specialized, but the palatine arch appears to be generalized (Figs. 4–7). In Leptoglaninae, teeth are found only on the jaws and pharyngeal arch. The multicuspoid jaw teeth of the genus *Tetracamphilius* are a notable specialization, especially for such small species, but the palatine arch of *Tetracamphilius* (Fig. 19) and pharyngeal arches are relatively generalized. The pharyngeal teeth are large and conical, not multicuspoid. The gill arches of Leptoglaninae, char-

acterized by reduced gill rakers, appear to be morphologically generalized and relatively unspecialized. Those of *Leptoglanis* (Fig. 8b) are morphologically very similar to those of *Zaireichthys* (Fig. 8c–e). The hyoid arch also appears to be relatively generalized and exhibits little osteological variation. Catfish families (e.g., Bagridae, Schilbeidae) often exhibit considerable range in the number of branchiostegal rays. Leptoglaninae all have 4–8 branchiostegal rays. The lowest observed count of 4 occurs in the tiny species *Psammphyletria nasuta*; the highest counts of 6–8 occur in the largest species *Leptoglanis xenognathus*.

The pectoral fin girdle, as in catfishes generally, comprises three main bony elements: postem-poral-supracleithrum, scapulocoracoid, and cleithrum (Diogo et al. 2001). There are also a meso-coracoid bone, a cartilaginous complex radial, and a single bony proximal radial. Some catfishes families, such as the African Claroteidae and Asian Bagridae, normally have two bony proximal radials, but Amphiliidae including Leptoglaninae usually have only one (Fig. 9a–b). This nomenclature follows Diogo et al. (2001) and authors cited therein. Much of the variation in leptoglanin pectoral girdle morphology (Fig. 9a–c) evidently is related to the variation in pectoral fin spines from stout, rigid, and serrate to slender, flexible, and non-serrate, and the corresponding presence or absence of a mechanism to lock the pectoral fin spine in erect position.

The paired fins, dorsal fin, and caudal fin show great variety of structure and numerous specializations. This is of course reflected in their girdles and other bony supporting structures.

One outstanding feature is the presence of dorsal and pectoral fin spines with locking mechanisms in *Zaireichthys*. In this genus the pectoral fin spine is also strongly serrate. All other leptoglanins lack locking mechanisms for the dorsal and pectoral spines, and only one other species, *Tetracamphilius pectinatus*, has a serrated pectoral fin spine (Fig. 9c). In *Psammphyletria* the pectoral fin rays are morphologically virtually the same as the pelvic fin rays. These fish effectively have two pairs of pelvic fins, an anterior pair (the pectoral fins) and a posterior pair (the true pelvic fins).

The axial skeleton exhibits numerous striking morphological differences. The range of vertebral counts from 33 to 44 is only a pale reflection of this. In some species of *Zaireichthys* the neural and hemal spines are relatively slender and morphologically generalized (Figs. 5c, 9–11b). In *Leptoglanis*, *Dolicamphilius*, and *Psammphyletria*, on the other hand, these processes are hugely expanded and morphologically highly specialized (Figs. 1d; 12; 13d–e; 16a,c). *Tetracamphilius* and some species of *Zaireichthys* are intermediate in this respect (Figs. 11a, 14b). The degree of specialization of the dorsal and anal fin pterygiophores is correlated closely with that of the neural and hemal processes (Figs. 1d; 5c; 9; 10c; 11; 12a,b; 13d–e; 14; 16a,c).

The caudal fin ray formulas of leptoglanins exhibit a remarkable range of principal fin ray counts, from 7/8 in *Leptoglanis xenognathus* and *Zaireichthys rotundiceps* down to 5/6 in *Psammphyletria* (Table 1). Caudal fin shape also varies markedly, from deeply forked, moderately forked, truncate or rounded (Figs. 1c; 5b; 9; 10b; 11; 12a–b; 13c,e; 14; 16).

Despite these great differences in the caudal fin shape and ray counts, the caudal fin skeleton shows remarkably little morphological variation (Figs. 1d; 5c; 9; 10c; 11a,b; 12a; 13d,e; 14b; 16c). It consists mainly of a single upper and single lower hypurals. Sometimes the two elements are entirely separate, as in *L. xenognathus* (Fig. 1d). They may be partially fused, as in species of *Tetracamphilius* (Figs. 14b, 16a,c), or entirely fused, as in *Psammphyletria* (Figs. 13d,e). The primitive principal caudal fin count in catfishes is 8/9 (Lundberg and Baskin 1969). This number occurs in several species of *Amphilius* and other Amphiliinae (Table 1). It is reasonable to assume that 7/8 is the most primitive caudal fin ray count in leptoglanins. This primitive count, however, does not appear to be associated with an equally primitive arrangement of the caudal fin skeleton. In leptoglanins the caudal fin skeleton consists mainly of a single upper and single lower hypural ele-

ment. This may indicate that the presence of 7/8 principal caudal fin rays in *Leptoglanis* and in one species of *Zaireichthys* is due to independent re-expression of a primitive catfish character trait. The dorsal and pectoral fin spine locking mechanisms and pectoral fin spine serrae of *Zaireichthys* may be further examples of the same phenomenon.

DISCUSSION

AFRICAN CATFISH FAMILIES AND LEPTOGLANINAE.— The freshwater catfishes of Africa currently are classified in seven families: Bagridae, Claroteidae, Mochokidae, Schilbeidae, Clariidae, Malapteruridae and Amphiliidae. Their phylogenetic relationships and higher classification are not well understood. All members of the first four families generally differ from Leptoglaninae and agree with each other in sharing the primitive catfish characteristics of the defensive tripod, an unencapsulated swim bladder, and 8/9 principal fin rays. The defensive tripod, an effective anti-predator device, consists of more or less stout, serrated dorsal and pectoral fin spines that can be locked in erect position. Bagridae is a large family present only in Africa and Asia. The large endemic African family Claroteidae was recently removed from Bagridae (Mo 1991). Thus African Bagridae now includes only the endemic African genus *Bagrus*. *Bagrus* differs from all other bagrids, from Claroteidae, and from all other African catfishes in having a dorsal fin with 10-11 soft rays. There are only six or seven species. They are all large, with flat head and long barbels. Claroteidae, Mochokidae, and Schilbeidae, with diverse head and body shape, usually have 7 soft dorsal fin rays. The exclusively African Mochokidae have highly specialized jaws with pedicellate multicupid teeth for browsing on algae, and strongly branched barbels. No other African catfishes have branched barbels. Osteological characters of Mochokidae, especially of the jaws, cranium, and pectoral girdle, indicate that they probably are related to the Auchenoglanidinae, a subfamily presently assigned to Claroteidae. Close relationship between Mochokidae and Doradidae, a South American family with branched barbels, seems unlikely. Schilbeidae and Clariidae are shared by Africa and Asia. Schilbeidae all have a laterally compressed body, a very long anal fin, and long barbels. Clariidae are distinguished from all other African catfishes by having a more or less elongate, eel-like body form and eel-like locomotion and a highly apomorphic cranium. Clariid pectoral fins have a stout serrated spine with a mechanism to lock it into erect condition, but the dorsal fin is entirely soft-rayed. The clariid dorsal fin has numerous rays, and extends the entire length of the body, unless interrupted posteriorly by the adipose fin. Then the dorsal fin with the adipose fin extends virtually the entire length of the body. The caudal fin invariably is rounded. Given the distinctive and specialized characteristics of Mochokidae, Schilbeidae, Clariidae, and Malapteruridae, it is difficult to sustain hypotheses of close relationships between any of them and Leptoglaninae.

The most viable hypothesis of a close relationship between Leptoglaninae and another family of African catfishes is with Amphiliidae. Leptoglaninae agrees with Amphiliidae and differs from other African catfish groups in two major ways: (1) absence of the defensive tripod (except in *Zaireichthys*); and (2) bony encapsulation of the swim bladder. The hypothesis of Amphiliidae-Leptoglaninae relationship is strengthened by presence of a "transverse interscapular bony bridge" in *Andersonia leptura* (He 1999; pers. obser.), a member of the rheophilic amphiliid subfamily Doumeinae. Apart from *Andersonia*, this character is known only in Leptoglaninae. Leptoglaninae differs from the two other amphiliid subfamilies, Amphiliinae and Doumeinae, in having an entirely different life style and in lacking unculiferous pads on the ventral surface of their paired fins. *Andersonia* is a highly specialized plated doumein, present in the Nile and other Sudanic drainage systems. It is not closely related to Leptoglaninae. The possibility that Amphiliidae or

Leptoglaninae might be closely related to South American or Asian catfishes is beyond the scope of the present work.

PLEOMERISM IN LEPTOGLANINAE.—Pleomerism, the tendency among related fish species for vertebral number to be correlated with maximum body length (Lindsey 1975), has been documented in several catfish families: Lindsey (1975; Ictaluridae and Mochokidae); Roberts (1983; sisorid genus *Bagarius*); Roberts and Vidthayanon (1991; Pangasiidae). The phenomenon often can be used by catfish systematists to distinguish closely related species differing in size. It may sometimes prove useful in predicting adult size of species known only from very small or immature specimens, and in detecting valid species formerly placed in synonymy (Lindsey 1975). Maximum standard length of leptoglanins ranges from a little under 20 mm to 65 mm (consult material examined) and total number of vertebrae from 34 to 44 (Table 2).

To simplify the present discussion, leptoglanins may be divided into four size classes: 1) less than 20 mm; 2) 20–30 mm; 3) 30–50 mm; and 4) over 50 mm. The ranges of total vertebral counts recorded for these classes are, respectively, 35 (only a single species, *T. clandestinus*); 34–37 (six species); 34–44 (six species); and 38–41 (only a single species, *Leptoglanis xenognathus*).

It may be noted that 34 is close to the lowest known vertebral count recorded in catfishes.

The very lowest vertebral counts in *P. delicata* (33), *Z. zonatus* (34), and *T. clandestinus* (35) indicate that these probably are indeed very small species. The highest counts, 43–44 in *Dolichamphilius brieni*, may indicate that this very rare species gets considerably larger than the 26.9–31.2 mm standard length of the only two specimens known. This count is also almost certainly related to the exceptionally elongate or slender body of this species (see discussion of relationship between pleomerism and body elongation in Lindsey, 1975). While the number of abdominal vertebrae (19) is not exceptional, the numbers of postabdominal vertebrae (24–25) and peduncular vertebrae (17) are the highest found in Leptoglaninae. The only known species that might be congeneric with *D. brieni*, *D. longiceps*, has a less elongate body with only 40 vertebrae.

The lowest total vertebral counts recorded in Leptoglaninae occur in the smallest species, *P. delicatus* (33), and in the stoutest species, *Z. heterurus* (33–34).

ZOOGEOGRAPHY OF LEPTOGLANINAE.—The geographical distribution of Leptoglaninae contrasts strikingly with that of the two other amphiliid subfamilies. Basic information on distribution of Amphiliidae is provided by Skelton and Teugels (1986). All three subfamilies are well represented in the Congo basin. Amphiliinae occur throughout virtually all of tropical Africa, including the Upper and Lower Guinean coastal areas, the Ogooué basin, Angolan coastal basins, and most of eastern and southern Africa. Doumeinae also occur in Upper and Lower Guinea, the Ogooué, and Angolan coastal basins, but are absent in southern and eastern Africa.

The only leptoglanin known from north of the Congo basin, *Zaireichthys camerunensis*, has been reported only from the Niger basin (Risch 1992). The Niger basin is part of the Nilo-Sudanic ichthyofaunal province recognized by Roberts (1975). It embraces the Nile, Chad, Niger, Senegal and Volta basins. Most Nilo-Sudanic fish genera occur in all of these basins, and further collecting may result in discovery of *Z. camerunensis* in other Nilo-Sudanic drainages. It is highly unusual for an essentially Congolese fish group to have close phyletic relationship to fishes otherwise found only in the Niger basin. Another instance of disjunct distribution involving Nilo-Sudanic and Congolese fishes is provided by the rheophilic cichlid genus *Steatocranus*, with six endemic species in the Congo basin and one in the Volta basin (Roberts and Stewart 1976).

The striking difference in the distribution patterns of Amphiliinae and Doumeinae versus Leptoglaninae may well lay in their different habitat preferences. Amphiliinae and Doumeinae are current-loving or rheophilic fishes typically living in high gradient streams with rocky substrate. They often occur at high elevations in mountain streams, and some species may be classed among

the oribatic or mountain-loving African fishes (Roberts 1975). Such fishes often occur in separate drainages on opposite sides of drainage divides, possibly because of numerous stream captures as mountain tops are eroded by their drainages. Leptoglaninae, on the other hand, are nearly all restricted to very large lowland streams, inhabiting extensive low-gradient areas where the substrate is predominantly or entirely fine sand. Such species are unlikely to cross over mountain divides. On the other hand, they are likely to have very extensive ranges within any particular river basin, as indeed seems to be so for several Congolese leptoglanins. *Leptoglanis xenognathus* and *Zaireichthys mandevillei* are known from the Lower Congo (Stanley Pool), Ubangui, and Lualaba. *Tetracamphilius pectinatus* also has an extensive range within the Congo basin.

A SPECIALIZED LIFESTYLE.— This account of Leptoglaninae may be concluded by a consideration of the unusual "lifestyle" of the more specialized taxa. We are concerned here with all of the species in the genera *Leptoglanis*, *Dolichamphilius*, and *Psammphyletria*, two species of *Tetracamphilius*, and one of *Zaireichthys*. These are all small or very small species. The largest known specimen of *Leptoglanis* is 65 mm and the largest known *Dolichamphilius* only 32 mm. *Psammphyletria nasuta* reaches only 23.7 mm. *Psammphyletria delicatus* is perhaps the smallest catfish in Africa. The largest specimen is only 20.5 mm. Although only two specimens are known, this probably is close to its maximum size. *Tetracamphilius angustifrons* is known up to 39.4 mm. *Tetracamphilius clandestinus*, at only 19.2 mm, is possibly the smallest of all known African catfishes. Finally, we have *Zaireichthys mandevillei*, of which the largest known specimen is only 26.7 mm. Despite the fact that these species are all small, and that several of them are among the smallest of all of the African freshwater fish species, they are known only from the mainstreams of two of the largest rivers in Africa, the Congo and its largest tributary, the Ubangui.

These species live only in what may be described as great aquatic deserts, the outstanding feature of which is sand. These sandy deserts or plains often appear to be featureless. Seemingly uniform sandy stretches inhabited by Leptoglaninae are often very extensive, but individual fish are not uniformly scattered over wide areas. Just as in the great African deserts, the sandy terrain has some features frequented by more organisms than others. In the Ubangui River, where the greatest diversity of Leptoglaninae has been found, they are most abundant in (1) sand riffles, where water flows in streams from vast shallow areas into deeper water; (2) edges of sand bars, where vast featureless sand flats suddenly slope into deeper water; and (3) edges of hollows in the sand caused by large rocks. An effective way to collect leptoglanins is to search for any kind of unusual feature in the sand, then push a fine-meshed push-net deeply into it. The little fish often come out on top of the sand when the net is removed from the water, or it may be necessary to let the sand filter out through the mesh of the push-net. This is particularly effective for collecting small species and small specimens of the larger species, but apparently is not so effective for catching the larger species such as *Leptoglanis xenognathus*, presumably because they are too mobile. These may be caught occasionally by seining at night. Fishing with a push-net in large uniform sandy areas (sand flats) produces almost no specimens of Leptoglaninae, even if there is a good current. Leptoglanins only occur in habitats with flowing water.

The aquatic insect larvae, crustaceans, and other small animals fed upon by leptoglanins probably are most abundant in the special niches in the aquatic sand desert occupied by the leptoglanins. Leptoglanins are perhaps the only fishes in the Congo basin that can successfully exploit this special food resource. Total or near total exemption from predation by fish may be another benefit conveyed by their small size and habitat. Their sand-diving behavior, mentioned above, may be related to their feeding as well as to predator avoidance. Also possibly involved in detecting potential food organisms and predators is the sense of olfaction. Leptoglanins have large olfactory organs.

While living in large rivers and having small body size have some obvious advantages, there

probably are some disadvantages. How do they adjust to the marked habitat changes during the annual cycle of low and high water periods? How do such tiny fish locate each other when it is time to mate? During high water periods characterized by swift current and massive changes in the sand banks, the leptoglanins presumably are widely dispersed. How do they manage to come together again? During periods of low water they are found mainly in special places in the sand deserts, such as riffles, sand-bar ridges or fall-offs, and troughs or holes created by isolated logs or rocks. Individuals finding such a place are likely to encounter conspecifics if they remain there. As mentioned above, at least some leptoglanins have fairly large olfactory organs. These might function in intraspecific communication as well as in finding food and avoiding predators. Probably all leptoglanins produce copious amounts of mucus. This mucus, secreted by the pectoral axillary gland, might include pheromones or might itself act as a pheromone.

Sand-dwelling catfishes with a lifestyle and sand-diving behavior comparable to that of Leptoglaninae apparently do not exist in the rivers of tropical Asia. I have searched for them without success, especially in the mainstream of the Mekong and in its larger tributaries, but also in other large Asian rivers. The only ecological equivalents among catfishes appear to be some of the very small tropical South American Trichomycteridae and Pimelodontidae.

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FIGURES 1-20

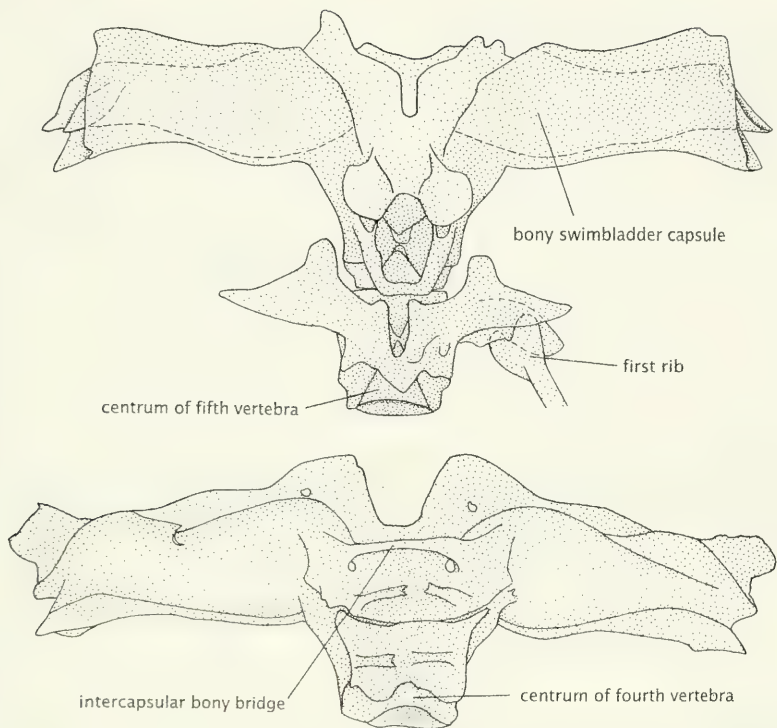


FIGURE 1. *Leptoglanis xenoganthus*, 41.4 mm, Stanley Pool. Dorsal and ventral views of the bony swim bladder capsules. The intercapsular bridge is a shared specialization or synapomorphy apparently common to all leptoglanins and to the doumein amphiliid genus *Andersonia*.

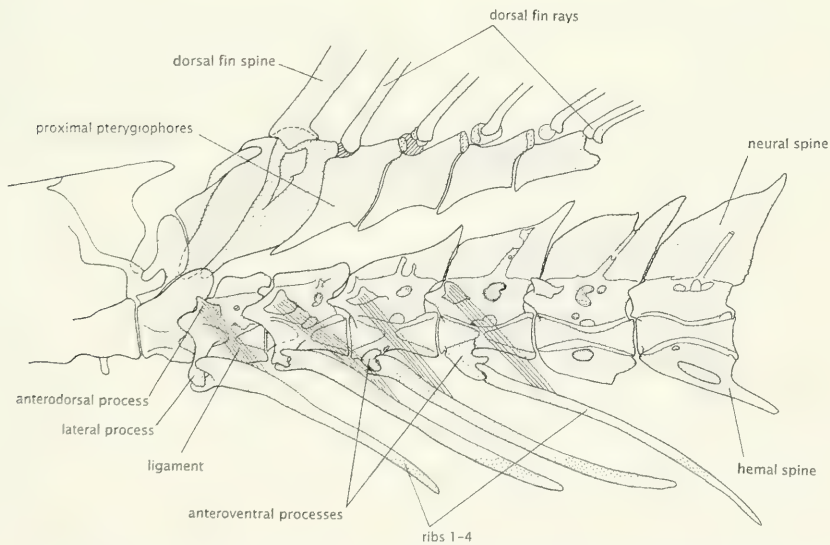


FIGURE 2. *Leptoglanis xenognathus*, 54.5 mm, Stanley Pool. Anterior portion of vertebral column and associated structures. Note specialized bicapital and ligamental attachment of ribs.

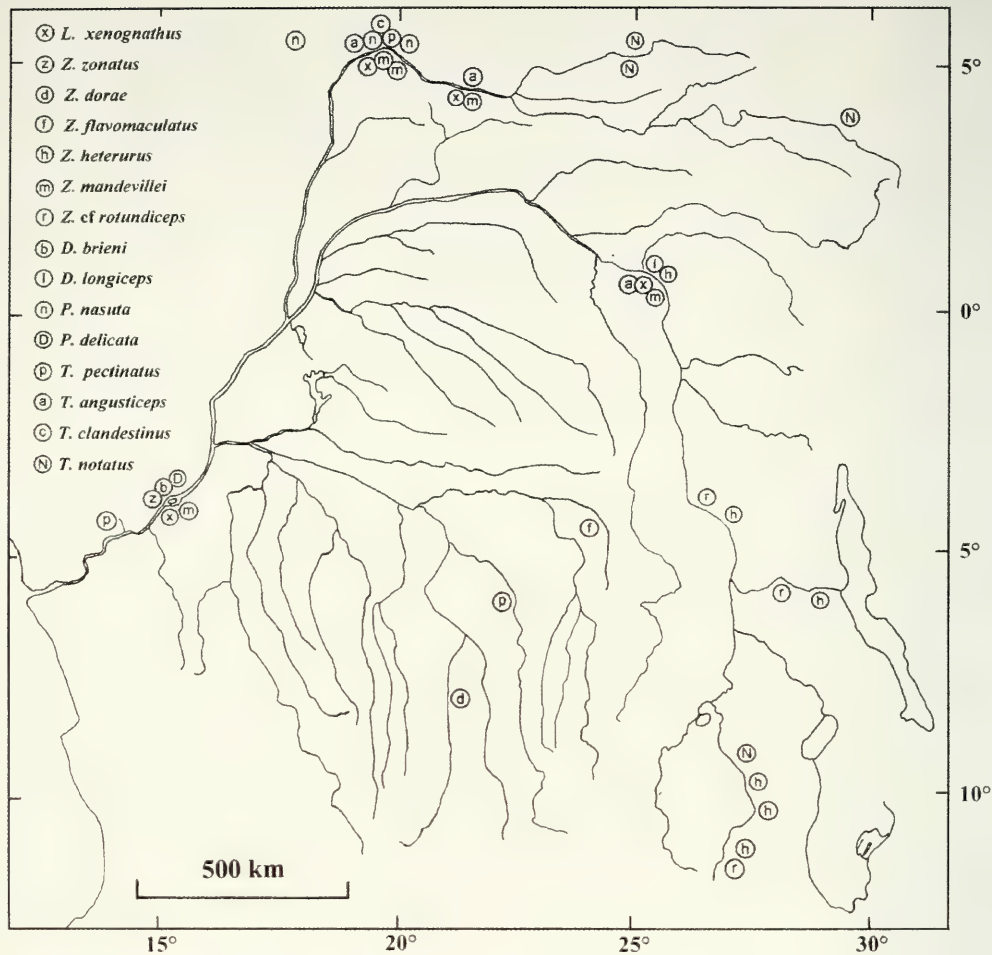


FIGURE 3. Distribution of Leptoglaninae in the Congo basin. Note clustering of species records on the Congo mainstream near Kinshasa (formerly Leopoldville), on the upper Congo mainstream or Lualaba at Kisangani (formerly Stanleyville), and especially in the Ubangui River upstream from Bangui. This reflects collecting activity as well as presence of favorable habitat.

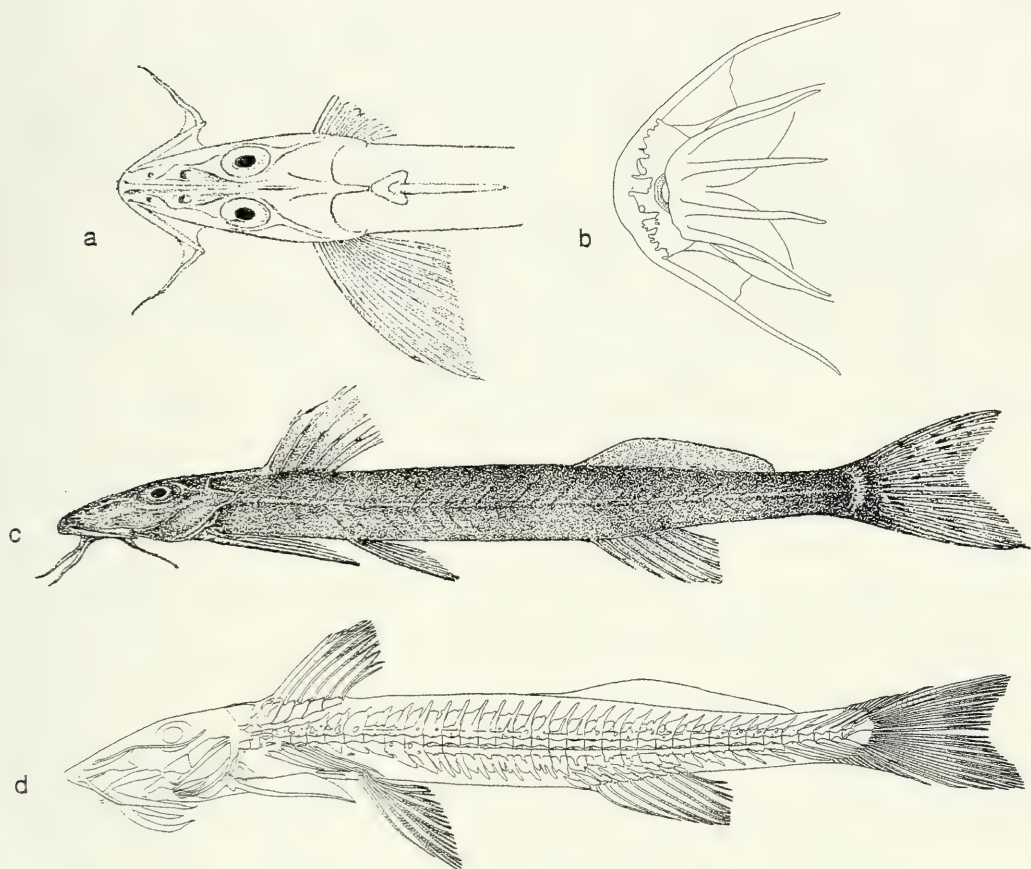


FIGURE 4. *Leptoglanis xenognathus*: a and c, holotype, total length 55 mm, Ubangui, dorsal view of head and full lateral view; b, 62.2 mm, Stanley Pool, ventral view of head; d, 53.4 mm, Stanley Pool, axial skeleton (vertebrae 21+18=39) (a and c from Boulenger 1911, Fig. 272).

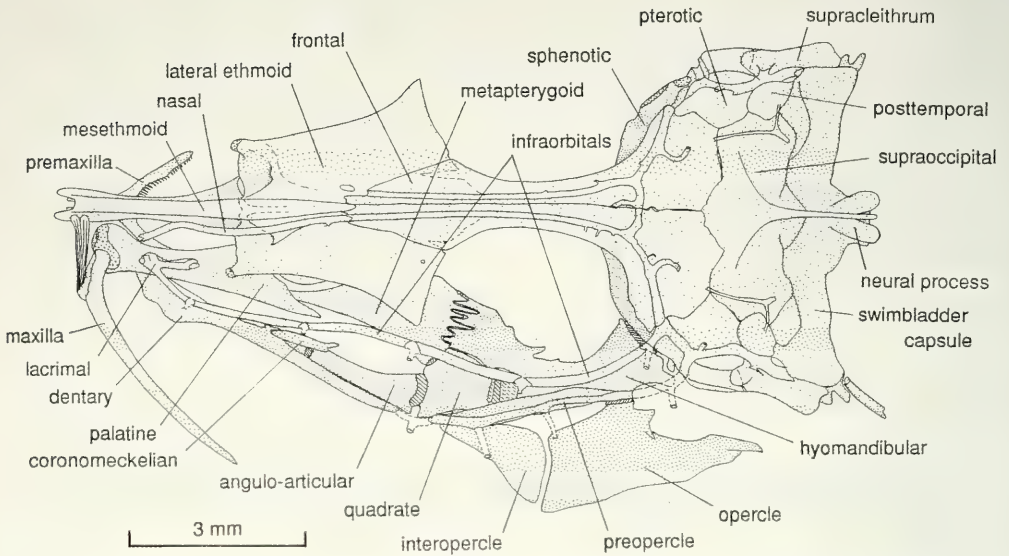


FIGURE 5. *Leptoglanis xenognathus*, 53.4 mm, Stanley Pool. Cranium, suspensorium and jaws (dorsal view).

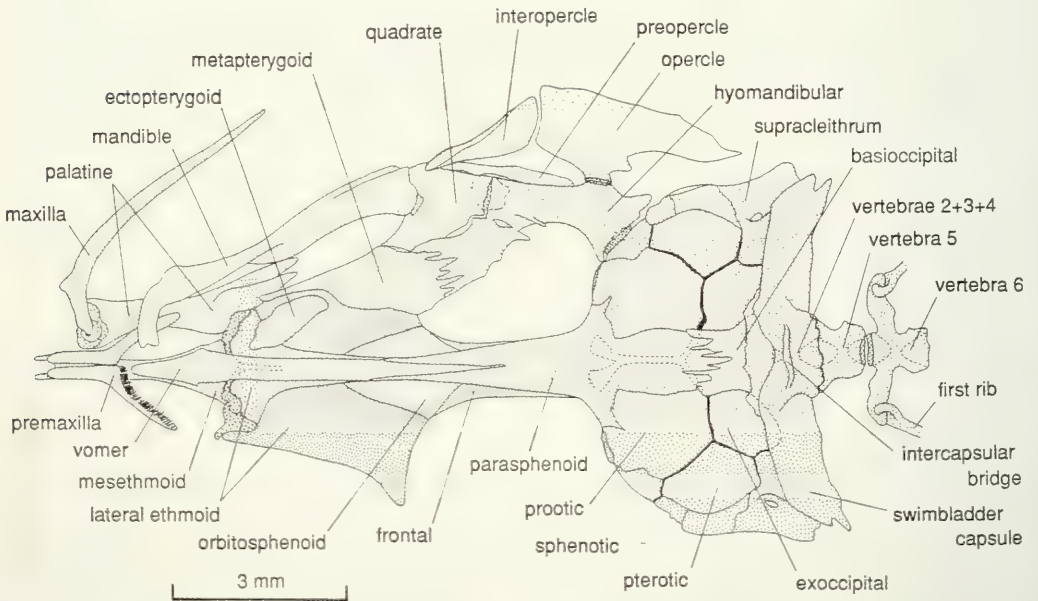


FIGURE 6. *Leptoglanis xenognathus*, 53.4 mm, Stanley Pool. Cranium, suspensorium and jaws (ventral view).

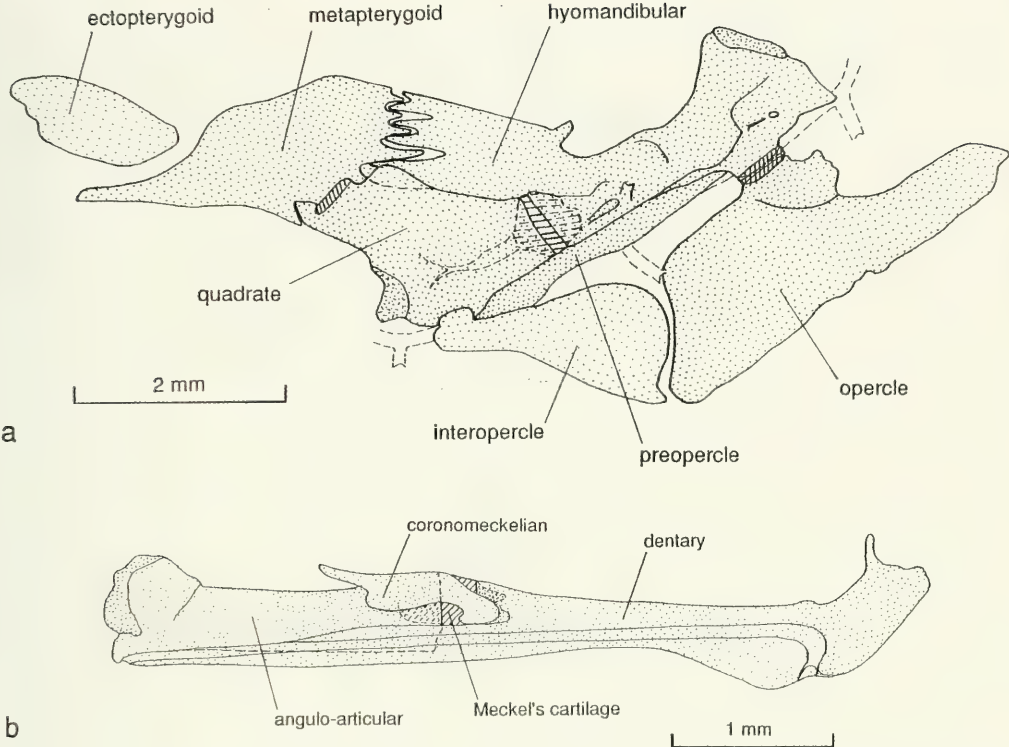


FIGURE 7. *Leptoglanis xenognathus*, 53.4 mm, Stanley Pool. a, suspensorium and jaws (medial view); b, lower jaw (lateral view).

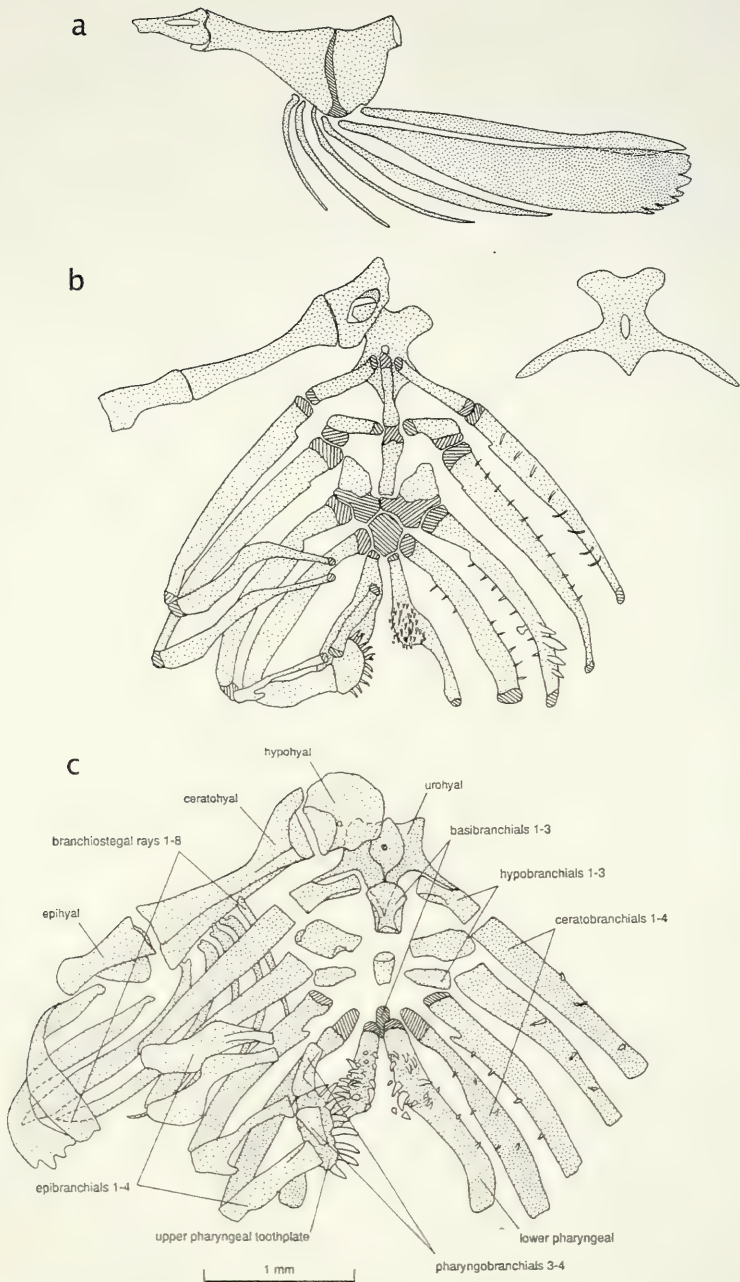


FIGURE 8. Leptoglaninae, hyoid and gill arches. a-b, *Leptoglanis xenognathus*, 54.5 mm, Stanley Pool; c, *Zaireichthys zonatus*, 18.1 mm, Kinsuka.

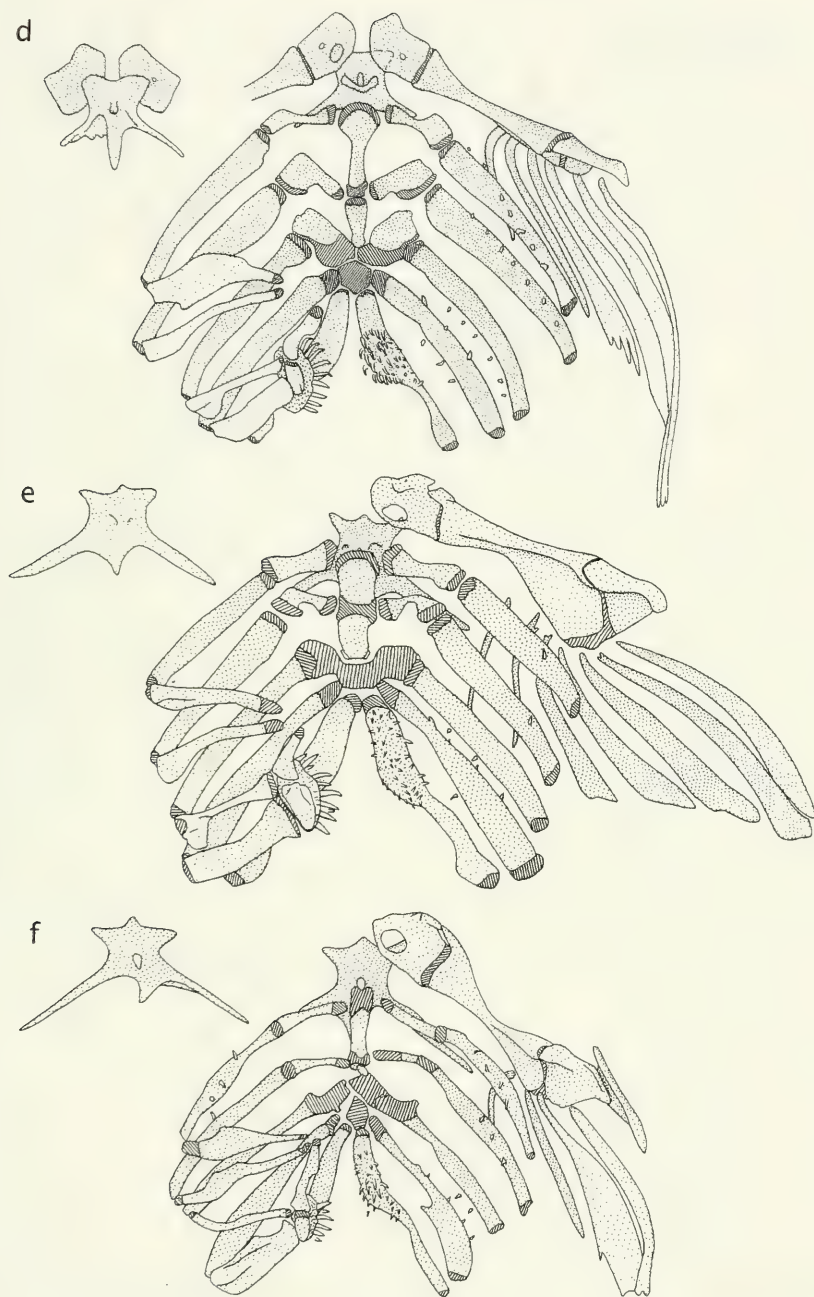


FIGURE 8 (cont.). d, *Zaireichthys camerunensis*, 30.0 mm, rivière Dele; e, *Zaireichthys mandevillei*, 22.3 mm, Banda; f, *Psammophyletria nasuta*.

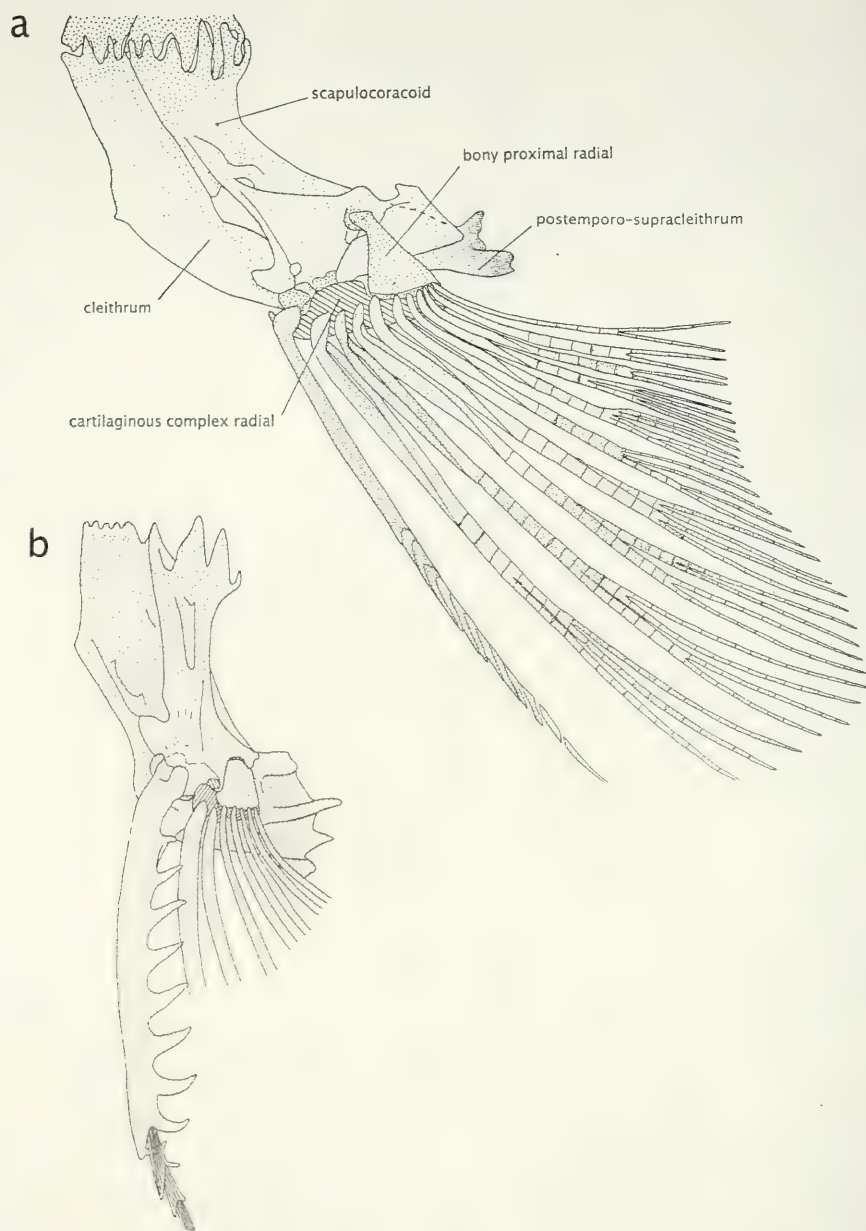


FIGURE 9. Leptoglaninae, paired fins and their girdles. a, *Leptoglanis xenognathus*; pectoral girdle and fin, 54.9 mm, Stanley Pool; b, *Zaireichthys zonatus*, pectoral girdle and fin (pectoral fin spine locked in erect position), 18.1 mm, Kinsuka.

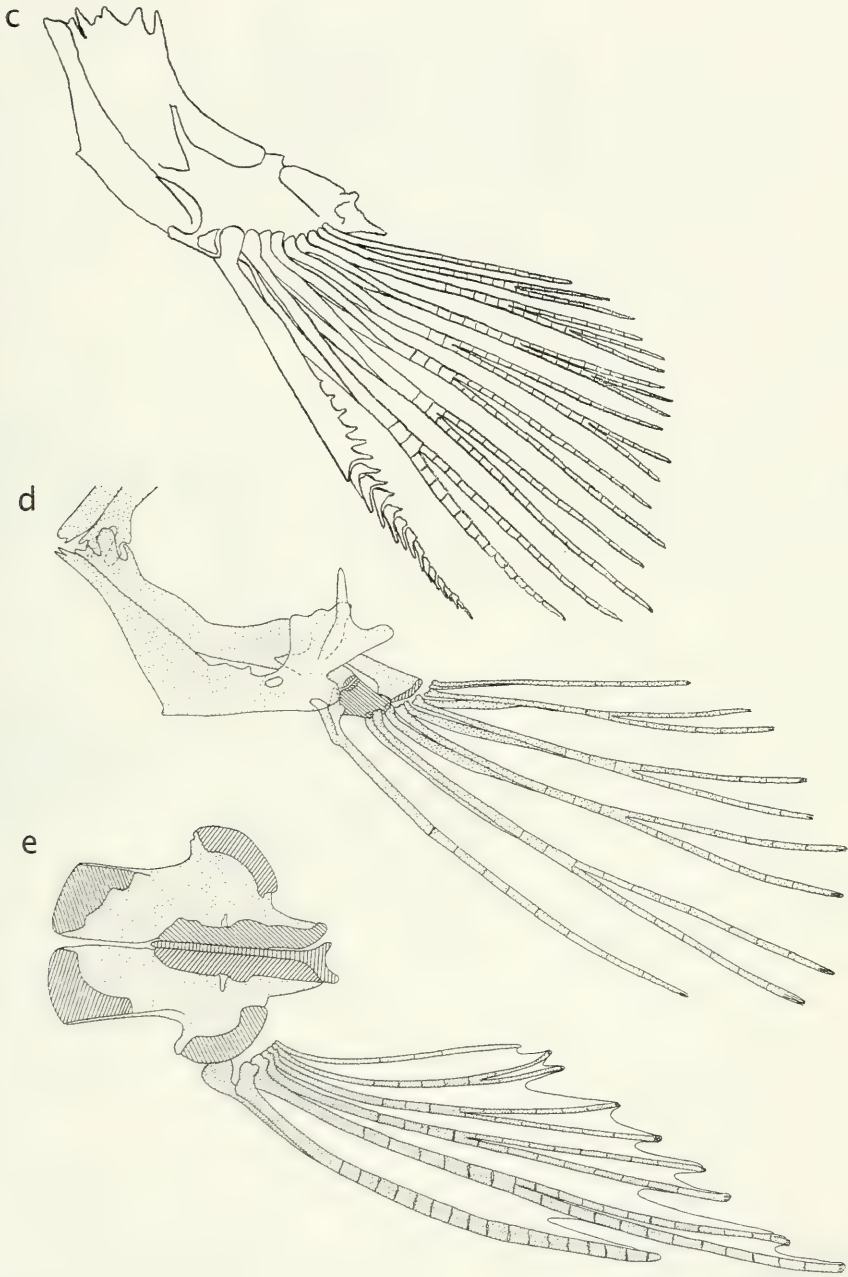


FIGURE 9 (cont.). c, *Tetracamphilus pectinatus*, pectoral girdle and fin, Luaia watershed; d, *Psammophyletria nasuta*, pectoral girdle and fin, 23.2 mm, Banda; e, *Dolicamphilus brevis*, pelvic girdle and fin, 31.2 mm, Stanley Pool.

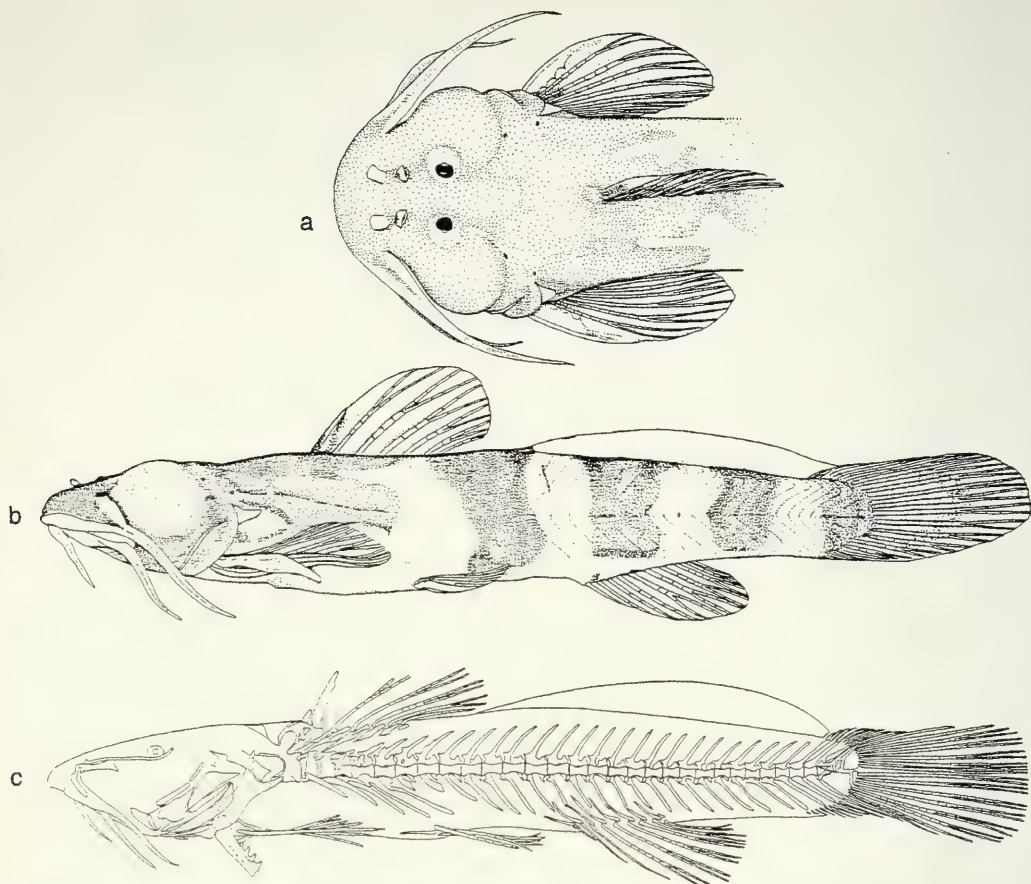


FIGURE 10. *Zaireichthys zonatus*, rapids below Stanley Pool. a, dorsal view of head (24.5 mm holotype); b, lateral view of body (24.5 mm holotype); c, lateral view of axial skeleton (18.1 mm paratype) (vertebrae 16+18=34).

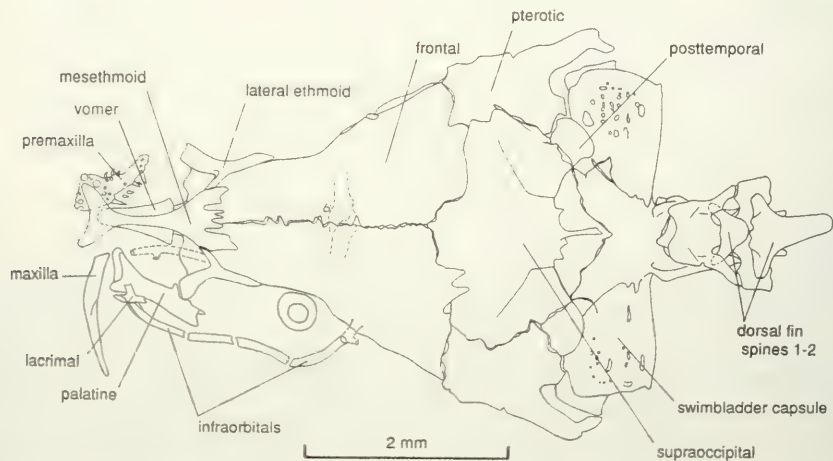


FIGURE 11. *Zaireichthys zonatus*, 18.1 mm, rapids below Stanley Pool. Dorsal view of cranium (with upper jaw).

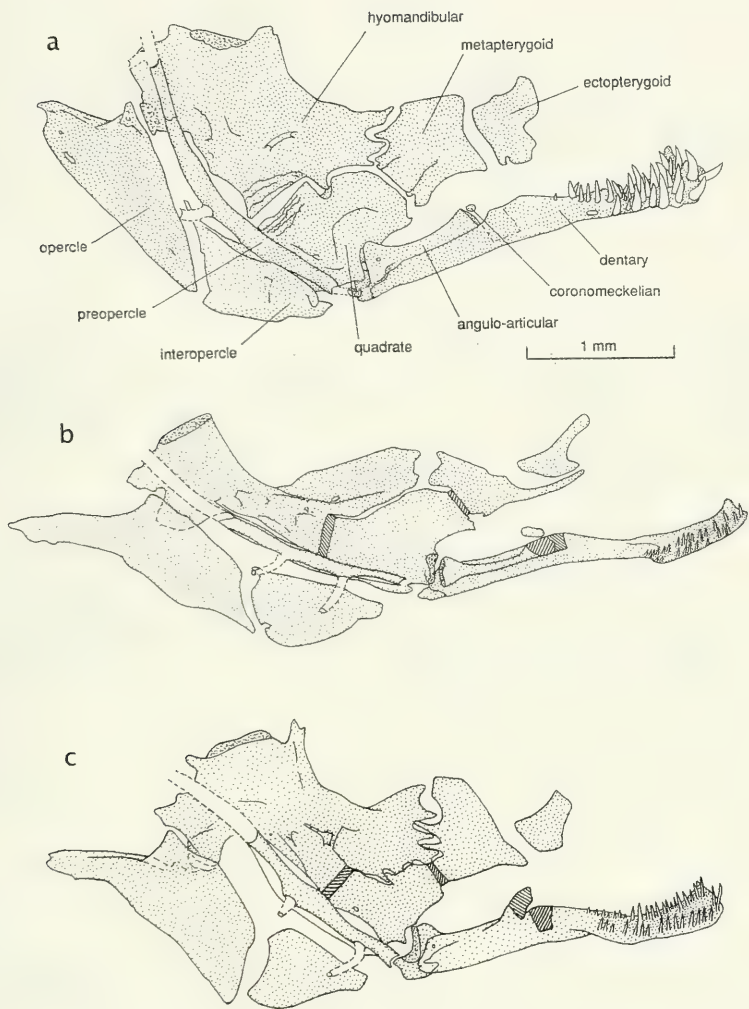


FIGURE 12. *Zaireichthys*. Suspensorium and lower jaw. a, *Z. zonatus*, 18.1 mm paratype, rapids below Stanley Pool; b, *Z. camerunensis*, 30.0 mm, rivière Dele; c, *Z. mandevillei*, 22.3 mm, Banda.

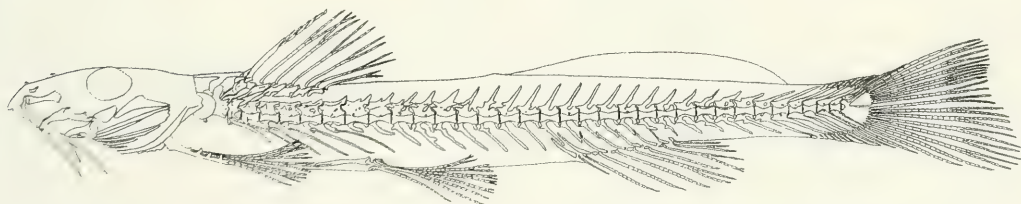


FIGURE 13. *Zaireichthys camerunensis*, 24.1 mm, rivière Dele. Axial skeleton (vertebrae 20+18=38).

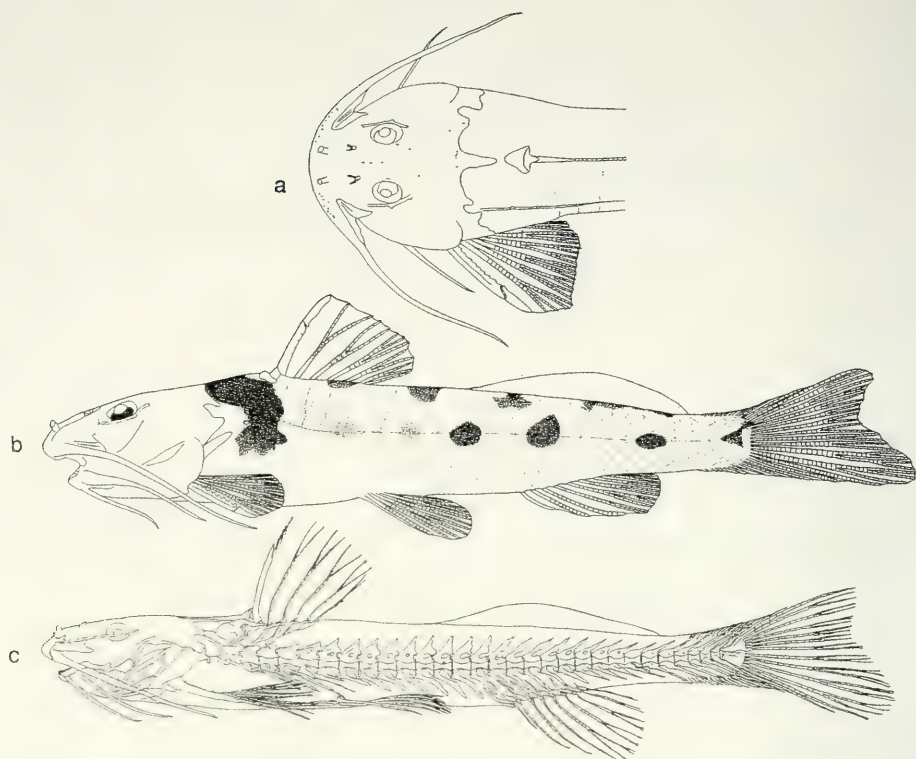


FIGURE 14. *Zaireichthys heterurus*. a, dorsal view of head, 31.4 mm holotype; b, lateral view, 31.4 mm holotype; c) lateral view of axial skeleton, 23.0 mm paratype (Lulindi) (vertebrae 16+17=33).

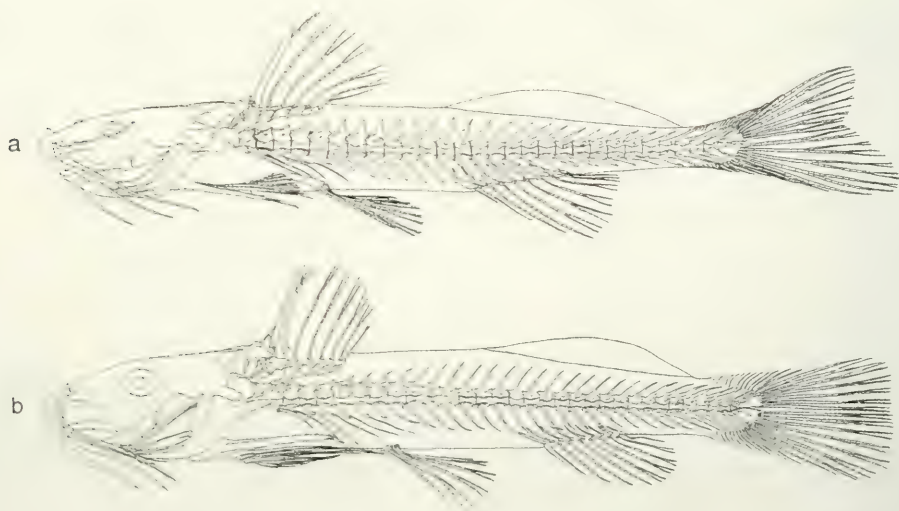


FIGURE 15. *Zaireichthys*, axial skeleton. a, *Z. mandevillei*, 21.5 mm, fleuve Ubangui near Banda (vertebrae 17+17=34); b, *Z. rotundiceps*, 24.1 mm, rivière Luwoyeye (vertebrae 18+17=35).

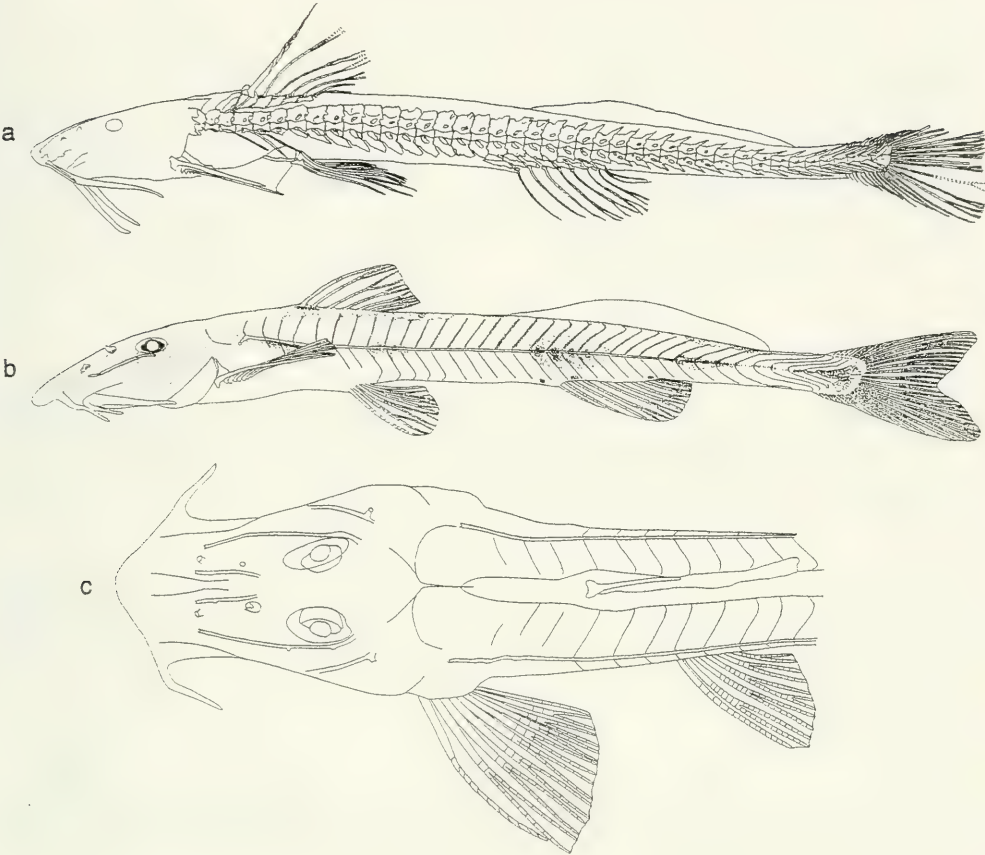


FIGURE 16. *Dolicamphilius*. a, *D. brieni*, 31.2 mm paratype, Stanley Pool, axial skeleton (vertebrae 18+24-43); b and c, *D. longiceps*, 42.2 mm holotype, Chutes Wagenia near Kisangani, lateral view; dorsal view of head and paired fins.

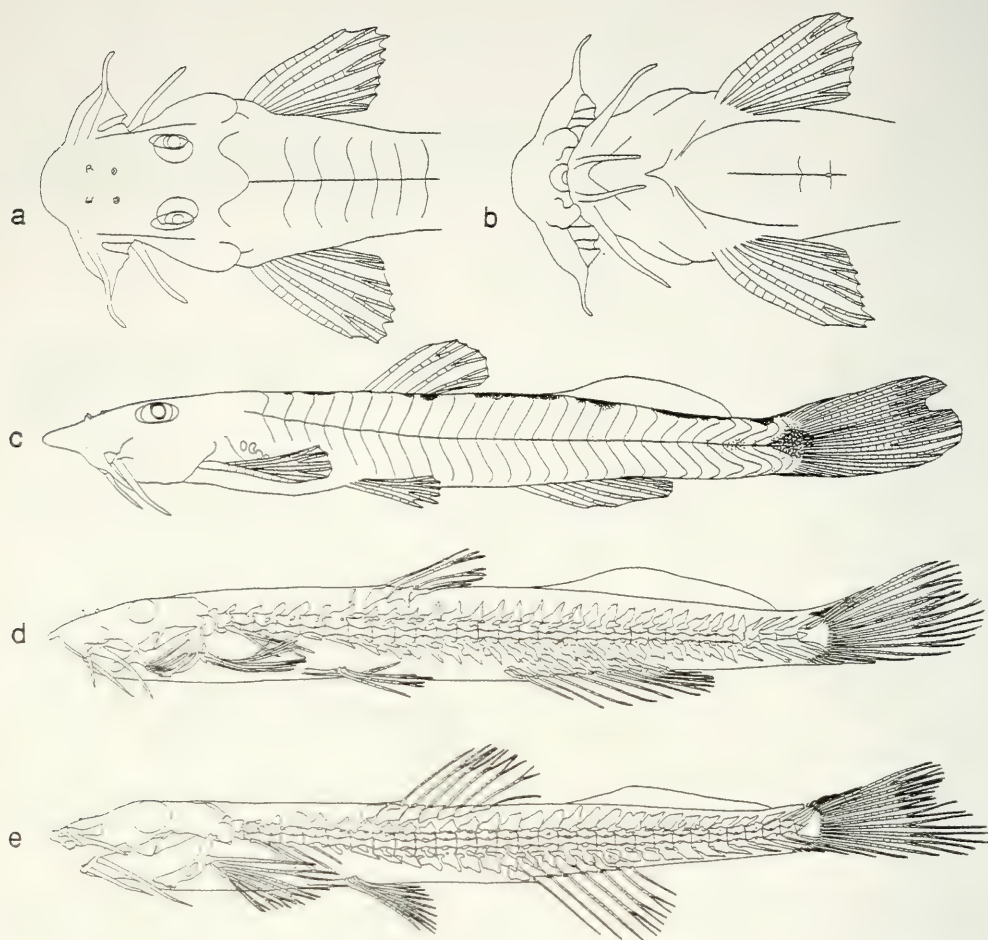


FIGURE 17. *Psammphyletria*. a-c, *P. nasuta*, 23.5 mm holotype, Ubangui, dorsal and ventral view of head, full lateral view; d, *P. nasuta*, 23.2 mm paratype, Ubangui, axial skeleton (vertebrae 18+18=36); e, *P. delicata*, 19.5 mm paratype, Stanley Pool, axial skeleton (vertebrae 17+16=33).

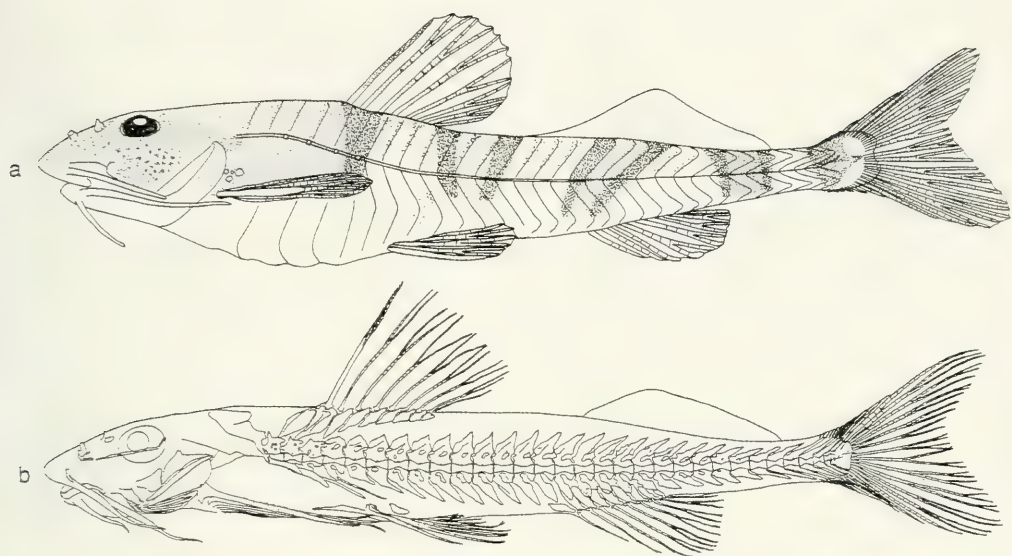


FIGURE 18. *Tetracamphilius pectinatus*. a, 33.7 mm gravid female holotype, LuaLa watershed, full lateral view; b, 28.3 mm paratype, LuaLa watershed, axial skeleton (vertebrae 18+18=36).

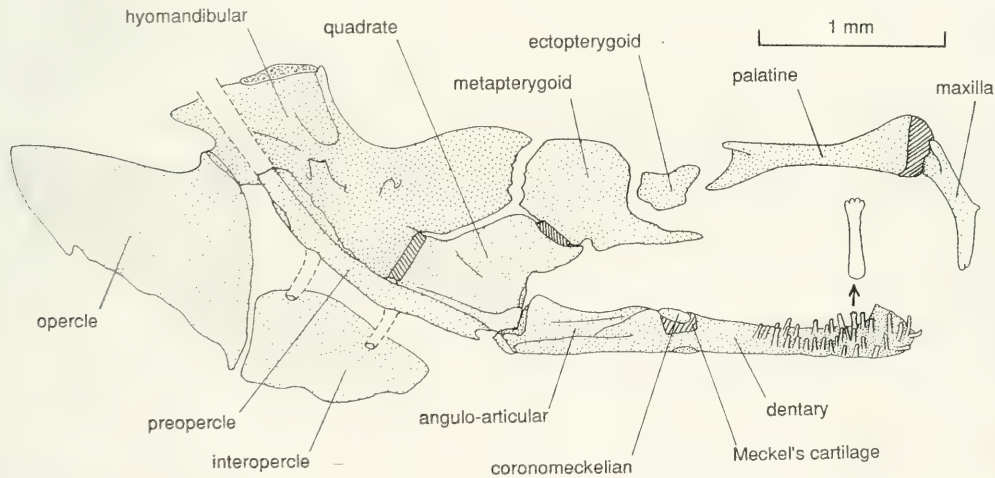


FIGURE 19. *Tetracamphilius angustifrons*, 22.3 mm, Ubangui, medial view of suspensorium and lower jaw.

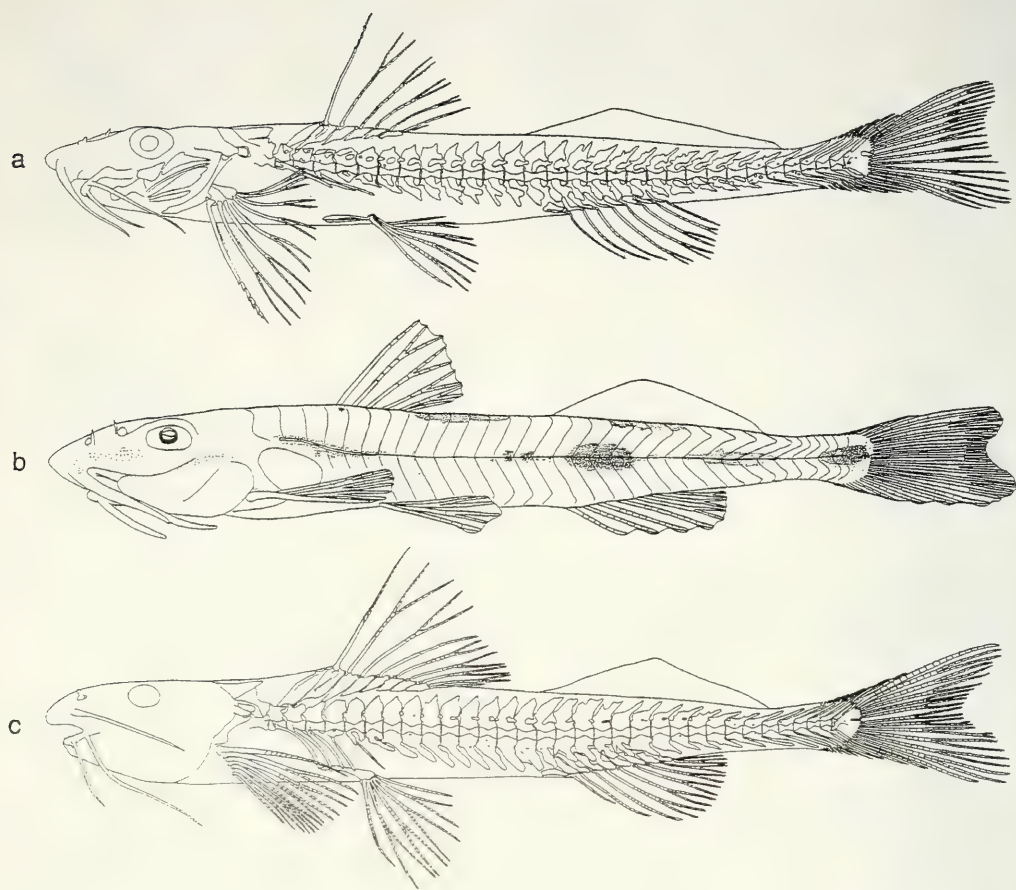


FIGURE 20. *Tetracamphilius*. a, *T. angustifrons*, 19.1 mm, Ubangui, axial skeleton (vertebrae $18+17=35$); b, *T. clandestinus*, 17.8 mm holotype, Ubangui, full lateral view; c, *T. notatus*, 25.9 mm, rivière Chinko, axial skeleton (vertebrae $19+18=37$).

Four Species of the Spider Genus *Steatoda* (Araneae: Theridiidae) from the Gaoligong Mountains, Yunnan, China

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Four species of the genus *Steatoda* are described from the Gaoligong Mountains region of Yunnan Province, China. Three new species, i.e., *Steatoda mainlingoides*, *Steatoda pardalia*, and *Steatoda tortoisea*, are described as is the previously unknown female of *Steatoda terostiosa* Zhu, 1998.

There are 16 species of the genus *Steatoda* known from China (Zhu 1998; Platnick 2002). In this paper we describe three new species and the hitherto unknown female of *Steatoda terostiosa* Zhu, 1998, which were collected in the Gaoligong Mountains by the first and second Sino-America expeditions, 1998 and 2000 respectively. The type specimens are deposited in the College of Life Science, Hunan Normal University, and some paratypes are in California Academy of Sciences.

MATERIALS AND METHODS

Specimens were fixed in 75% ethanol for 24 hours, then transferred to 85% ethanol for preservation. Vulvae were cleared in lactic acid. Examination was via an Olympus Tokyo BH-2 stereomicroscope. The following leg segment measurements were taken (femur, patella + tibia, metatarsus, and tarsus) and these measurements summed to give total length. All measurements are in mm. All length and width measurements are of the largest dimension of the structure in question. All scale bars equal 1.0 mm except figs. 22 and 23 in which they equal 0.1 mm.

ABBREVIATIONS USED.— AER=anterior eye row; ALE=anterior lateral eye, AME=anterior median eye, MOQ=median ocular quadrangle, MOQA=MOQ anterior, MOQP=MOQ posterior, PER=posterior eye row, PLE=posterior lateral eye, PME=posterior median eye, PME-PME=interval between PMEs, PME-PLE=interval between PME and PLE.

Steatoda mainlingoides, new species

Figures 1–8

TYPES.— Holotype ♀ and paratype ♂ from native forest at pass over Gaoligongshan at 2100m, Nankang, 36 air km SE TengChong, 24°50' N, 98°47' E, Baoshan Prefecture, Yunnan, China, collected 4–7 October 1998 by C. Griswold, D. Kavanaugh and C.-L. Long, deposited in HNU (No. 98-TC-7).

ETYMOLOGY.— The specific name refers to its similarity to *Steatoda mainlingensis* (Hu and Li 1987).

DIAGNOSIS.— This new species is similar to *Steatoda mainlingensis*, but can be distinguished by: (1) the narrow median markings on the abdominal dorsum (Fig. 1), whereas that of *S. mainlin-*

gensis has broad median and posterior triangles (Zhu 1998: fig. 229A); (2) the subtriangular epigynum (Fig. 5), whereas that of *S. mainlingensis* is ellipsoid (Zhu 1998: fig. 229B); (3) the vulval tube is longer and curved (Fig. 8), whereas that of *S. mainlingensis* is very short and straight; and (4) the S-shaped conductor and short embolus of male palpal organ (Figs. 2, 3) are very different from *S. mainlingensis* (Zhu 1998: fig. 229D, E).

FEMALE.— Carapace and sternum black. Carapace integument with small punctures along grooves, margins ornamented with hairs. Cervical and radial grooves distinct, caput somewhat elevated. Fovea transversely concave. AER recurved, PER almost straight. Chelicerae, palpi, endites and leg femora black-brown, other leg segments red-brown. Chelicerae with fang orange-yellow, promargin with two teeth and no retromarginal tooth (Fig. 7). Abdominal dorsum deep grayish black, covered with white-yellow hairs; with white forming a crescent pattern anteriorly, a series of small markings on the median line, and two pairs of markings laterally (Fig. 1). Center region of venter grayish black, with yellow-brown striae laterally. Spinnerets brown to yellow-brown, surrounded by white membranous ring. Epigynum subtriangular (Fig. 5), protruding posteromedially (Fig. 6), spermathecae ovoid, connective tube curved (Fig. 8).

MALE.— Body coloration, patterns and eye arrangement as in female, only leg formula differs. Palpal bulb with S-shaped conductor (Fig. 3) enlarged at distal end (Fig. 2), embolus conical, tapered (Figs. 2, 4).

MEASUREMENTS.— ♀ total length 7.45–11.20. ♂ 6.20–7.50. Holotype ♀ total length 9.90. Carapace length 2.70, width 2.00; abdomen length 6.50, width 5.70. Eye sizes and intervals: AME=ALE=PME=PLE 0.25; AME-AME =AME-ALE 0.05; PME-PME= PME-PLE 0.15; MOQ length 0.44, anterior width 0.50, posterior width 0.55; CH 0.55. Leg measurements: ♀ I: 4.30 + 4.75 + 3.50 + 1.70 = 14.15, II: 3.90 + 3.50 + 2.50 + 1.40 = 11.30, III: 2.60 + 2.90 + 2.00 + 1.20 = 8.70, IV: 3.50 + 4.50 + 3.30 + 1.80 = 13.10; leg formula I, IV, II, III. % I: 5.30 + 5.50 + 4.10 + 1.90 = 16.80, II: 5.00 + 4.50 + 3.30 + 1.80 = 14.40, III: 3.50 + 3.50 + 2.50 + 1.50 = 11.00, IV: 4.70 + 4.90 + 3.90 + 1.90 = 12.40; leg formula I, II, IV, III.

MATERIAL EXAMINED

CHINA.— Yunnan: Baoshan Prefecture: pass over Gaoligongshan at 2100m. Nankang, 36 air km SE TengChong, 24°50' N, 98°47' E, native forest, 4–7 October 1998, C. Griswold, D. Kavanaugh and C.-L. Long (holotype ♀, paratype ♂, HNU No. 98-TC-7); native forest at 2300m, Luoshuidong, 28 air km E TengChong, 24°57' N, 98°45' E, flight trap over stream, 26–31 October 1998, C. Griswold, D. Kavanaugh and C.-L. Long (1 ♀ 1 ♂ CAS, 2 ♀ HNU No. 98-TC-6). Nujiang Prefecture: Nujiang State Nature Reserve, Qiqi He, 9.9 air km W Gongshan, 27°43' N, 98°34' E, 2000m, 9–14 July 2000, H.-M. Yan, D. Kavanaugh, C.E. Griswold, H.-B. Liang, D. Ubick and D.-Z. Dong (1 ♂ subadult HNU No. 00-QF-56).

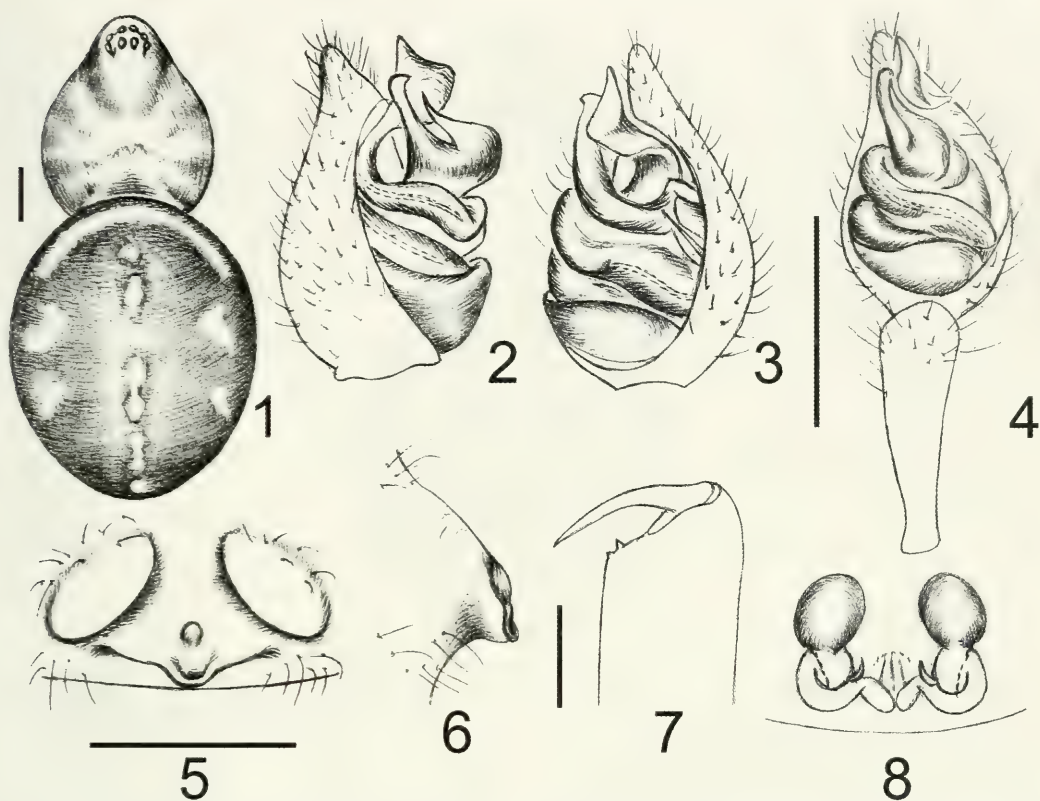
Steatoda pardalia, new species

Figures 9–13

TYPES.— Holotype ♀ and paratype ♂ from Gaoligongshan in Nujiang State Nature Reserve at 2775m near No. 12 Bridge Camp area, 16.3 air km W of Gongshan, 27°43' N, 98°30' E, Nujiang Prefecture, Yunnan Prov., China, collected 15–19 July 2000 by H.-M. Yan, D. Kavanaugh, C.E. Griswold, H.-B. Liang, D. Ubick and D.-Z. Dong, deposited in HNU (No. 00-QD-12).

ETYMOLOGY.— The specific name refers to the abdomen dorsal pattern, which is similar to leopard's spots (Fig. 11).

DIAGNOSIS.— This new species is very distinct from other Chinese *Steatoda*. The pale network

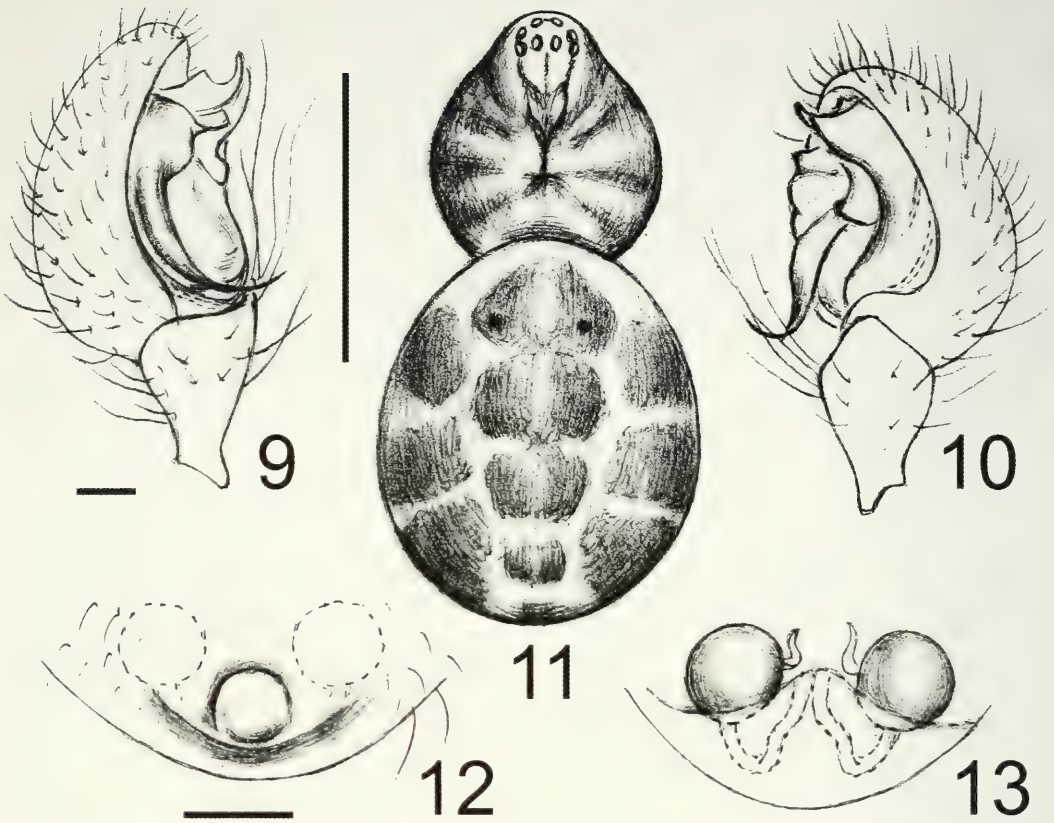


FIGURES 1-8. *Steatoda mainlingoides*, new species. 1, 5-8. Female. 2-4. Male left pedipalpus. 1. Habitus, dorsal. 2. Prolateral. 3. Retrolateral. 4. Ventral. 5. Epigynum, ventral. 6. Epigynum, lateral. 7. Chelicera, retrolateral. 8. Vulva, dorsal.

pattern on the abdominal dorsum (Fig. 11) is somewhat similar to *Steatoda tortoisea*, new species (Fig. 21), but *S. pardalia* can be distinguished by (1) lacking the epigynal scape (Fig. 12) characteristic of *S. tortoisea* (Fig. 22) and (2) the thick, meandering copulatory duct (Fig. 13) that differs from the short, curved duct of *S. tortoisea* (Fig. 23).

FEMALE.— Carapace brown, margin black-brown, lateral margins smooth. Cervical groove indistinct, head region slightly elevated. AER procurved, PER slightly procurved. Fovea transversely concave, two V-shaped markings behind eye region to fovea. Sternum brown, with hairs. Chelicera brown, promargin having three teeth and no retromarginal tooth. Endite and labium brown proximally, milk white distally. Palpi and legs yellow-brown but middle section of femora and distal ends of patellae and tibiae black-brown. Abdomen ovoid, dorsum gray-black, clothed with pale network pattern, dividing the dorsum into 11 black patches, five in middle and three on each side (Fig. 11). Abdomen brown ventrally with one pair of white scale markings. Periphery of spinnerets black-brown, colulus distinct, color same as spinnerets. Posterior margin of epigynum procurved, with thickened rim, rim of atrium protruding (Fig. 12). Spermathecae spherical, connective duct V-shaped, inner arm extending forward to atrium (Fig. 13).

MALE.— Habitus as in female except lateral margins of carapace serrate. Palpal bulb from prolateral view (Fig. 9) with anterior part of median apophysis robust, cubical, posteriorly elongate, curved into a sickle-shaped part, from retrolateral view (Fig. 10), embolus short, conical, accompanied by the conductor on its right side.



FIGURES 9-13. *Steatoda pardalia*, new species. 9, 10. Male left pedipalpus. 11-13. Female. 9. Prolateral. 10. Retrolateral. 11. Habitus, dorsal. 12. Epigynum, ventral. 13. Vulva, dorsal.

MEASUREMENTS.— ♀ total length 2.93. Carapace length 1.70, width 0.96; abdomen length 1.76, width 1.43. ♂ total length 2.85. Carapace length 1.11, width 1.00; abdomen length 1.74, width 1.36. Eye sizes and intervals: ♀/♂: AME=ALE 0.10, PME=PLE 0.11; AME-AME 0.04, AME-ALE 0.03, PME-PME 0.09, PME-PLE 0.04; MOQ length= anterior width 0.20< posterior width 0.23, carapace height ♀ 0.26, ♂ 0.23. Leg measurements: ♀ I: $1.20 + 1.34 + 0.89 + 0.69 = 4.12$, II: $1.00 + 1.14 + 0.71 + 0.63 = 3.48$, III: $0.91 + 0.94 + 0.54 + 0.60 = 2.99$, IV: $1.14 + 1.30 + 0.80 + 0.63 = 3.87$; leg formula I, IV, II, III. ♂ I: (missing) + $1.57 + 1.49 +$ (missing) = (not calculated), II: $1.29 + 1.11 + 0.80 + 0.59 = 3.79$, III: $1.06 + 0.97 + 0.67 + 0.53 = 3.23$, IV: $1.34 + 1.29 + 0.81 + 0.68 = 4.12$; femur I probably longer than femur IV, leg formula probably I, IV, II, III.

DISTRIBUTION.— Yunnan, China.

MATERIAL EXAMINED

Only the types.

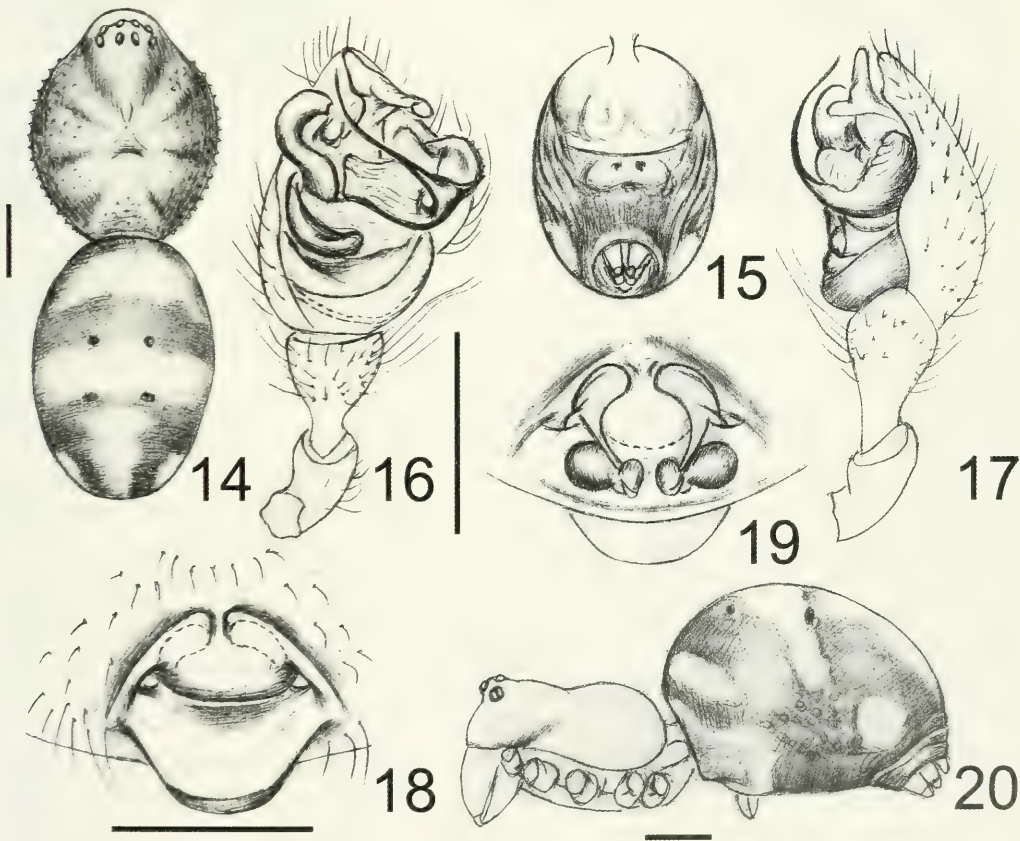
Steatoda terastiosa Zhu, 1998

Figures 14–20

Steatoda terastiosa Zhu 1998:347, fig. 232A–C. Platnick 2002.

NOTE.— The male was described by Zhu (1998:346). We describe the female for the first time.

FEMALE.— Carapace, sternum, endites and labium flaming red (Fig. 20). Carapace clothed with short black hairs that are denser on the lateral margins than on the median. Cervical and radial grooves distinct, darker, caput elevated, with long black hairs. AER recurved, PER slightly recurved; bases of ALE and PLE contiguous. Clypeus protruding. Fovea shallow, subtriangular. Sternum with dense black hairs, triangular, posterior end long and pointed between coxae IV. Chelicerae red brown, with two small promarginal teeth and no retromarginal tooth. Distal ends of labium and endite pale white, endite with black margin. Palpal trochanter and coxa and trochanters of legs flaming red, remaining segments black-brown. Abdomen subspherical, dorsum brown with three distinct pairs of muscular depressions, the second largest and third smallest; white forming two transverse bands on anterior half, one longitudinal median band and one pair of round marks laterally on the posterior half (Fig. 14). Abdominal venter with large white, square mark before spinnerets, gray patches beside white mark and surrounding spinnerets; base of anal tubercle with regularly arranged brown hairs. Epigynum trapezoid, an ellipsoid atrium on anterior half, the pos-



FIGURES 14–20. *Steatoda terastiosa* Zhu, 1998. 14–17. Male. 18–20. Female. 14. Habitus, dorsal. 15. Abdomen, ventral. 16. Palpal organ, ventral. 17. Palpal organ, retrolateral. 18. Epigynum, ventral. 19. Vulva, dorsal. 20. Habitus, lateral.

terior half recurved, thickened, with black margin (Fig. 18). Spermathecae spherical, connecting duct anterior, funnel-shaped (Fig. 19).

MALE.— (Figs. 14–17): Body smaller than female; for description see Zhu (1998:347, fig. 232A–C).

MEASUREMENTS.— ♀ total length 11.43. Carapace length 3.43, width 2.97; abdomen length 5.77, width 5.09. Eye sizes and intervals: AME=ALE 0.17; AME-AME 0.11; AME-ALE 0.20. PME 0.19; PLE 0.21, PME-PME 0.14, PME-PL 0.23, MOQ length 0.40, anterior width 0.43, posterior width 0.47; carapace height 0.29. Leg measurements: I: $4.06 + 4.69 + 3.57 + 1.83 = 14.15$, II: $3.43 + 3.60 + 2.71 + 1.54 = 11.28$, III: $2.91 + 2.86 + 2.09 + 1.31 = 9.17$, IV: $4.37 + 4.63 + 3.31 + 1.66 = 13.97$; leg formula: I, IV, II, III.

DISTRIBUTION.— Yunnan, China.

MATERIAL EXAMINED

CHINA.— Yunnan Province: **Kunming Prefecture:** Kunming, Heilongtan District, Kunming Institute of Botany botanical gardens, $25^{\circ}08' \text{ N}$, $102^{\circ}45' \text{ E}$, 1950m, 21–23 June 2000, D. Kavanaugh and C.E. Griswold (2 ♀ HNU No. 00-KB-10, 1 ♀ 1 ♂ CAS).

Steatoda tortoisea, new species

Figures 21–23

TYPES.— Holotype ♀ from Nujiang, $30^{\circ}06' \text{ N}$, $97^{\circ}12' \text{ E}$, Yunnan Province, China, collected 30 July 1981 Jia-Fu Wang, deposited in HNU (No. 97-102). Paratype, 1 ♀ subadult, from Liuku, Nujiang Prefecture, Lushui Co., Liuku Township, 800m, $25^{\circ}52' \text{ N}$, $98^{\circ}51' \text{ E}$, Yunnan Prov., China, collected 25–26 June 2000 by D. Kavanaugh, C.E. Griswold, H.-M. Yan and D. Ubick, deposited in HNU (No. 00-LK-9).

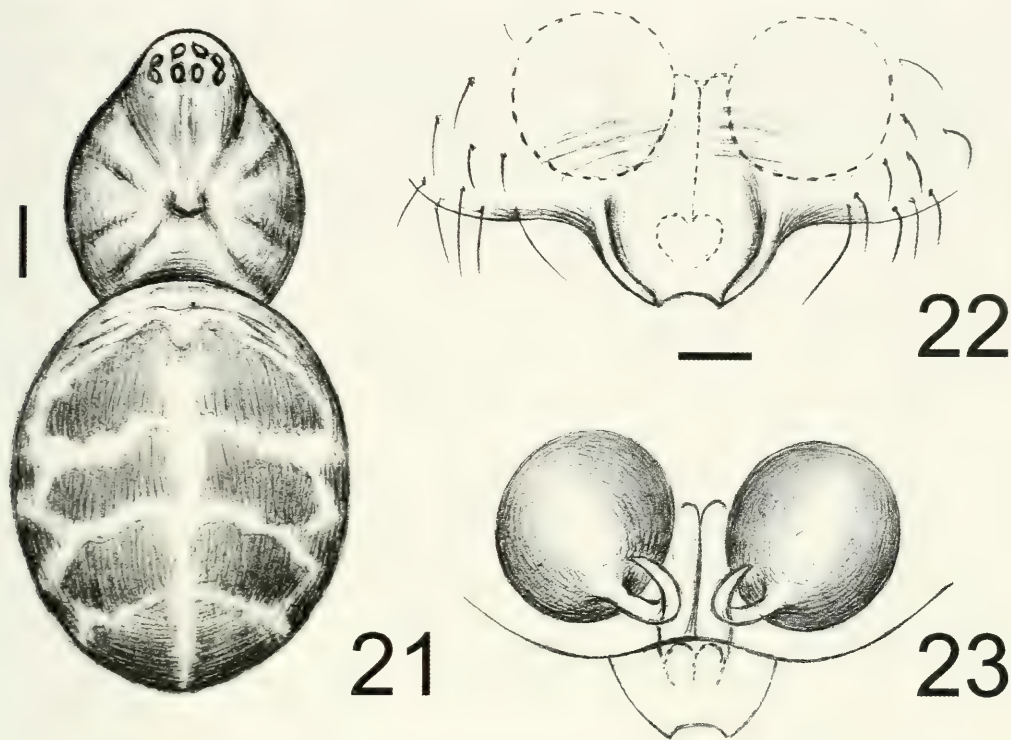
ETYMOLOGY.— The specific name is derived from the tortoise shell-like pattern of the abdomen dorsum (Fig. 21).

DIAGNOSIS.— The vulva is most similar to *Steatoda cingulata* (Thorell 1890), but *S. cingulata* lacks the scape characteristic of *S. tortoisea* (Fig. 22), and the abdominal patterns of these two species are distinct.

FEMALE.— Carapace pear-shaped, red-brown to black-brown. Cervical groove clear, caput elevated. AER strongly recurved, PER almost straight. ALE and PLE contiguous at base. Fovea transversely concave, radial grooves indistinct. Thoracic region clothed with red-brown hairs. Sternum, chelicerae, endites and labium red-brown, chelicerae with 2 promarginal teeth and no retromarginal tooth. Labium wider than long. Palpi and legs red-brown to black-brown. Abdominal dorsum ovoid, black-brown, with tortoise shell-like pattern, three pairs of distinct muscle impressions, the second pair largest (Fig. 21). Abdominal venter brown, with a square white marking behind epigastric groove and a pair of pale subaxial striae, with ring-like mark surrounding the spinnerets. Epigynum with scape, its lateral margins turned up towards the median (Fig. 22). Vulva with two large spherical spermathecae (Fig. 23).

MALE.— Unknown.

MEASUREMENTS.— Holotype ♀ total length 9.27; carapace length 3.97, width 3.76; abdomen length 5.51, width 4.55. Eye sizes and intervals: AME=ALE=PME=PLE 0.23; AME-AME =PME-PLE 0.09; AME-ALE 0.06; PME-PLE 0.13; MOQ length 0.51, anterior width 0.49, posterior width 0.46; carapace height 0.17. Leg measurements: I: $4.50 + 5.20 + 3.50 + 1.40 = 14.60$, II: $3.50 + 3.50 + 2.60 + 1.00 = 10.60$, III: $2.60 + 2.50 + 2.05 + 1.05 = 8.20$, IV: $3.90 + 4.55 + 3.40 + 1.05 = 12.90$;



FIGURES 21–23. *Steatoda tortoisea*, new species, holotype female. 21. Habitus, dorsal. 22. Epigynum, ventral. 23. Vulva, dorsal.

leg formula: I, IV, II, III.

DISTRIBUTION.— Yunnan, China.

MATERIAL EXAMINED

Only the types.

ACKNOWLEDGMENTS

Support for this research came from the China Natural History Project, the Foundation of Natural Science of the Education Department of Hunan Province (China), the California Academy of Sciences and the US National Science Foundation grant DEB BSI 074632456. We are grateful to Prof. Heng Li and Prof. Chun-Lin Long for support for the 1998 and 2000 Sino-American-expeditions to the Gaoligong Mountains and to Prof. Zhi-ling Dao for organizing the expeditions. We also thank all the collectors who did the difficult fieldwork and provided us with specimens. This is Scientific Contribution no. 23 from the California Academy of Sciences Center for Biodiversity Research and Information (CBRI) and contribution no. 16 from the China Natural History Project (CNHP).

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A New Species of *Bufo* (Anura: Bufonidae) from Myanmar (Burma), and Redescription of the Little-Known Species *Bufo stuarti* Smith 1929

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A new species of *Bufo* is described from the Rakhine State near the Rakhine Yoma Elephant Range in western Myanmar. This species is morphologically similar to *Bufo melanostictus*, but it is distinguished by its smaller body size at maturity, the bright breeding coloration of the males, and its advertisement call. The new species brings the total number of bufonid species known to occur in Myanmar to seven; all are referred to the genus *Bufo*. Additionally, *Bufo stuarti* Smith 1929 is redescribed from the type specimen and more recently acquired specimens from the vicinity of the type locality. Lastly, a key to the *Bufo* of Myanmar is provided.

Recent fieldwork in western Myanmar has resulted in the discovery of a new species of bufonid that appears to be closely related to *Bufo melanostictus*. Further, the senior author during a visit to the Zoological Survey of India, Calcutta was afforded the opportunity to examine the type specimen of *Bufo stuarti*, one of the few southern Asian bufonid types that was not examined and redescribed by Dubois and Ohler (1999). *Bufo stuarti* is a little known species that has been reported only from northern Myanmar and Assam, India (Smith 1929; Frost 2002). Because of the dearth of information on the species, and because we have obtained new material from the vicinity of the type locality, "Putao Plain, N.E. Burma," the holotype is herein redescribed with additional notes based on our newly acquired materials.

MATERIALS AND METHODS

Animals were collected by hand by the authors. Latitude and longitude were recorded using a Garmin 12 GPS with the datum set to WGS 84. Animals were euthanized and then preserved in 10% buffered formalin before being transferred to 70% ethanol. Specimens are deposited in the California Academy of Sciences (CAS). Museum symbolic codes follow Leviton et al. (1985).

Measurements were taken using digital calipers to the nearest 0.1 mm (instrumental error of \pm 0.2 mm). Measurements follow Dubois and Ohler (1999). The following measurements were used in the analysis: snout vent length (SVL), head length (HL), head width (HW), jaw to nares length (MN), jaw to eye (MPE), jaw to front of eye (MAE), distance between front of eyes (IFE), distance between back of eyes (IBE), internarial space (IN), distance from eye to nares (EN), snout length (SL), nostril to tip of snout (NS), tympanum diameter (TympD), eye to tympanum distance (ET), forelimb length (FLL), hand length (HAL), first finger length (FFL), third finger length (TFL), tibia length (TL), foot length (FL), femur length (F), fourth toe length (FTL), inner metatarsal

tubercle length (IMT), outer metatarsal tubercle length (OMT), parotoid length (ParL), and parotoid width (ParW).

Ranges and means are provided in Table 1 for all of the above measurements and ratios for HL/SVL, HW/SVL, ParW/ParL, FEM/SVL, TL/FEM, OMT/IMT, EN/MN, ParL/SVL, ParW/HW are included.

Statistical analysis was carried out on measurements recorded for the lectotype of *Bufo melanostictus* (ZMB 3462), given in Dubois and Ohler 1999, and from seventeen *Bufo melanostictus* from throughout Myanmar (N=18), the new species (N=5), and *Bufo stuarti* (N=3) in the collections of the California Academy of Sciences. To eliminate the need for allometric corrections (Hayek et al. 2001), only adult specimens were included in analysis. SPSS Base 10.0 for Macintosh (SPSS Inc. 1999) was used for statistical analysis.

Calls were analyzed using Signal 3.1/RTSD 1.1 (Engineering Design 1999) software and a Kay Elemetrics DSP SonaGraph model 5500.

SPECIES DESCRIPTION

Bufo crocus Wogan sp. nov.

Figures 1-3

HOLOTYPE.— CAS 220192 adult male from Myanmar, Rakhine State, Gwa Township, Rakhine Yoma Elephant Sanctuary, Ye Bya Stream Camp, 17°41'47.0" N, 94°38'48.7" E., elev. 83 m, collected 25 April 2001 by J.B. Slowinski, G.O.U. Wogan, Htun Win, Thin Thin and Kyi Soe Lwin.

PARATYPES (4 specimens).— CAS 220193–220195 from Myanmar, Rakhine State, Gwa Township, Rakhine Yoma Elephant Sanctuary, Ye Bya Stream Camp, 17°41'47.0" N, 94°38'48.7" E, collected 25 April 2001 by J. B. Slowinski, G.O.U. Wogan, Htun Win, Thin Thin and Kyi Soe Lwin. CAS 220331 from Myanmar, Rakhine State, Gwa Township, Rakhine Yoma Elephant Sanctuary, 17°42'14.0" N, 94°38'54.3" E, collected 26 April 2001 by J.B. Slowinski, G.O.U. Wogan, Htun Win, Thin Thin and Kyi Soe Lwin.

DIAGNOSIS.— A moderately sized *Bufo*, snout-vent length in males 54.6–59.1 mm females 67.6–67.8 mm, body stout, cornified canthal, pre-orbital and post-orbital crests present, and weakly defined uncornified parietal ridges (terminology follows Dubois and Ohler 1999). *Bufo crocus* possesses a protruding snout and a subterminal mouth and its head is wider than long. It has prominent singular subarticular tubercles. Breeding males are bright yellow in coloration.

DESCRIPTION OF HOLOTYPE (Fig. 1).— For ease in comparison with other Asian bufonids, the description follows the format of Dubois and Ohler (1999).

(A) **SIZE AND GENERAL ASPECT:** (1) specimen of medium size (SVL 54.6 mm).

(B) **HEAD:** (2) head width (18.7 mm) is greater than head length (16.1 mm), (3) snout protruding (SL 5.9 mm), (4) canthus rostralis distinct, (5) interorbital space concave, distance between front of eyes (7.9 mm) slightly greater than half of distance between back of eyes (15.1 mm), (6) nostrils rounded, closer to tip of snout (NS 2.1 mm) than to eye (3.8 mm), (7) pupil horizontal, (8) tympanum (TYMPD 2.2 mm) ovular, verticle, distinct and located 1.0 mm from eye (ET), (9) pineal ocellus absent, (10) vomerine ridge absent, (11) tongue longer than wide, and unnotched, (12) supratympanic fold absent, (13) parotoid glands present, oval, prominent, and less than twice as long (ParL 10.7 mm) as wide (ParW 5.7 mm), (14) canthal, preorbital, supraorbital, postorbital, supratympanic and (faint) parietal ridges present.

(C) **FORELIMBS:** (16) forelimb (12.7 mm) longer than hand (11.0 mm), enlarged, (17) fingers long, (18) relative length of fingers, shortest to longest: II<I<IV<III, (19) tips of fingers rounded,



FIGURES 1–2. (1) *Bufo crocus*, holotype, CAS 220192 male; (2) *Bufo crocus*, paratype, CAS 220193 female. Photos by Hla Tun.

not enlarged, without grooves, (20) fingers without dermal fringe, webbing absent, (21) subarticular tubercles prominent, rounded, single, (22) prepollex oval; one palmar tubercle large prominent and reniform; numerous small rounded and pointed tubercles covering palm and fingers.

(D) HINDLIMBS: (23) femur (20.3 mm) and tibia (20.4 mm) of approximately equal length, (24) toes long, toe IV half the length of the femur, (25) relative length of toes shortest to longest $I < II < V < III < IV$, (26) tips of toes rounded, not enlarged, without grooves, (27) webbing (follows Myers and Duellman, 1982) $I2-3III1-2 \ 1/2III11/2-3 \ 1/2IV3 \ 2/3-1 \ 1/2V$, (28) dermal fringe along toe V absent, (29) subarticular tubercles more prominent than the supernumerary tubercles, (30) inner metatarsal tubercle prominent and round (1.5 mm), (31) tarsal fold absent, (32) outer metatarsal tubercle prominent (absent from left foot), numerous tubercles on the plantar surface of the foot and toes.

(E) SKIN: (33) anterior of snout and region between eyes and anterior portion of dorsum with dense flattened keratinized warts, posterior portion of dorsum with less dense keratinized flattened warts, flank with scattered glandular warts, (34) dorso-lateral folds absent, (35) forelimb, tarsus, and leg with flattened keratinized warts, tips of fingers and toes keratinized, (36) row of keratinized warts along lower lip, rest of ventral side with glandular flattened warts, not spiculate, (37) parotoid glands present.

(F) COLORATION IN PRESERVATIVE: (38) dorsal and lateral parts of head and body are light tan, keratinized warts are black as are ridges, (39) dorsal parts of limbs are light tan, keratinized warts are black, (40) ventral parts of head body and limbs are light with indistinct dark mottling, throat region blue.

COLORATION IN LIFE: (38B) dorsal and lateral parts of head and body are bright yellow with black keratinized warts, (39B) dorsal parts of limbs are bright yellow with black keratinized warts, tips of toes and fingers are black, (40B) ventral parts of head body and limbs are white with pink, throat yellow.

(G) MALE SEXUAL CHARACTERS: (41) nuptial spines on prepollex and fingers I and II, dorsal side of finger I covered entirely, (42) inner openings of vocal sac present, round, (43) forearm enlarged.

VARIATION WITHIN THE PARATYPIC SERIES.— The tubercles on the hands and feet vary in number and density and prominence. The palmar tubercle is reniform or round. The subarticular tubercles of CAS 220195 are more prominent than those of the holotype.

SKIN: All of the paratypes agree with the description of the holotype, but the degree of black keratinizations varies. CAS 220193 and 220194 have spiculate warts on the flanks and ventral side.



FIGURE 3. Maps with collection localities of *Bufo crocus* and *Bufo stuarti*. Collection localities of holotypes are indicated by stars.

In both of these specimens, the ventrum is almost entirely covered in minute spiculate asperities.

COLORATION: The other males of the paratype series agree with the coloration of the holotype except that they are a slightly darker tan shade, and the degree of mottling on the ventrum varies. The females of this species differ markedly in coloration. In preservative (38) dorsal and lateral parts of the head and body are tan to brown, in CAS 220193 there is an indistinct pattern of black mottling intermixed with an umber background, keratinized warts are black as are ridges, (39) dorsal parts of limbs are brown, (40) ventral parts of head, body and limbs are light with dark mottling, the mottling varies in degree

In life (38B) the dorsal and lateral parts of head and body are brown with black and red marbling, (39B) dorsal parts of limbs are light brown, (40B) ventral parts of head, body, and limbs are white with dark mottling.

NATURAL HISTORY.— Description of habitat: *Bufo crocus* is found in primary evergreen forest. Thus far, it is known only from two localities in the Rakhine Division in Myanmar. It is expected that as additional surveys are carried out the range will be extended, however, surveys conducted to the north and south of this region have not produced any individuals of this species.

REPRODUCTIVE BEHAVIOR.— Males in breeding condition are bright yellow. This degree of sexual dichromatism has been observed in several other species of *Bufo*: *B. macrotis* (Taylor 1962).

B. kisoensis (Drewes and Vindum 1994), *B. periglenes* (Savage 1966), *B. leutkeni* (Villa 1972), *B. peripatetes* (Savage and Donnelly 1992), and *Bufo stuarti* (Smith 1940). Drewes and Vindum (1994) suggest that in voiced species (as is *B. crocus*) it is unlikely that the dichromatism plays a roll in mate selection.

Breeding occurs in congruence with the earliest rains of the monsoons, generally in late April to early May. This species is an explosive breeder, hundreds were observed after heavy rains during the night of April 26, 2001. Individuals were gathered around pooled water bodies. Males were actively calling and amplexus was observed. Neither egg deposition nor larvae were observed.

COMPARISONS AND REMARKS.— *Bufo crocus* differs from all of the following Asian *Bufo* belonging to the *Bufo bufo*, *Bufo viridis*, *Bufo stomaticus*, *Bufo stejnegeri*, and *Bufo orientalis* groups (*sensu* Inger 1972) in possessing cephalic crests: *B. bufo*, *B. bankorensis*, *B. gargarizans*, *B. wrighti*, *B. japonicus*, *B. minshanicus*, *B. tibetanus*, *B. viridis*, *B. calamita*, *B. raddei*, *B. surdus*, *B. latastei*, *B. luristanica*, *B. orientalis*, *B. dodsoni*, *B. stomaticus*, *B. olivaceus*, *B. dhufarensis*, *B. beddomi*. It differs from *B. asper* and *B. juxtasper* (Inger's 1972 *Bufo asper* group) in lacking a tarsal ridge. It can be distinguished from *Bufo biporcatus*, *B. divergens*, *B. philippinicus*, *B. parvus*, *B. quadriporcatus*, and *B. claviger*, the members of the *Bufo biporcatus* group (Inger 1972), through the presence of melanophores in tissue surrounding the vocal sac (Inger 1972). It is distinguished from the *B. scaber* group (Dubois and Ohler 1999) (*B. scaber*, *B. parietalis*, *B. silent-valleyensis*, *B. atukoralei*, *B. kotagamai*) in that it lacks very prominent parietal ridges.

Bufo crocus is tentatively placed in the *Bufo melanostictus* group based on Inger's (1972) suite of characters, but differs from all other species in this group. Included herein are comparisons with all currently recognized species from Inger's 1972 defined group (*Bufo melanostictus*, *B. parietalis*, *B. stuarti*, *B. himalayanus*), and Dubois and Ohler's (1999) redefined *Bufo melanostictus* group (*B. melanostictus*, *B. himalayanus*, *B. cyphosus*, *B. microtypanum*, *B. noellerti*, *B. stuarti*). From *Bufo stuarti*, *B. crocus* can be distinguished by its very distinct cephalic ridges, which are lacking in *B. stuarti*. From *B. microtypanum*, it differs in having a tympanum that is much larger in relation to the eye and in the absence of double distal tubercles on fingers three and four. It is readily distinguishable from *B. noellerti* both on the basis of geography, *B. noellerti* is endemic to Sri Lanka, and in the absence of a dark patch extending from the tympanum onto the flanks (see Manamendra et al. 1998); from *B. cyphosus* by the absence of symmetrical stripes on the female's ventrum (Dubois and Ohler 1999); and from *B. himalayanus* in that it possesses a distinct supratympanic cephalic crest. *Bufo crocus* differs from *B. melanostictus* in its smaller body size, in possessing weak parietal ridges and singular subarticular tubercles, and in the absence of paired warts between the parotoid glands.

Of the above species, *B. crocus* appears most similar to *Bufo melanostictus*. Besides differing in the above mentioned characters, it also differs in its call, reproductive behavior, and habitat preference. The advertisement calls of the two species differ markedly in structure, dominant frequency, duration and pattern (Figs. 4–5). The *B. melanostictus* call recorded from Myanmar is consistent with findings reported by Grosjean and Dubois (2001) in that it is comprised of a series notes made up of a variable number of pulses. The call of *Bufo crocus* consists of a series of notes without the distinct pulses.

Smith (1917), van Kampen (1923), and Church (1960) reported *Bufo melanostictus* as breeding throughout the year. Boulenger (1912) however, reported the breeding season as March and April on the Malay Peninsula. *Bufo crocus* as reported above is an explosive breeder in which breeding occurs with the earliest monsoon rains. Unlike *B. melanostictus*, it is also not commonly found outside of this breeding period. Additional searches carried out at the type locality in June of 2001, and late January 2002 yielded only one individual. Lastly, the two species are found in

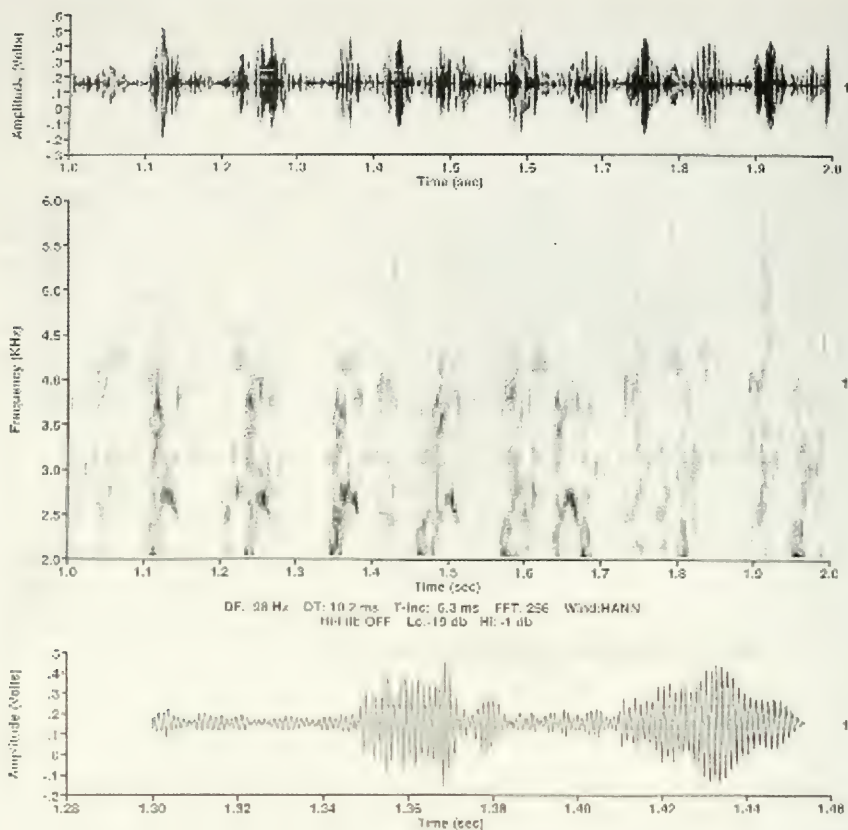


FIGURE 4. Call of *Bufo crocus* (CAS 220331) recorded on April 26, 2001 at 22:35 hrs. Temperature 28.05° C, 90% humidity after heavy rain. Myanmar. (A) spectrogram; (B) oscillogram; (C) detailed oscillogram of notes 3 and 4.

very different habitat types. *Bufo melanostictus* is primarily a commensalistic species (Inger 1966; Berry 1975; Inger et al. 1984; Dutta and Manamendra-Arachchi 1996; Dutta 1997; Inger 1997; Iskandar 1998) and *Bufo crocus* is found in primary evergreen forest.

ETYMOLOGY.— The specific epithet, *crocus*, is Latin for yellow or saffron. This is in reference to the bright yellow breeding coloration of the males.

REDESCRIPTION OF *BUFO STUARTI* SMITH, 1929
Figures 3, 6-7

In 1929, Malcolm Smith described *Bufo stuarti*¹, with the type being deposited at the Zoological Survey of India in Calcutta (ZSI 19985). The following redescription of the type specimen (Fig. 6) follows the format of Dubois and Ohler 1999:

(A) SIZE AND GENERAL ASPECT: (1) a medium sized frog (SVL 71.3 mm) (note that difference in SVL from Smith's description (73.0 mm) may differ due to time in preservation, or the current use of a more precise measuring device).

(B) HEAD: (2) head of medium size, wider (26.2 mm) than long (21.9 mm) (3) snout obtuse, protruding beyond mouth, (4) canthus rostralis distinct, (5) interorbital space slightly concave, (6)

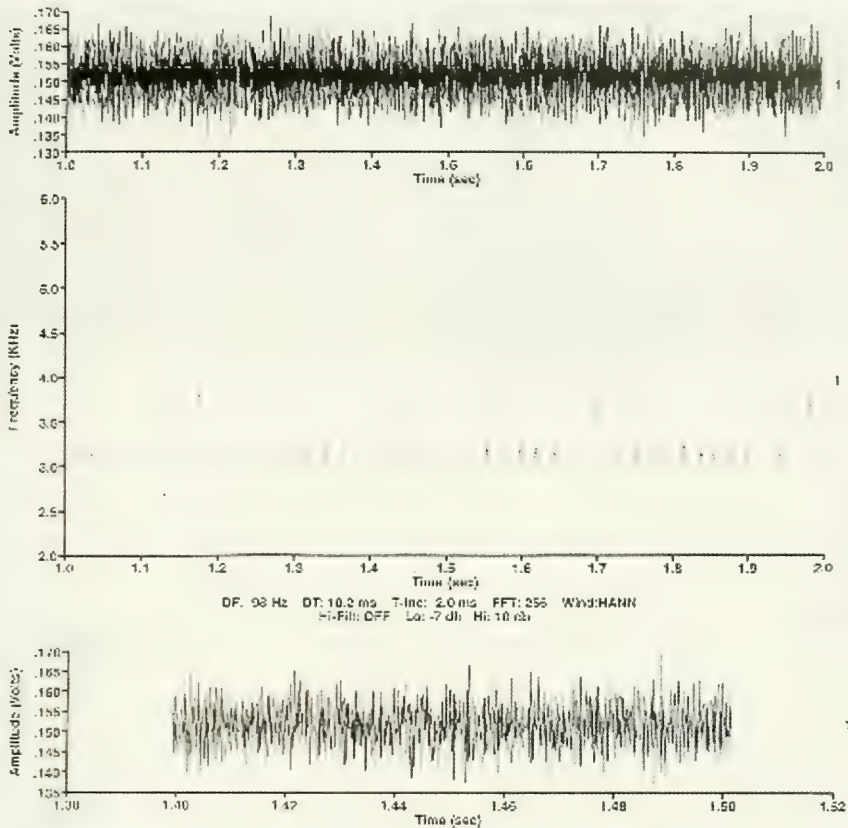


FIGURE 5. Call of *Bufo melanostictus* (USNM/field series 35608) recorded on March 2, 2002 at 21:00 hrs. Temperature 22.0° C. Myanmar. (A) spectrogram; (B) oscillogram; (C) detailed oscillogram of notes between 1.4 and 1.5 seconds.

nostrils closer to snout than eye, (7) pupil not observed, (8) tympanum 2.4 mm in diameter, oval and vertical, distinct, (9) pineal ocellus absent, (10) vomerine ridge not observed, (11) tongue not observed, (12) supratympanic fold absent, (13) parotoid glands present, reniform and long (18.4 mm), (14) cephalic ridges absent.

(C) FORELIMBS: (16) arms robust and enlarged, (17) fingers long and thin, (18) relative length of fingers 3>4>1>2, (19) tips of fingers not enlarged, rounded, grooves absent, (20) fingers without dermal fringe, (21) subarticular tubercles prominent, (22) prepollex rounded and very prominent, one prominent rounded palmar tubercle.

(D) HINDLIMBS: (23) leg measurements not recorded, (24) toes long, (25) relative length of toes 1<2<5<3<4, (26) tips of toes rounded, not enlarged without grooves, (27) webbing formulae I1-2 1/2II2-21/2III2-3IV2 1/2-1 1/2 V (28) dermal fringe along toe V absent, (29) subarticular tubercles indistinct, (30) inner metatarsal tubercle long and prominent, (31) tarsal fold absent, (32) outer metatarsal tubercle present, round and prominent; numerous tubercles on the plantar surface of the foot.

(E) SKIN: (33) head and anterior of dorsum granular, posterior of dorsum with large keratinized spiculate warts, (34) dorso-lateral fold absent, (35) dorsal parts of limbs with keratinized warts, (36) throat, chest, belly and thighs granular, (37) parotoid glands present.



FIGURES 6–7. (6) *Bufo stuarti*, holotype ZSI 19985. Photo by G.O.U. Wogan. (7) *Bufo stuarti*, CAS 224954. Photo by Hla Tun.

(F) COLORATION: (38) dorsal and lateral parts of the head and body are tan olive with brown on warts, (39) dorsal parts of limbs are tan olive, (40) ventral parts of head, body, and limbs are whitish tan.

(G) MALE SEXUAL CHARACTERS: (41) nuptial spines present on digits I, II, III (42) vocal sacs present.

Recent herpetological surveys made in the vicinity of the type locality have yielded three adult *Bufo stuarti* (Fig. 5). Herein I include these specimens in order to provide a more thorough description of *B. stuarti*. Ranges and means are provided in Table 1.

Additional observations on the recent specimens: (5) interorbital space distinctly concave, (7) pupil horizontal (Fig. 7), (10) vomerine ridge absent, (11) tongue not emarginate, (13) parotoid glands of CAS 224954 have a slightly triangular shape. CAS 221317 and 221439 are elongate and approximately twice as long as wide. (30, 32) measurements of the inner and outer metatarsal tubercles show that the outer metatarsal tubercle is larger. (33) the dorsal and lateral parts of the head and body of CAS 221317 and CAS 224954 are more coarsely granular and warty, however, CAS 224954 lacks asperities on the head. (34) dorsal parts of limbs are very granular with large asperities and warts. (38) CAS 221317 dorsal and lateral parts of the head and body are dark brown to tan, with a faint mid-dorsal line, parotoids umber, sides are white with tan and dark brown warts. CAS 224954 dorsal and lateral parts of the head and body are dark brown to umber with a black w shaped pattern, black triangular mark between eyes, faint mid-dorsal line, parotoids umber, (39) CAS 221317 and CAS 224954 dorsal parts of limbs are barred with light tan, (40) CAS 221317 ventral surfaces of head, body, and limbs light with dark brown mottling varying in density, CAS 224954 is heavily mottled with dark brown on a light tan background.

¹ Original description (Smith 1929): "Adult male collected on the Putao plain, N.E. Burma, near the Tibetan frontier by Dr. Murray Stuart, after whom it is named. Habit like that of *B. melanostictus*. Crown without bony ridge; snout as long as the upper eyelid, prominent, projecting forwards beyond the lower jaw; canthus rostralis distinct; loreal region almost verticle; interorbital space a little broader than the upper eyelid; tympanum distinct, half the diameter of the eye. First finger a little longer than second, third finger nearly twice as long as second; two well marked carpal tubercles, the outer larger and flatter than the inner. Toes half webbed, the membrane not reaching the tips of the third and fifth toes, subarticular tubercles, not very prominent; no tarsal fold, two well marked metatarsal tubercles. The tarso-metatarsal articulation reaches to the tip of the snout; the heels meet when the legs are folded at right angles to the body. Skin of the head fairly smooth, of the back and limbs above with smooth warts of moderate size. Parotoids well developed, elongate, twice as long as broad, parallel with each other. Skin of the lower parts coarsely granular. Nuptial asperities on the inner three fingers. Pale olive above, uniform; brownish-white below. From snout to vent 73 mm. *Bufo stuarti* is closely related to *B. stomaticus* Lutken from which it can be distinguished by the more prominent snout, the strong canthal ridges and by the absence of a tarsal fold."

TABLE 1. Means and ranges for morphometric characters.

Character state	<i>Bufo crocus</i>			<i>Bufo crocus</i>			<i>Bufo melanostictus</i>			<i>Bufo melanostictus</i>			<i>Bufo stuarti</i>		<i>Bufo stuarti</i>	
	males (N=3)			females (N=2)			males (N=9)			females (N=9)			male	females (N=2)		
	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.		Min.	Mean	Max.
SVL	54.6	56.533	59.1	67.6	67.7	67.8	70.5	77.878	93.4	67.8	91.644	150.4	60.7	61.0	68.6	76.2
HL	16.1	17.233	18.0	19.2	19.35	19.5	21.7	23.867	28.5	20.7	28.611	46.1	17.2	17.0	18.95	20.9
HW	18.7	20.567	21.5	24.2	24.2	24.2	27	30.822	38.9	26.2	36.122	62.2	21.6	23.3	25.05	26.8
MN	13.6	15.033	16.9	16.0	16.4	16.8	18.6	20.222	23.1	16.8	24.611	37.3	14.2	13.9	16.0	18.1
MPE	5.4	6.0	6.5	6.0	6.35	6.7	5.8	7.956	11.5	4.9	11.233	18.5	3.6	4.0	5.3	6.6
MAE	11.2	11.567	11.8	11.9	12.25	12.6	15.2	16.244	18.1	12.0	18.711	28	10.4	9.9	11.5	13.1
IFE	7.5	7.767	7.9	8.9	9.05	9.2	8.0	9.911	14.3	7.2	11.311	18.8	8.2	8.1	8.8	9.5
IBE	15.1	16.0	16.5	17.7	18.45	19.2	17.9	20.789	25.7	17.4	22.822	35.7	15.6	15.9	17.0	18.1
IN	2.6	3.233	3.8	4.2	4.2	4.2	3.5	4.522	6.0	3.1	5.244	8.7	3.6	3.5	3.9	4.3
EN	3.8	4.867	6.8	4.5	4.55	4.6	4.1	4.744	5.9	3.7	5.667	8.3	3.7	4.1	4.7	5.3
SL	5.9	6.567	7.1	8.4	8.5	8.6	6.9	8.278	10.4	7.0	9.5	15.9	6.5	6.2	7.1	8.0
NS	2.1	2.30	2.6	2.7	2.75	2.8	2.1	2.867	4.3	2.0	3.111	5.6	6.5	2.2	4.2	6.2
TympD	2.1	2.433	3.0	2.9	3.3	3.7	4.2	5.027	6.1	4.2	5.211	7.2	2.2	1.7	2.45	3.2
ET	1.0	1.067	1.2	1.5	1.55	1.6	0.8	1.727	2.5	1.4	3.011	6.2	1.2	1.4	1.65	1.9
ParW	5.7	6.233	6.8	7.9	7.9	7.9	6.8	8.0	9.5	5.6	7.144	11.0	13.4	10.9	12.35	13.8
ParL	10.7	11.133	11.4	11.9	12.4	12.9	14.1	16.878	21.1	13.8	21.211	37.2	5.3	6.4	14.25	22.1
FLL	12.7	13.3	13.9	15.3	15.95	16.6	16.1	18.711	25.2	14.4	20.389	29.7	16.1	16.3	18.15	20.0
HAL	11.0	13.2	14.8	15.8	16.0	16.2	16.0	18.478	21.2	15.7	21.3	34.5	15.9	15.4	17.9	20.4
TL	20.4	20.9	21.3	24.7	24.8	24.9	25.5	29.944	36.0	24	32.564	51.7	25.8	24.9	28.45	32.0
FL	20.3	21.3	22.3	23.7	23.85	24	25.8	28.589	32.4	22.2	31.878	52.8	26.3	24.7	28.55	32.4
FEM	20.3	21.567	22.8	24.6	26.35	28.1	28.4	33.175	41.5	24.7	34.811	55.8	26.8	25.7	26.15	26.6
IMT	1.5	2.033	2.5	2.5	2.55	2.6	1.4	3.311	4.3	2.1	3.922	6.6	3.2	2.5	3.5	4.5
OMT	0.6	1.20	1.8	1.7	1.8	1.9	2.1	2.916	4.1	2.3	2.967	4.0	3.8	3.7	3.75	3.8
MPE/MAE	0.48	0.5181	0.55	0.5	0.518	0.53	0.37	0.4885	0.66	0.36	0.6375	1.54	0.35	0.4	0.4539	0.5
HL/SVL	0.29	0.3049	0.32	0.28	0.2858	0.29	0.29	0.3064	0.32	0.3	0.3132	0.33	0.28	0.27	0.2765	0.28
HW/SVL	0.34	0.3636	0.38	0.36	0.3575	0.36	0.37	0.3945	0.43	0.37	0.3927	0.41	0.36	0.35	0.3668	0.38
ParW/ParL	0.53	0.5593	0.6	0.61	0.6381	0.66	0.42	0.4753	0.52	0.27	0.349	0.43	2.53	0.49	1.3247	2.16
FEM/SVL	0.37	0.3817	0.41	0.36	0.3892	0.41	0.4	0.4203	0.45	0.36	0.3813	0.42	0.44	0.35	0.3852	0.42
TL/FEM	0.93	0.9705	1.0	0.89	0.9451	1.0	0.87	0.9234	0.99	0.89	0.9379	0.97	0.96	0.97	1.0859	1.2
OMT/IMT	0.4	0.5638	0.72	0.68	0.7054	0.73	0.22	0.7531	1.08	0.61	0.7962	1.14	1.19	0.82	1.1711	1.52
EN/MN	0.27	0.3186	0.4	0.27	0.2775	0.28	0.21	0.234	0.26	0.21	0.2316	0.27	0.26	0.29	0.2939	0.29
ParL/SVL	0.19	0.197	0.2	0.18	0.1832	0.19	0.2	0.2162	0.23	0.2	0.2294	0.29	0.09	0.1	0.1975	0.29
ParW/HW	0.29	0.3032	0.32	0.33	0.3264	0.33	0.24	0.26	0.29	0.16	0.2016	0.23	0.62	0.41	0.4995	0.59

DISCUSSION

Despite the taxonomic confusion within the Asian Bufonidae and particularly the genus *Bufo*, recent work (Dubois & Ohler 1999; Macey et al. 1998; Liu et al. 2000) has started to untangle the confusion surrounding these taxa. The taxonomic position of *Bufo stuarti* has remained uncertain because of its rarity in collections. Inger (1972) originally placed it in the *Bufo melanostictus* group thereby indicating the presence of cephalic ridges, however, Smith (1929) mentions a similarity with *Bufo stomaticus* in the original description (refer to footnote 1). In our examination of the type

and subsequent collections, no cephalic ridges were found. We suggest that additional studies should be undertaken before reassigning it to a different species group. *Bufo crocus* as mentioned previously is tentatively assigned to the *Bufo melanostictus* group based on the prescribed suite of characters from Inger’s 1972 designation. Its taxonomic position, however, is uncertain pending additional analysis.

As the Myanmar Herpetological Survey moves into new areas, assuredly new and interesting bufonids will be found in Myanmar. To date, no representatives of the genera *Ansonia*, *Leptophryne*, and *Pedostibes* have been found within Myanmar, although each has been reported in neighboring countries. Frost (2002), for instance, suggests that at least three bufonid species, two of *Ansonia* (*A. penangensis*, *A. malayana*) and one *Leptophryne* (*L. borbonica*) should occur in Myanmar. In addition, as work is carried out on widespread composite species, such as *Bufo melanostictus*, it is likely that additional species masquerading under this name will be discovered within Myanmar.

KEY TO THE *BUFO* OF MYANMAR

- 1. Cephalic ridges present 2
Cephalic ridges not present 3
- 2. Cephalic ridges run parallel to parotoids *B. parvus*
Cephalic ridges not parallel 5
- 3. Tympanum distinct 4
Tympanum not visible *B. burmanus*²
- 4. Tympanum of equal size to eye, parotoids small and round *B. macrotis*
Tympanum much smaller than eye, parotoids elongate *B. stuarti*
- 5. Tarsal ridge present, supratympanic ridges prominent *B. asper*
Tarsal ridge absent 6
- 6. Adult size, 62–150 mm; paired dorsal warts between parotoid glands *B. melanostictus*
Adult size, 54–67 mm; paired warts between parotoid glands absent *B. crocus*

MATERIAL EXAMINED

Bufo andrewsi: China, CAS 214911–214915, Yunnan Province, Nu Jiang Prefecture, village S of Gongshan, 27°42’13.7” N, 98°42’10.2” E, ca 1451 m.

Bufo asper: Malaysia, CAS-SU 14833, Pinang; Thailand, CAS 73689, Sritamarat, Nakon; Myanmar, CAS 222196, Mon State, Kyaik Hto Township, Kyaik-Hti-Yo Wildlife Sanctuary, tributary of Moe Baw Chaung, 17°29’48.5” N, 97°04’49.6” E.

Bufo bufo: China, CAS 16484–16487, Shanghai.

Bufo burmanus: Myanmar, MCZ 23440–23444, Chin State

Bufo crocus: Myanmar, CAS 220192–220195, Rakhine State, Gwa Township, Rakhine Yoma Elephant Sanctuary, Ye Bya stream camp, 17°41’47.0” N, 94°38’48.7” E; CAS 220331, Rakhine State, Gwa Township, Rakhine Yoma Elephant Sanctuary, 17°42’14.0” N, 94°38’54.3” E; CAS

² *Bufo burmanus* is maintained in this key in accordance with Frost 2002, but it should be noted that Dubois and Ohler (1999) synonymized this species with *B. pageoti*. *B. burmanus* is known only from Myanmar and has not been obtained in recent collections.

222923, Rakhine State, Gwa Township, Rakhine Yoma Elephant Wildlife Sanctuary, 17°35'03.9" N, 94°40'52.6" E; CAS 222970, Rakhine State, Gwa Township, Daung stream, 17°35'03.9" N, 94°40'52.6" E.

Bufo dhufarensis: Saudi Arabia, CAS 134168–134169, vicinity of Matri and Khasawiyah [16°58' N., 42°42' E – 16°56' N, 42°37' E], 20–25 m.

Bufo gargazians: China, CAS 194198–194201, Anhui Province, Luan Prefecture, 23 km SW and 10 km south of Yanzhihe, also 20 km WSW of Manshuihe (31°08' N, 116°01' E), Beimazhei.

Bufo himalayanus: China, CAS 177560–177568, Xizang (Tibet) Autonomous Region, Xigaze Prefecture, between Chinese check point at Zhangmu (Khasa) [28°07' N, 85°59' E] and the Nepal border on the Lhasa-Kathmandu Rd., 2100–2300 m.

Bufo macrotis: Myanmar, CAS 213551–213558, Yangon Division, Hlaw Ga Park, Mingalardon Township, 17°02'08.2" N, 96°06'00.6" E.

Bufo melanostictus: Myanmar, CAS 205186–205187, Rakhine State, Gwa Township, ca 300 m E of Pleasant Beach Resort, 17°43'28.8" N, 94°32'36.1" E; CAS 222981, Rakhine State, Taung Gok Township, Taung Gok Town, 18°50'31.8" N, 94°12'31.8" E, 11 m; CAS 213763, Magwe Division, Shwe Set Taw Wildlife Sanctuary, Pwint Byu Township, Oak Pho Camp, 20°19'38.5" N, 94°34'27.1" E; CAS 213621, Magwe Division, Shwe Set Taw Wildlife Sanctuary, Mimbu (Sagu) Township, 20°03'34.3" N, 94°35'37.7" E; CAS 220562, Magwe Division, Saw Township, Saw Town, Forest Department office, 21°08'52.9" N, 94°09'36.6" E; CAS 219956–219957, Chin State, Min-Dat District, Kanpetlet Township, Nat Ma Taung National Park, Saw stream, 21°10'16.0" N, 94°04'26.1" E; CAS 219775, Ayeyarwady Division, Pya Bon District, Bogalay Township, Mein Ma Hla Kyun Wildlife Sanctuary, West Htaw Pai Camp, 15°51'06.3" N, 95°18'40.6" E; CAS 213880, Magwe Division, Shwe Set Taw Wildlife Sanctuary, Lap Pan Taw Camp, Minbu (Sagu) Township, 20°06'56.1" N, 94°36'38.4" E.

Bufo microtympanum: India, CAS 94446, 12.9 km NE of Munnar; CAS 104227–104228, India, Madras State, Palni Hills, Kodaikanal.

Bufo orientalis: Saudi Arabia, CAS 139542–139543, near Al Hada at 20°22' N, 40°16' E, ca 2000 m.

Bufo parvus: Malaysia, CAS-SU 3242–3243, Perak; CAS-SU 3237, Perak, Gunong Kledang.

Bufo pentoni: Saudi Arabia, CAS 119214, Al Lith, 20°09' N, 40°17' E, ca 20 m.

Bufo raddei: China, CAS 166809–166819, Ningxia Hui Autonomous Region, Yinnan Prefecture, along the south shore of the Yellow River (Huang He), Shenjiatan (37°28' N, 105°18' E).

Bufo scaber: Sri Lanka, CAS 85271, India, CAS 104139, Madras State, Kanyakumari District (Cape Comorin District) Mylaudi Village, 4 mi. W. Jamestown.

Bufo stomaticus: Afghanistan, CAS 96172, Khost; Nepal, CAS-SU 15315, above Tambur River.

Bufo stuarti: Myanmar, CAS 221436, Kachin State, Putao District, Naung Mon Township, Aureinga Camp, 27°17'36.4" N, 97°51'50.0" E; CAS 221432, Kachin State, Putao District, Naung Mon Township, Aureinga Camp, 27°17'32.4" N, 97°51'56.4" E; CAS 221317, Kachin State, Putao District, Machanbaw Township, Ahtonga Village, 27°15'41.8" N, 97°48'06.9" E; CAS 221485, Kachin State, Putao District, Machanbaw Township, rd between Ahtonga and Babaw, 27°15'27.2" N, 97°50'32.4" E; CAS 224954, Kachin State, Putao District, Ba Bawt Village, 27°21'33.4" N, 97°54'56.1" E, 640 m; CAS 224955, Kachin State, Putao District, Ba Bawt Village, 27°22'39.3" N, 97°53'46.7" E, 556 m; ZSI 19958, "Putao Plain, N. Myanmar" (Kachin State).

Bufo surdus: Iran, CAS 158247, Seistan and Baluchestan Province, W slope of Kuh-e-Taftan, 2250 m.

Bufo viridis: Turkey, CAS 217837–217845, Icel Province, Anamur, 36°04'17.7" N, 32°52'03.4" E, 6 m.

ACKNOWLEDGEMENTS

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***Cottoclinus canops*, a New Genus and Species of Blenny (Perciformes: Labrisomidae) from the Galápagos Islands**

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We describe *Cottoclinus* new genus, type species *C. canops* novum, from two specimens from Española Island, Galápagos Islands. The new genus is assigned to the labrisomid tribe Mnierpini Hubbs. The tribe is redefined and considered sister to the Labrisomini. It is united by nine synapomorphies: 1) body elongate to moderately elongate (depth 13%–22% of standard length); 2) spinous dorsal fin with no incision in outline, anterior rays soft and flexible; 3) anal fin rays all thickened, and fleshy at tips; 4) head blunt with upper jaw projecting; 5) lower lip interrupted by a pair of grooves outlining a frenum on chin; 6) lips thick and inflated; 7) scales expanded posteriorly forming pockets; 8) membrane of anal fin rays incised almost to base of rays; 9) belly and pectoral base naked. The two currently recognized monotypic genera in the tribe, *Dialommus* Gilbert 1891 and *Mnierpes* Jordan and Evermann 1896, are considered synonyms. The name Mnierpini is retained for the tribe. *Cottoclinus* differs from *Dialommus* in that there is no fleshy pigmented vertical bar across the eye separating two flat windows, and the posterior mandibular teeth are not abruptly smaller and set lower than the anterior teeth. *C. canops* is considered the basal member of the clade leading to *D. fuscus* and *D. macrocephalus*.

In 1964 Boyd W. Walker and Edmund S. Hobson of the University of California, Los Angeles, participated in a University of California expedition to the Galápagos Islands aboard the M/V *Golden Bear*, operated by the California Maritime Academy. They were able to make large collections of fishes at a number of the islands. Included in the material that they returned with were two specimens of a labrisomid blenny from a tidepool on Española (Hood Island), the southernmost Galápagos Island. Until recently, these two undistinguished-looking specimens had languished on a shelf with other unidentified material. Eventually they were brought to the attention of one of us (JSS). In concert with the other two authors of this paper, it was determined that they represented an undescribed genus and species. It is the purpose of this paper to describe the genus and species and to present a hypothesis of relationships.

MATERIALS AND METHODS

Type specimens of the new species are deposited in the Department of Ichthyology of the California Academy of Sciences (CAS), San Francisco. Measurements are straight-line (point to point) and made with dial calipers and recorded to the nearest 0.1 mm. Length of specimens is given as standard length (SL), the distance from the front of the upper lip to the base of the caudal fin. Body depth is measured vertically from the origin of the anal fin; body width is taken just posterior to the gill opening. Head length (HL) is measured from the front of the upper lip to the pos-

* The order of authorship was randomly determined.

terior end of the opercular membrane, and snout length is from the upper lip to the fleshy edge of the orbit. Orbit diameter is the greatest fleshy diameter, and interorbital width is the least fleshy width.

***Cottoclinus* McCosker, Stephens, and Rosenblatt, new genus**

Type species *Cottoclinus canops*, new species.

DIAGNOSIS.— That of the single included species.

ETYMOLOGY.— From the generic names *Cottus* and *Clinus*, in reference to the cottid-like appearance of this blenny. Gender masculine.

***Cottoclinus canops* McCosker, Stephens, and Rosenblatt, new species**

Figs. 1–4, Table 1

MATERIAL EXAMINED.— Holotype: CAS 217107 (formerly W64–35), an immature male, 45.2 mm SL, from a low tidepool on the south side of Punta Suarez, Isla Española (Hood), Galápagos Islands, collected on 18 Feb. 1964 by M. Castro. Paratype: CAS 217108, an immature female, 54.4 mm SL, collected with the holotype.

DIAGNOSIS.— A moderate-sized mnierpin labrisomid blenny with the following characteristics: body moderately elongate (depth 4.4–5.1 in SL); head bulbous, slightly depressed; lips fleshy; posterodorsal corner of maxillary slips into a cheek pouch; nasal, orbital, and nuchal cirri small and fimbriate; breast and belly scaleless; scales membranously expanded posteriorly to form pockets; spinous dorsal fin rays nearly level, lower and less numerous than dorsal fin soft rays; one anal fin spine; interradial membrane of anal fin incised almost to base of each ray; all fin-rays unbranched; cornea convex, eyeball lacking a vertical bar and heavy pigmentation; teeth conical, stout, slightly recurved; medial teeth of dentary notably larger than lateral teeth; vomerine teeth present, palatine teeth absent.

DESCRIPTION.— Meristic values listed are those of the holotype, those for the paratype are in parentheses. (We have selected the larger of the two specimens to be the paratype in that it is bent and in poorer condition.) Counts: D XXI, 10 (XX, 10); A I, 19; P₁ xiii; P₂ I, 3; C xiii; branchiostegal rays 6, pored lateral line scales 47; vertebrae 10 + 25. Body depth about 4.5–5.1 in length. Head roughly quadrangular when viewed from front; its depth about 90% of width. Eyes set high, entering dorsal profile, cornea not divided. Lips fleshy, lower lip with a free ventral flap attached to a medial frenum. Mouth short; maxilla, which slips into cheek pouch, ends at level of posterior margin of pupil.

Premaxilla with a small, conical symphyseal tooth, followed by an outer row of 10 conical teeth that decrease in size posteriorly. A few vomerine teeth, palatine teeth absent. An interior patch of setiform teeth at head of premaxillary. Dentary of holotype with a pair of enlarged incisors at

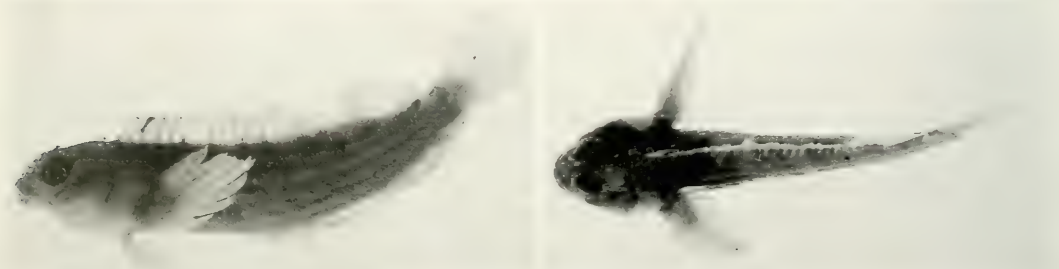


FIGURE 1. Lateral and dorsal views of holotype of *Cottoclinus canops*, CAS 217107, 45.2 mm SL.

symphysis, followed by 5 conical recurved teeth, increasing in size posteriorly; sixth tooth about 1/3 length of fifth, followed by a row of small, increasingly flattened teeth. A small medial patch of villiform teeth near symphysis. Dentition of paratype somewhat different: symphyseal teeth not so conspicuously enlarged; second through fifth teeth about 3/4 as long as symphyseals, then teeth 6 and 7 are conspicuously enlarged, about twice as long as symphyseal teeth, with teeth 8 through 11 similar in size to teeth 2 to 5.

Posterior nostril with a raised rim, anterior nostril with a short tube surmounted by a palmate tentacle with about 7 fimbriae. A small fimbriated supraorbital

TABLE 1. Measurements in millimeters of the holotype and paratype of *Cottoclinus canops*, new species.

	Holotype	Paratype
Standard length	45.2	55.4
Head length	15.0	16.8
Head width	10.3	13.3
Head depth	7.2	9.1
Orbit	3.3	3.4
Preal distance	23.0	29.2
Longest pectoral ray	13.2	14.3
Body depth at anal origin	8.8	12.2
Caudal peduncle depth	4.3	4.9
Longest dorsal fin spine	5.1	—
Longest caudal ray	9.8	11.7

cirrus dorsally on the eyeball, and a pair of fimbriated nuchal cirri arising from a common base on the nape on either side of the first dorsal fin spine.

Dorsal fin spines 1–20 subequal, but spines 18–20 decrease in length, resulting in a distinct notch between the spinous dorsal fin and the soft dorsal fin. Margin of soft dorsal fin rounded, 2nd through 5th rays longest. Last dorsal fin ray free from caudal peduncle. Anal fin spine 1/3 (1/2) as long as first soft-ray. Anal fin soft-rays thickened, their membranes incised almost to the base, except for the last 6 rays. Pectoral fan-shaped, rays 7–9 longest; rays 9–13 thickened. Pelvic spine splint-like, soft-rays one and two stout, soft ray 3 slender, but almost as long as second.

Body scaled except for breast, belly, an area anterior to pectoral fin, and an area at nape extending back along first 4 or 5 dorsal fin spines. Scales with posterior membranous caudal expansions, forming pockets, particularly on lower sides. Lateral-line scales pored, the pore openings being located along the mid-dorsal scale margins; posteriorly, pores become obsolete.

Cephalic sensory pores (Fig. 2) mostly minute, numerous, many appearing as skin pricks. The following is based on the condition of the holotype. Mandibular (M) series with six pores on each side, the first along the symphysis, the following four evenly spaced, the last more separated. Six preopercular (PO) pores closely following the posteriormost mandibular pore. A series of four pores above maxilla, followed by an upward-arching row of approximately eight small pores. Two pores above upper lip in advance of the anterior nostril, followed by three pores (the middle pore lacking on left side of holotype above the anterior frontal region). A single median interorbital or commissural (C) pore is followed by a pore pair, then a single median supratemporal (MST) pore that is closely followed by another pore pair. The orbits are surrounded by numerous minute infraorbital (IO), postorbital (PO), and supraorbital (SO) pores. Additional rows of minute pores are located between the POP and PO regions. There are few preorbital pores, although two nasal pores (N) lie between, and just medial to, the anterior and posterior nostrils. A row of minute pores

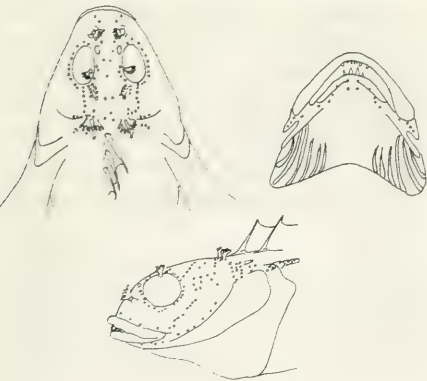


FIGURE 2. Lateral (left), dorsal (right) and ventral (below) views of cephalic sensory pores of holotype of *Cottoclinus canops*, CAS 217107, 45.2 mm SL.

passes from the mid-PO region to form a "T"-shaped juncture alongside the ST pores. Several minute pores lie distal to the nuchal cirri, which are followed by a large lateral supratemporal (ST) pore.

Body coloration in isopropyl alcohol tan, with a suggestion of 3 or 4 diffuse bars. Head of holotype profusely spotted with brown flecks, these less conspicuous in the paratype. Upper lip with a brown mark at the corner of mouth and another near midline, the latter one continued on lower lip. Middle and lower pectoral rays brown. Caudal fin of holotype with the suggestion of 3 vague bars. Eyeball pigmented dorsally, but no suggestion of a pigmented vertical bar across eye.

ETYMOLOGY.— From the Greek *kanon*, rule or standard, and *ops*, eye, in reference to the normal structure of the cornea.

RELATIONSHIPS.— Hubbs (1952) established the tribe Mnierpida (*sic*) within his subfamily Labrisominae (now Labrisomidae) for the reception of the genera *Mnierpes* and *Dialommus*. The tribe was defined by: 1) "a fleshy bar runs vertically across pupil of eye; 2) body elongate (depth 13%–17% of standard length); 3) spinous dorsal fin with anterior rays soft and flexible, with no incision in outline; 4) anal fin rays all enlarged and fleshy at tips; 5) head blunt with upper jaw projecting." To these we can add: 6) posterior dentary teeth abruptly smaller and set lower than the anterior teeth; 7) lower lip interrupted by a pair of grooves outlining a frenum on chin; 8) lips thick and inflated; 9) scales expanded posteriorly forming pockets; 10) membrane of anal fin rays incised almost to base of rays; and 11) belly and pectoral base naked. Although no cladistic analysis of relationships of all labrisomid genera has been attempted, the classification of Stepien et al. (1993, 1997) based on molecular data indicates that the tribe Labrisomini (genera *Malaccoctenus* and *Labrisomus*) is sister to the tribe Mnierpini (*sensu* Hubbs). The above 11 character states are synapomorphies of the Mnierpini with respect to the Labrisomini.

Cottoclinus shares all of these synapomorphies except 1 and 6. (Although *C. canops* is not as elongate as *D. fuscus* and *D. macrocephalus* — body depth 19.5% and 22% in holotype and paratype respectively — it is still relatively elongate in comparison to other labrisomids.) Relationships are best indicated by placing *Cottoclinus* as the basal member of the clade leading to *Mnierpes* and *Dialommus* (Fig 3). Those genera were separated by Hubbs on the basis of number of anal fin spines (1 versus 2), presence or absence of a supraorbital, and meristic and proportion-

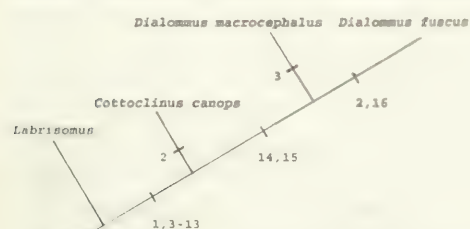


FIGURE 3. Cladogram of hypothesized relationships within the Mnierpini. Characters are: 1) orbital cirri present; 2) 1 anal fin spine; 3) 2 anal fin spines; 4) body elongate (depth 19–22% of SL); 5) anterior spinous dorsal fin rays flexible, without incision; 6) anal fin rays enlarged, tips fleshy; 7) head blunt, upper jaw projecting; 8) posterior dentary teeth smaller and lower than anterior; 9) chin frenum present; 10) lips thick and inflated; 11) posterior scale pockets; 12) membrane of anal rays incised; 13) belly and pectoral base naked; 14) body very elongate (depth 13–17% of SL); 15) a vertical fleshy bar across pupil; 16) orbital cirri absent.

al characters more suitable for the distinction of species than genera. *Dialommus* then would be characterized by the presence of 1 anal fin spine and the lack of an orbital cirrus (an autapomorphy), and *Mnierpes* by the presence of a supraorbital cirrus and 2 anal fin spines. One anal fin spine and no orbital cirri are each apomorphic features within the Labrisomidae. However, *Cottoclinus* shares one apomorphic and one plesiomorphic character state with each.

Inasmuch as *Cottoclinus* has 1 anal fin spine, and if the phylogeny diagrammed in Figure 3 is valid, two hypotheses can be erected. Either the common ancestor of *Dialommus* and *Mnierpes* had one anal fin spine and an anal fin spine was gained in *Mnierpes* as a reversal, or the common ancestor had two anal fin spines and an anal fin spine was lost independently in *Cottoclinus* and *Dialommus*.

In either case, the synapomorphies of the complex corneal modifications (Graham and Rosenblatt 1970) and the condition of the mandibular dentition would have been present in the common ancestor of *Dialommus* and *Mnierpes*. The anal fin spine-pterygiophore relationship in *Mnierpes* is essentially identical to the plesiomorphic condition in *Labrisomus* and *Malacoctenus*, and both *Cottoclinus* and *Dialommus* have lost the first spine but retained the first pterygiophore (Fig. 4). (The phylogeny as diagrammed in figure 3 reflects the independent loss of an anal fin spine.) Therefore, we cannot reject either hypothesis on the basis of available evidence.

The common possession of the dentition and corneal specializations in the monotypic genera *Dialommus* and *Mnierpes* indicates common ancestry and the species *D. fuscus* and *M. macrocephalus* should therefore be regarded as congeneric. *Dialommus* Gilbert 1891 (type species *D. fuscus* Gilbert 1891) is senior to *Mnierpes* Jordan and Evermann 1896 (type species *Clinus macrocephalus* Günther 1861), and *Mnierpes* is a junior synonym of *Dialommus*.

REMARKS.— The membranous posterior prolongation of the scales to form pockets and the separation and thickening of the anal fin rays have been hypothesized as adaptations to amphibious life; the former would hold water, and the latter would aid in clinging to sloping surfaces and in terrestrial locomotion (Clark 1932; Graham 1970). These modifications are already present in *Cottoclinus*, indicating that the ancestor of the fuscus-macrocephalus clade must have attained considerable terrestriality even before the modifications of the eye had developed.

In January 2002, JMc and JSS returned to Española and collected in tidepools contiguous with the type locality of *C. canops*. They were unable to access the pool sampled in 1962 but were able to collect from two pools within a km of that site. In general, the pools were devoid of large fish. The following species were collected: one each of *Muraena lentiginosa*, *Echidna nocturna* and *Uropterygius macrocephalus*; several *Scorpaena mystes*, *Acanthemblemaria castroi*, *Starksia galapagensis* and *Ogilbia deroyi*; numerous *Dialommus fuscus* (in the 1962 collection, 24 *D. fuscus* were collected from the same pool as the two *C. canops*) and *Malacoctenus zonogaster*; and hundreds of small *Tomicodon chilensis*.

Recent El Niño events (1982–1983 and 1997–1998) have had strong effects on tidepool and shallow subtidal species at the Galápagos. For example, the abundant shallow-water chaenopsid, *Acanthemblemaria castroi*, had largely disappeared following the most recent El Niño (JMc and C. C. Baldwin, personal observations), but it is once again abundant, and the conspicuous midwater pomacentrid, *Azurina eupalama*, has not been seen at Galápagos since 1977. We consider the possibility that *Cottoclinus canops* might be a naturally-occurring casualty of a recent El Niño event.

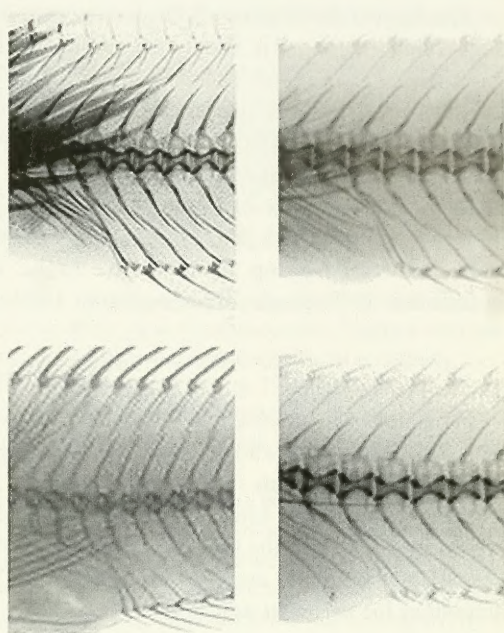


FIGURE 4. Lateral view of radiographs of anterior anal fin and supporting elements. (Images have been slightly enlarged or reduced to facilitate comparison.) Upper left, *Cottoclinus canops*, holotype, CAS 217107, 45.2 mm SL. Upper right, *Dialommus fuscus*, CAS 23754, 68 mm SL. Lower left, *Labrisomus dendriticus*, CAS 46577, 88.5 mm SL. Lower right, *Dialommus macrocephalus*, CAS 213855, 63 mm SL.

The known distribution of *Dialommus macrocephalus* is from Cape San Lucas to the Bay of Panama and *D. fuscus* is widely distributed within the Galápagos archipelago and Cocos Island (Costa Rica). *Cottoclinus canops* is known only from the Galápagos. Based on the basal position of *C. canops*, it could be argued that the tribe evolved on the Galápagos and that the progenitor of *D. macrocephalus* invaded the mainland from there or from Cocos Island.

The tribal name Mnierpini, based on a generic junior synonym, is retained in accordance with Article 40.1 of the Code of Zoological Nomenclature: "When the name of a type genus of a nominal family-group taxon is considered to be a junior synonym of the name of another nominal genus, the family-group name is not to be replaced on that account alone" (International Commission on Zoological Nomenclature 1999).

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