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THE CABALLO MUERTO COMPLEX AND ITS PLACE IN THE ANDEAN CHRONOLOGICAL SEQUENCE

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ABSTRACT

The Caballo Muerto complex in the Moche Valley, Peru, is a group of early ceramic mounds, which were constructed sequentially between 1500 and 400 B.C. Recovered ceramics show that most decoration and vessel forms cover the entire time span of the complex. When the Caballo Muerto complex is compared with other early sites in Peru. however, most types of ceramic decoration cannot be correlated with either the Initial Period (1800–900 B.C.) or the Early Horizon (900–200 B.C.). Thus, the distinction between the two periods is very vague. Attention is also paid to the fact that sites dating to the Initial Period and the Early Horizon on the coast have radiocarbon dates several hundred years earlier than supposedly comparable ones in the highlands. It is suggested that the so-called Chavin or Early Horizon sites bearing modeled adobe friezes on the coast actually predate the major constructions at Chavin de Huantar and Kotosh in the highlands and that certain iconographic and architectural configurations originated on the coast and diffused to the highlands. Basically, the Chavin phenomenon was not the widespread unifying force that has been proposed by most investigators. Instead, throughout early ceramic times (1800–200 B.C.) several regional polities developed and thrived both on the coast and in the highlands.

THE CABALLO MUERTO COMPLEX

The complex of early ceramic mounds known as Caballo Muerto is located on the north side of the Moche Valley on the north coast of Peru. Investigations of the complex by the author lasted from July 1973 to December 1974. Though Caballo Muerto is known primarily for the presence of adobe friezes at Huaca de los Reyes (Moseley and Watanabe, 1974:154–161; Pozorski, 1975:211–251, 1976:63–92, 1980:

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100–110, 1982:235–249), there are also chronological data, particularly concerning ceramics, that need to be presented in order to fully appreciate the significance of the complex.

Architectural Sequence

The complex consists of eight platform mounds of varying sizes that are distributed over an area of 2 km^2 (Fig. 1). Each mound is a corporate labor structure that has, or probably once had, a pair of small parallel wing structures extending out from its front face to form a large "U." The consistent "U" pattern plus the relatively large size of the mounds suggests that all shared a similar nondomestic function. In addition to the eight main mounds, the presence of a small niched room called the Hall of the Niches just south of Huaca Cortada (Fig. 1) indicates the possible existence of a ninth platform mound.

Among these mounds, however, certain architectural features differ which suggest gradual chronological change. Five features were useful in deriving a constructional sequence: 1) mound location, 2) main mound size and configuration, 3) large mound-small mound association, 4) mound orientation, and 5) entry pattern. The resultant seriation (Table 1) indicates that the mounds cluster into three groups—Group I consists of Huaca Cortada with the adjacent Hall of the Niches which is probably part of a small mound, Huaca Herederos Chica, and Huaca Herederos Grande; Group II contains Huaca de los Reyes, Huaca Curaca, and Huaca San Carlos; and Group III is made up of Huaca La Cruz and Huaca Guavalito.

There are two basic mound locations—on flat terrain or on a rocky hillside. Huaca Herederos Grande, Huaca Herederos Chica, Huaca Cortada, and Huaca Curaca are all built on flat terrain. Huaca de los Reyes is basically constructed on flat terrain except that its western half is situated on a natural flat-topped 6-m rise. The remaining three mounds, Huaca San Carlos, Huaca La Cruz, and Huaca Guavalito are all built on rocky hillsides in order to take advantage of the natural base to add height to the principal part of each mound.

A second characteristic is the size and configuration of the main mound. Huaca Herederos Grande and Huaca Cortada are large multitiered platform mounds about equal in volume and height; the length (defined as the distance along the principal site axis) of each mound is greater than the width (perpendicular to the main site axis). Huaca Curaca consists of two adjoining flat platforms of ascending height. In a much more elaborate sense, the main construction of Huaca de los Reyes has the same configuration (Pozorski, 1980:101–102, 1982: 232–235). On a much simpler level, Huaca San Carlos has the same layout. For all three mounds, the length is again greater than the width, or

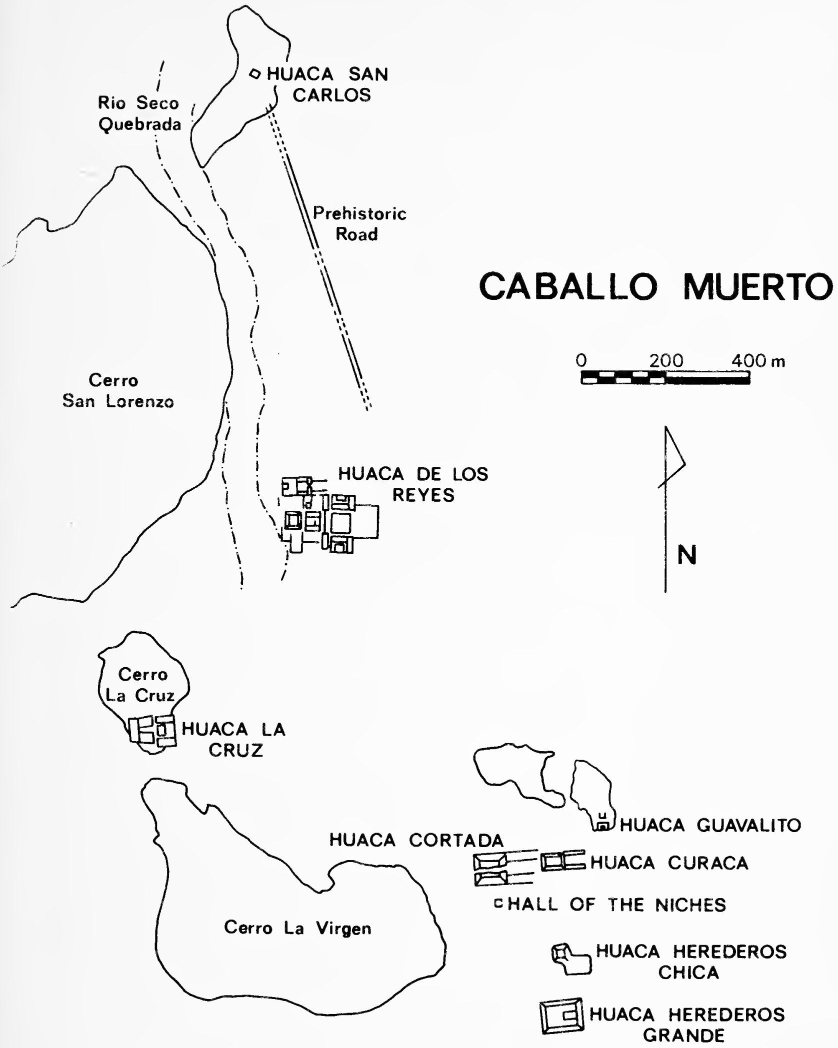

Fig. 1.—Map of the Caballo Muerto Complex showing the distribution of its component mounds.

very nearly the same. The final two sites, Huaca La Cruz and Huaca Guavalito, have main mounds that are wider than they are long.

The phrase "large mound-small mound association" describes a repetitive pattern of one small mound situated laterally and adjacent to

Table 1.—*Architectural component seriation of the Caballo Muerto mounds.*

Group	Mound	Flat terrain	Large mound-small mound associa-tion	Large multi-tiered	Small	E10°N	Central staircase	Small ridge	2 Flat plat-forms	E5°N	E35°S	Paired stair-cases	Hillside	High and narrow	S10°E
I	Cortada	+	+	+		+	+								
	Niches	+	+		+	+	+?								
	H. Chica	+	+		+	+	+								
	H. Grande	+	+	+		+	+								
II	Reyes 1 & 2	+	+				+	+	+	+		+			
	Curaca 1[1]	+				+	+		+						
	San Carlos						+		+		+		+		
III	La Cruz					+	+					+	+	+	
	Guavalito											+	+	+	+

[1] Data from Huaca Curaca construction phase 2 are insufficient for inclusion in the seriation.

a much larger mound. This association exists in three places within Caballo Muerto: 1) between Huaca Herederos Chica (small mound) and Huaca Herederos Grande (large mound), 2) between the Hall of the Niches (small mound) and Huaca Cortada (large mound), and 3) between the subsidiary mounds and the main mounds of Huaca de los Reyes. Proximity and similar orientation make these associations significant.

Mound orientation is another architectural seriation characteristic. Five of the mounds have a common orientation, with the open end of the "U" directed E10°N (magnetic north). Huaca de los Reyes, oriented E5°N, varies slightly. Major orientation shifts occur in Huaca San Carlos, opening E35°S, and Huaca Guavalito, at S10°E, respective 45° and 90° shifts from the predominant mound orientation.

The fifth characteristic is entry pattern, which is concerned with access to the main mound as one passes through each site. Huaca Herederos Grande, Huaca Cortada, Huaca Curaca, and Huaca San Carlos all have central staircases, each located along the principal site axis. Huaca Herederos Chica probably has or had a central staircase. Huaca de los Reyes and Huaca La Cruz have both central staircases and paired staircases bilaterally symmetrical with respect to the main site axis. At Huaca de los Reyes, however, the central staircase is the predominant access pattern whereas at Huaca La Cruz the opposite is true. At Huaca Guavalito, the concept of central staircases appears to have been abandoned altogether.

The resultant seriation of the Caballo Muerto mounds is supported by the position of Huaca Curaca, a Group II mound, relative to Huaca Cortada, a Group I mound. Huaca Curaca is situated such that it blocks the entrance to the main plaza in front, or east, of Huaca Cortada, indicating that Huaca Curaca is later in date.

The Caballo Muerto architectural seriation is based on the principal constructions of each mound. There are indications of later architectural additions and overlap in artifact assemblages which suggest extended use of some mounds during and/or after construction of other mounds (Pozorski, 1976:114–120). This is evident for construction phase 2 of Huaca Curaca which dates to the time of the main construction of Huaca Guavalito. In addition, Luis Watanabe (personal communication) recovered ceramics from the uppermost levels at Huaca Herederos Chica which apparently date to the Group III occupation of the complex.

Radiocarbon Dating

In general, the radiocarbon dates from each group of mounds support the relative mound sequence (Table 2). Two dates from the same cul-

Table 2.—*Radiocarbon dates for the Caballo Muerto complex.*

	Group	Caballo Muerto mound	Radiocarbon date
400 B.C.	III	Huaca Guavalito	440 B.C. ± 70 (Tx-1939)
		Huaca Curaca, Phase 2	
		Huaca La Cruz	
	II	Huaca San Carlos	
		Huaca Curaca, Phase 1	
		Huaca de los Reyes, Phase 2	
		Huaca de los Reyes, Phase 1	850 B.C. ± 60 (Tx-2180)
			1190 B.C. ± 60 (Tx-1973)
			1360 B.C. ± 80 (Tx-1972)
			1730 B.C. ± 80 (Tx-1974)
1400 B.C.			
	I	Huaca Herederos Chica	1090 B.C. ± 60 (Tx-1937)
		Huaca Herederos Grande	1500 B.C. ± 70 (Tx-1938)
		Hall of the Niches	
		Huaca Cortada	
1800 B.C.			

tural context at Huaca Herederos Chica, 1090 B.C. ± 60 (Tx-1937) and 1500 B.C. ± 70 (Tx-1938), average 1300 B.C. From construction phase 1 at Huaca de los Reyes, four dates also averaging 1300 B.C. are available from the same context—850 B.C. ± 60 (Tx-2180), 1190 B.C. ± 60 (Tx-1973), 1360 B.C. ± 80 (Tx-1972), and 1730 B.C. ± 80 (Tx-1974). For the Group III mounds, a single date of 440 B.C. ± 70 (Tx-1939) was taken from a sealed floor of Huaca Guavalito. Though there is some overlap in the dating of the Group I and Group II mounds, it is clear that most of the mounds in these two groups predate 1000 B.C. The Group III mounds appear to date well after 1000 B.C., with a terminal construction date of about 400 B.C.

Nonceramic Artifacts

The validity of the ordering of the architectural sequence is strengthened by nonceramic artifacts at some Group I and Group II mounds which are similar to artifacts found at the early coastal site of Gramalote that has six radiocarbon dates ranging from 1590 to 1100 B.C. (Pozorski and Pozorski, 1979:418–421). These artifacts, found at Huaca Herederos Chica, Huaca Cortada, and Huaca de los Reyes, include jet mirrors, stone bowl fragments, hammerstones, smooth stones, stone paint palettes, and shell paint palettes. In addition, at the same three mounds there are impressions of simple weaving, knitting, and straight-paired twining preserved in adobe roofing fragments that are similar to actual cloth specimens found at Gramalote (Conklin, 1974:77–92).

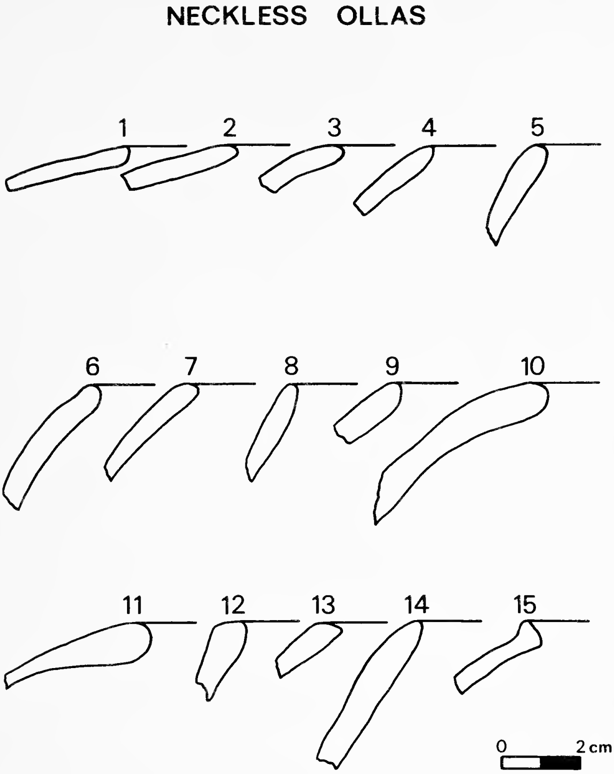

Fig. 2.—Neckless olla rim profiles from Caballo Muerto.

Ceramics

The seriation of ceramic material is continuous when arranged according to the stratigraphic evidence and the architectural sequence. Absolute differences in ceramic traits are few, however, with most differences in terms of degree rather than presence or absence.

Of a total of 10,240 sherds, the majority were found within architectural fill and fallen wall debris, though a significant portion was associated with plastered floors. Thin (3–6 mm) coarse utilitarian ware, both oxidized and reduced, makes up the bulk of the collection and varies from 80% to 90% of the Group I assemblage to 65% to 70% for the later mounds. Oxidized and reduced fine ware constitutes the remainder of the sample.

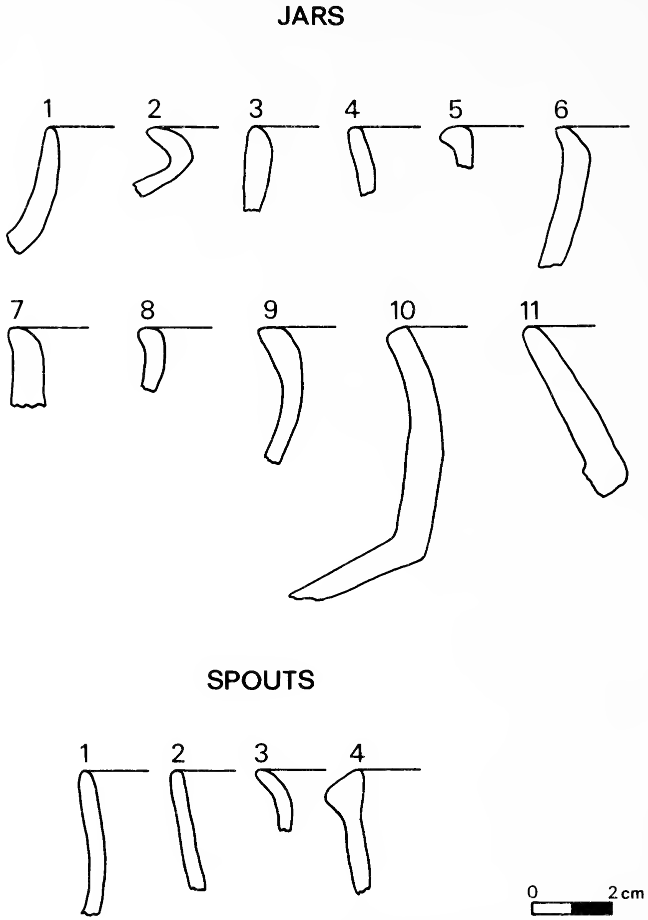

Fig. 3.—Jar and spout rim profiles from Caballo Muerto. Spout rims 1–3 are from stirrup spout vessels and spout rim 4 is from a single-neck bottle.

Sixty-five percent of the 679 rim sherds found are made of coarse ware. Vessel forms are limited to neckless ollas, short neck jars, open bowls with straight or everted sides, stirrup spout bottles, and, rarely, tall single-neck bottles (Figs. 2–4). Some partially restorable vessels were encountered, indicating that most bottle forms and bowls were flat-bottomed whereas neckless ollas and jars were generally round-bottomed. Jars and bowls occur among types of both coarse ware and fine ware. Neckless ollas are restricted to coarse ware types, whereas stirrup spout bottles are virtually limited to fine ware types.

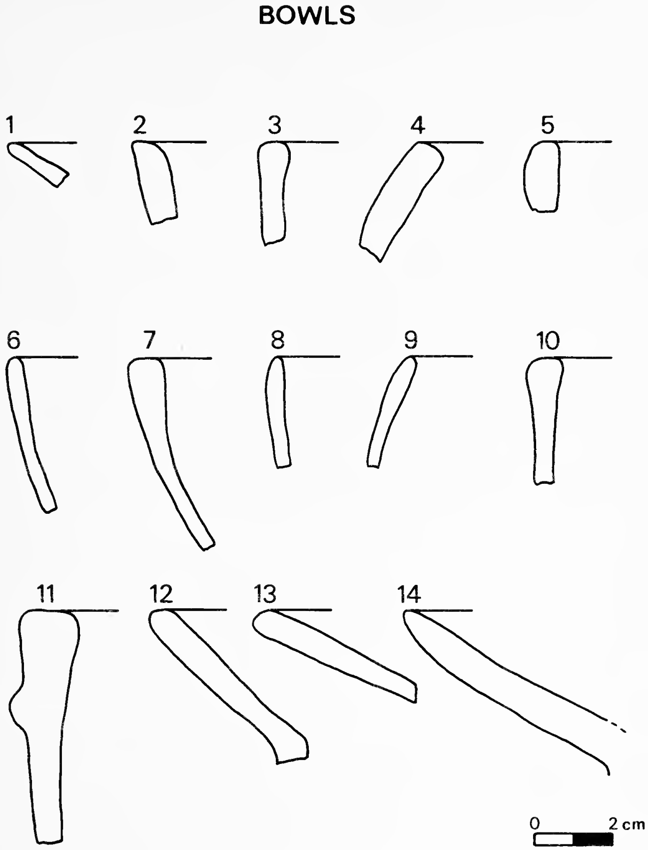

Fig. 4.—Bowl rim profiles from Caballo Muerto.

Neckless ollas predominate throughout, but are especially frequent at the earlier mounds. Neckless olla rim 8 (Fig. 2) seems chronologically significant because, though present at all of the mounds, it occurs only in the first construction phase at Huaca Guavalito. Neckless olla rim form 9 (Fig. 2) is present only at Huaca de los Reyes and later mounds. Diagnostic jar rim forms include numbers 3 and 7 (Fig. 3) for the early part of the sequence and numbers 9 and 10 for the end—within construction phase 2 of Huaca Curaca and at Huaca Guavalito.

Of the numerically significant bowl rims, the absence of form 6 (Fig. 4) separates Huaca Guavalito and phase 2 of Huaca Curaca from the other mounds. Stirrup spout fragments (Fig. 14) were present at all

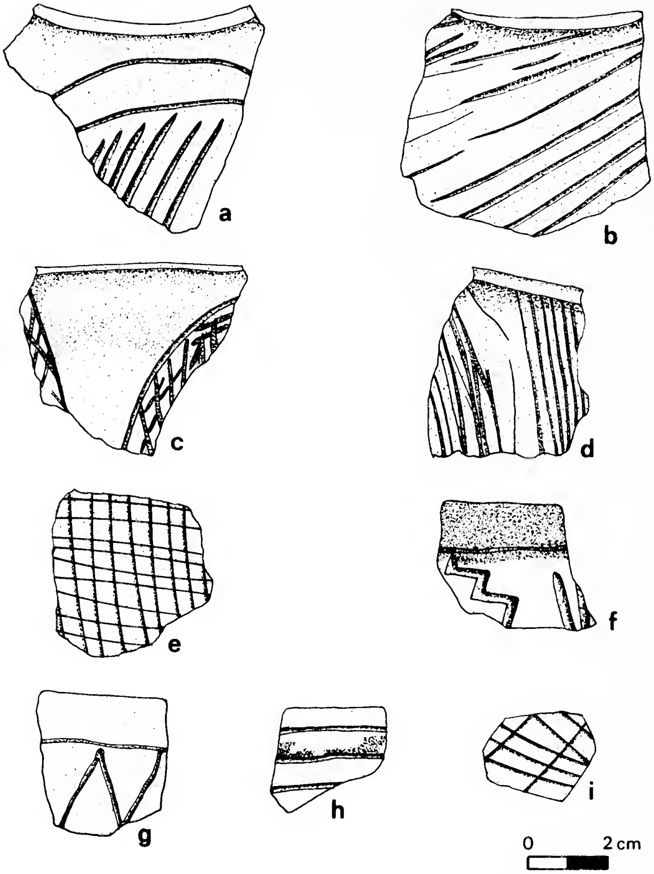

Fig. 5.—Incised and crosshatched sherds from Caballo Muerto: *a–c, e* are from Huaca Herederos Chica, *d* is from Huaca Guavalito, *f* and *h–i* are from construction phase 2 of Huaca de los Reyes and *g* is from construction phase 2 of Huaca Curaca.

sites, and much more common than definable stirrup spout rim forms (Fig. 3). The only two definite single-neck bottle rims found within the entire complex came from construction phase 2 of Huaca Curaca. Specific rim forms are not numerous enough to be considered diagnostic in themselves, but several fragments of stirrup spout arcs indicate that all examples are without decorative modeling and are trapezoid or rectangular in profile.

A total of 856 decorated sherds were recovered, 70% of which are made of fine ware. From the beginning of the sequence, there are numerous modes of decoration, most of which persist throughout the

Table 3.—*Distribution of Caballo Muerto ceramic decorative modes 1 through 7 by number and percentage.*

Context	Decorative modes						
	1	2	3	4	5	6	7
Group I (totals)	*36 (38%)*	*21 (21%)*	—	*87 (27%)*	*1 (13%)*	*15 (43%)*	*3 (21%)*
Cortada	8 (8%)	6 (6%)	—	13 (4%)	—	3 (8%)	—
Niches	10 (11%)	4 (4%)	—	7 (2%)	—	3 (8%)	—
H. Chica	17 (18%)	11 (11%)	—	66 (21%)	1 (13%)	9 (26%)	3 (21%)
H. Grande	1 (1%)	—	—	1 (0%)	—	—	—
Group II (totals)	*30 (31%)*	*54 (54%)*	*2 (33%)*	*117 (37%)*	*2 (25%)*	*11 (31%)*	*4 (29%)*
Reyes 1	2 (2%)	2 (2%)	—	6 (2%)	—	—	2 (14%)
Reyes 2	26 (27%)	52 (52%)	1 (17%)	107 (34%)	2 (25%)	8 (23%)	2 (14%)
San Carlos	—	—	—	1 (0%)	—	3 (8%)	—
Curaca 1	2 (2%)	—	1 (17%)	3 (1%)	—	—	—
Group III (totals)	*30 (31%)*	*25 (25%)*	*4 (67%)*	*114 (36%)*	*5 (62%)*	*9 (26%)*	*7 (50%)*
Curaca 2	18 (19%)	6 (6%)	1 (17%)	65 (20%)	—	7 (20%)	2 (14%)
La Cruz	1 (1%)	1 (1%)	—	3 (1%)	—	—	—
Guavalito	11 (11%)	18 (18%)	3 (50%)	46 (15%)	5 (62%)	2 (6%)	5 (36%)
Total for caballo Muerto complex	*96 (100%)*	*100 (100%)*	*6 (100%)*	*318 (100%)*	*8 (100%)*	*35 (100%)*	*14 (100%)*

1) Punctation.
2) Zoned punctation.
3) Zoned punctation, lines filled with graphite.
4) Incision.
5) Patterned burnishing.
6) Crosshatching.
7) Incised raised bands.

chronological sequence, with new modes simply added to the repertoire (Tables 3–7). For the Group I mounds, there are 13 modes of decoration: 1) fine-line incision (1 mm or less wide), 2) broad-line incision (more than 1 mm wide), both of which are executed in wet paste forming geometric patterns (Figs. 5a–b, 10a–b, d, f–h, 11h, 15a–d); 3) circular and diagonal punctation, both unzoned and zoned by incised lines (Figs. 8c–e, 9b–g, 16a–d); 4) crosshatching (Figs. 5c, e, 10c, 11a–b, i); 5) combing, a type of decoration consisting of a series of parallel, non-overlapping incised lines made by use of an implement with six to nine teeth; 6) raised ribs or bands, usually marked by incisions executed transversely or obliquely to the length of the band (Fig. 12d); 7) modeling, probably part of figurines or figured vessels; 8) pattern burnishing, usually in the form of parallel lines; 9) appliqué bumps, measuring a few millimeters in each direction and usually bearing incision (Fig. 12h); 10) post-fired paint within and outside incised lines; 11) rim or lip incision (Figs. 13e, 17a); 12) square rim castellation; and 13) black zoning, probably consisting of graphite. There are also numerous examples of sherds bearing combinations of the above techniques.

For mounds of Groups II and III, all forms of decoration except rim castellation continue, usually in continuous succession, but with certain frequency fluctuations (Figs. 5d, f–i, 6c, 7d–g, 8a–b, f–h, 9a, h, 10e, 11c–g, 12a–c, e–g, 13a–d, f, 17b–e, 18a–d, 19a–d). A significant chronological marker separating these latter two groups from Group I is the use of a black, probably graphite, paint. It is used both as a filler of incision, often in combination with punctation or raised bands (Figs. 6a–b, 21e), and as black bands or zones painted on flat surfaces, usually demarcated by incised lines (Figs. 6d–f, 7a–c, e–g, 20a–e, 21a–b). Despite the presence of two black zoned sherds at Huaca Herederos Grande, these techniques statistically appear to be definite time markers, and are exclusively associated with two types of reddish brown burnished fine ware. The use of graphite or manganese as a slip entirely covering one or both surfaces of a vessel (Figs. 6g–h, 21c–d) is especially abundant at Huaca Guavalito and therefore further distinguishes this mound from other mounds within the complex.

The end of the mound sequence at Caballo Muerto is distinguished by four additional decorative modes. Plain and dentate rocker stamping (Fig. 13g–h) occurs only at Huaca Guavalito and in construction phase 2 of Huaca Curaca. One sherd recovered from Huaca Guavalito appears to be "brushed," bearing a dense cluster of multiple incisions that generally run in the same direction, but frequently overlap. Cane-stamped and incised circles (Fig. 22a–g), usually about 2 cm in diameter, exist in small numbers at the remodeled Huaca Curaca and in greater quantity at Huaca Guavalito. A lone example of stamped circles is seen in Huaca de los Reyes, but these are much smaller (4 mm in

Table 4.—*Distribution of Caballo Muerto ceramic decorative modes 8 through 14 by number and percentage.*

Context	Decorative modes						
	8	9	10	11	12	13	14
Group I (totals)	*6 (75%)*	—	*2 (67%)*	—	—	—	*2 (14%)*
Cortada	3 (38%)	—	—	—	—	—	—
Niches	—	—	1 (33%)	—	—	—	1 (7%)
H. Chica	3 (38%)	—	1 (33%)	—	—	—	1 (7%)
H. Grande	—	—	—	—	—	—	—
Group II (totals)	*2 (25%)*	—	—	—	—	—	*8 (57%)*
Reyes 1	2 (25%)	—	—	—	—	—	1 (7%)
Reyes 2	—	—	—	—	—	—	7 (50%)
San Carlos	—	—	—	—	—	—	—
Curaca 1	—	—	—	—	—	—	—
Group III (totals)	—	*35 (100%)*	*1 (33%)*	*1 (100%)*	*1 (100%)*	*1 (100%)*	*4 (29%)*
Curaca 2	—	3 (9%)	1 (33%)	1 (100%)	1 (100%)	—	1 (7%)
La Cruz	—	—	—	—	—	—	—
Guavalito	—	32 (91%)	—	—	—	1 (100%)	3 (22%)
Total for Caballo Muerto complex	*8 (100%)*	*35 (100%)*	*3 (100%)*	*1 (100%)*	*1 (100%)*	*1 (100%)*	*14 (100%)*

8) Incised raised bands with accompanying incised lines.
9) Incised raised bands with accompanying incised lines filled with graphite.
10) Incised raised bands with combing.
11) Incised raised bands with punctation.
12) Incised raised bands with punctation and combing.
13) Incised raised bands with graphite zoning.
14) Figurine or modeling fragments.

Table 5.—*Distribution of Caballo Muerto ceramic decorative modes 15 through 21 by number and percentage.*

Context	Decorative modes						
	15	16	17	18	19	20	21
Group I (totals)	—	*1 (33%)*	—	*1 (11%)*	—	—	*2 (50%)*
Cortada	—	—	—	—	—	—	—
Niches	—	—	—	—	—	—	—
H. Chica	—	1 (33%)	—	1 (11%)	—	—	2 (50%)
H. Grande	—	—	—	—	—	—	—
Group II (totals)	*6 (32%)*	*1 (33%)*	*1 (100%)*	*1 (11%)*	*2 (12%)*	—	—
Reyes 1	—	—	—	—	—	—	—
Reyes 2	2 (11%)	1 (33%)	1 (100%)	1 (11%)	2 (12%)	—	—
San Carlos	—	—	—	—	—	—	—
Curaca 1	4 (21%)	—	—	—	—	—	—
Group III (totals)	*13 (68%)*	*1 (33%)*	—	*7 (78%)*	*14 (88%)*	*32 (100%)*	*2 (50%)*
Curaca 2	2 (11%)	1 (33%)	—	—	—	2 (6%)	2 (50%)
La Cruz	—	—	—	—	—	—	—
Guavalito	11 (57%)	—	—	7 (78%)	14 (88%)	30 (94%)	—
Total for Caballo Muerto complex	*19 (100%)*	*3 (100%)*	*1 (100%)*	*9 (100%)*	*16 (100%)*	*32 (100%)*	*4 (100%)*

15) Incisiion filled with graphite.
16) Incision filled with postfired paint.
17) Incision associated with a white slip.
18) Appliqué.
19) Appliqué with accompanying incision.
20) Appliqué with combing.
21) Appliqué with punctation.

Table 6.—*Distribution of Caballo Muerto ceramic decorative modes 22 through 28 by number and percentage.*

	Decorative modes						
Context	22	23	24	25	26	27	28
Group I (totals)	—	*2 (3%)*	*2 (100%)*	*2 (33%)*	*2 (11%)*	—	—
Cortada	—	—	—	—	1 (5%)	—	—
Niches	—	—	—	—	1 (5%)	—	—
H. Chica	—	—	2 (100%)	1 (17%)	—	—	—
H. Grande	—	2 (3%)	—	1 (17%)	—	—	—
Group II (totals)	—	*47 (66%)*	—	*2 (33%)*	—	*1 (100%)*	—
Reyes 1	—	1 (1%)	—	—	—	—	—
Reyes 2	—	41 (58%)	—	2 (33%)	—	—	—
San Carlos	—	—	—	—	—	—	—
Curaca 1	—	5 (7%)	—	—	—	1 (100%)	—
Group III (totals)	*1 (100%)*	*22 (31%)*	—	*2 (33%)*	*16 (89%)*	—	*1 (100%)*
Curaca 2	—	13 (18%)	—	—	5 (28%)	—	—
La Cruz	—	—	—	2 (33%)	—	—	—
Guavalito	1 (100%)	9 (13%)	—	—	11 (61%)	—	1 (100%)
Total for Caballo Muerto Complex	*1 (100%)*	*71 (100%)*	*2 (100%)*	*6 (100%)*	*18 (100%)*	*1 (100%)*	*1 (100%)*

22) Appliqué with punctation and combing.
23) Graphite zoning and bands.
24) Rim castellation.
25) Rim incision.
26) Combing.
27) Combing with graphite zoning.
28) Rocker stamping and incision.

Table 7.—*Distribution of Caballo Muerto ceramic decorative modes 29 through 34 by number and percentage.*

Context	Decorative modes					
	29	30	31	32	33	34
Group I (totals)	—	—	—	—	—	—
Cortada	—	—	—	—	—	—
Niches	—	—	—	—	—	—
H. Chica	—	—	—	—	—	—
H. Grande	—	—	—	—	—	—
Group II (totals)	—	—	*1 (5%)*	—	—	—
Reyes 1	—	—	—	—	—	—
Reyes 2	—	—	1 (5%)	—	—	—
San Carlos	—	—	—	—	—	—
Curaca 1	—	—	—	—	—	—
Group III (totals)	*1 (100%)*	*1 (100%)*	*19 (95%)*	*7 (100%)*	*2 (100%)*	*1 (100%)*
Curaca 2	1 (100%)	1 (100%)	3 (15%)	2 (29%)	1 (50%)	—
La Cruz	—	—	—	—	—	—
Guavalito	—	—	16 (80%)	5 (71%)	1 (50%)	1 (100%)
Total for Caballo Muerto complex	*1 (100%)*	*1 (100%)*	*20 (100%)*	*7 (100%)*	*2 (100%)*	*1 (100%)*

29) Rocker stamping, appliqué, and incision.
30) Rocker stamping.
31) Circles.
32) Circles with central dots.
33) Concentric circles.
34) Brushing.

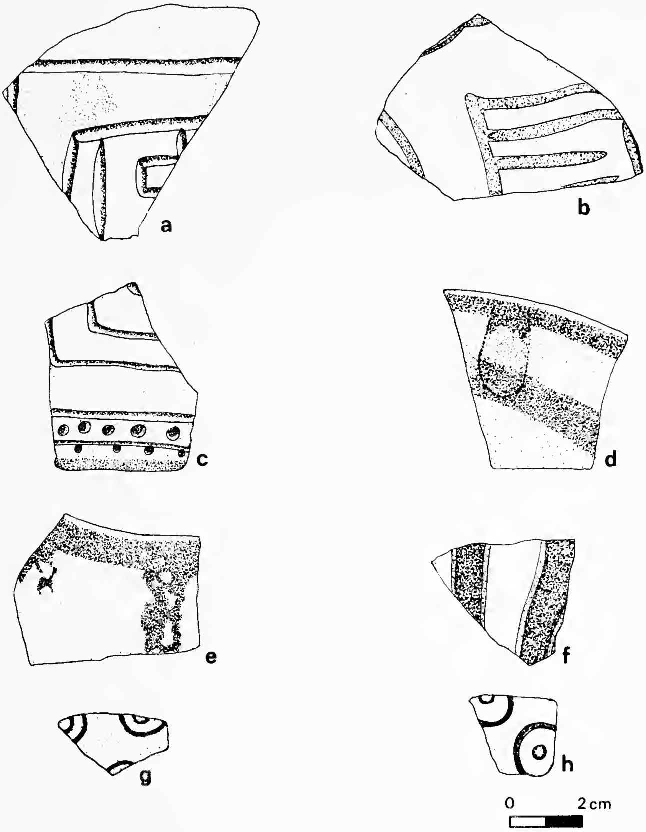

Fig. 6.—Decorated sherds from Caballo Muerto: *a* is from Huaca La Cruz, *b–d* and *g–h* are from Huaca Guavalito, *e* is from construction phase 2 of Huaca Curaca, and *f* is from construction phase 2 of Huaca de los Reyes. Sherds *a–b* have graphite within incised decoration, *c* is decorated with incision and punctation which is covered with an exterior graphite slip, *d–f* are decorated with painted graphite bands, and *g–h* have stamped circular decoration.

diameter) than the normal sized circles present at the other two mounds. The larger circles at Huaca Curaca and Huaca Guavalito occasionally contain either a small central circular punctate or a small central concentric circle (Fig. 6g–h). The circular designs are usually associated with the fine ware type that is covered completely with graphite or manganese, but are also present on a reddish brown fine ware. Broad-line incision executed upon the graphite covered fine ware represents the only possibility of naturalistic designs within the entire Caballo

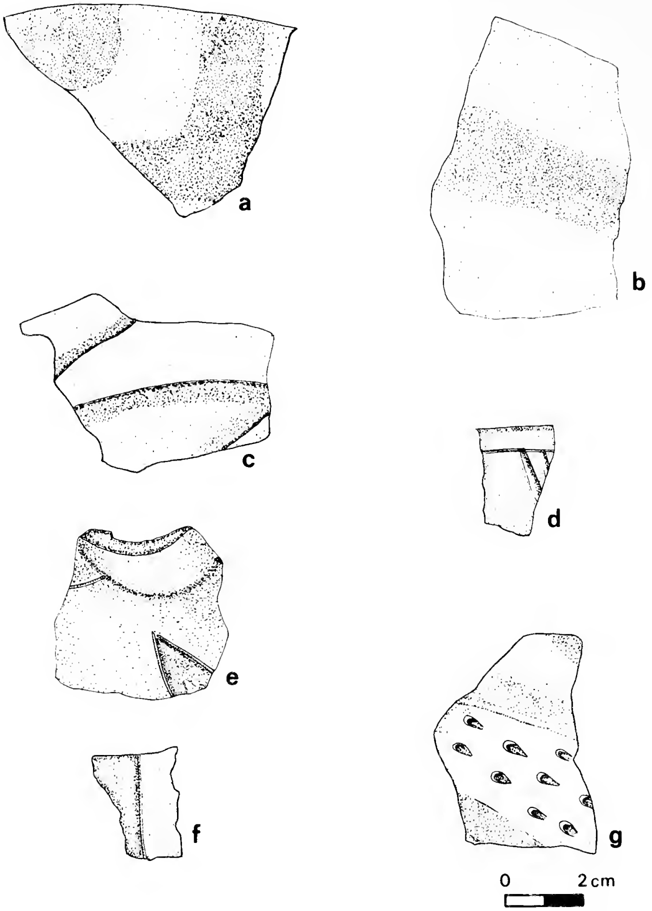

Fig. 7.—Decorated sherds from Caballo Muerto: *a* is from Huaca Guavalito, *b–e* and *g* are from construction phase 2 of Huaca de los Reyes, and *f* is from construction phase 1 of Huaca Curaca. Sherds *a–c* and *e–g* have painted zones and bands of graphite, *g* also has zoned punctation, and *d* has incised decoration.

Muerto complex. One example may represent a claw whereas a few others might once have been parts of feline motifs.

In comparing the Caballo Muerto ceramic assemblage with that of Gramalote, the correspondence is very close, especially for Groups I and II. The primary vessel form at Gramalote is the neckless olla with lesser quantities of jars and bottles. Decoration consists of incision, zoned punctation, and decorated raised ribs or bands.

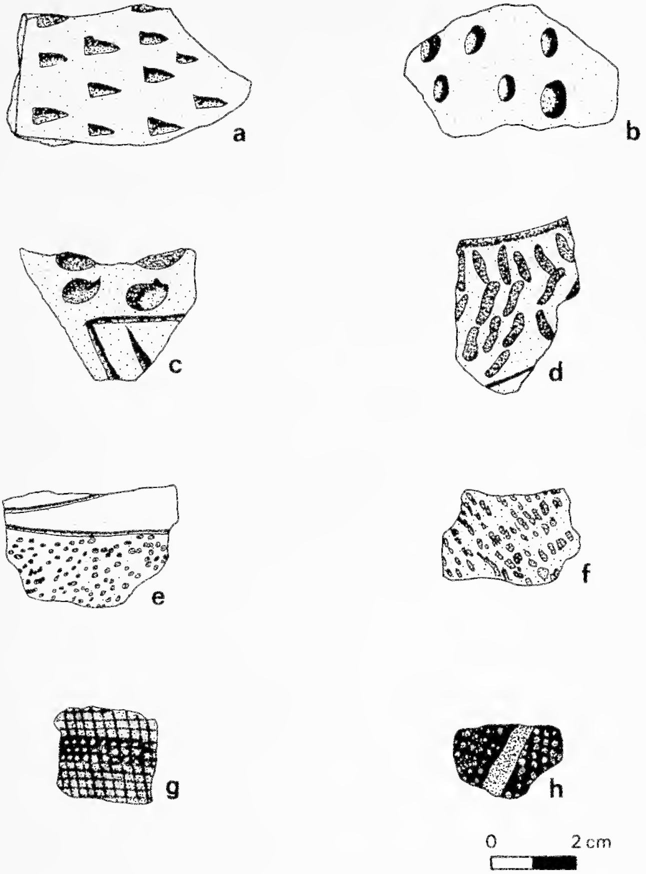

Fig. 8.—Sherds with punctation and zoned punctation from Caballo Muerto: *a* is from Huaca La Cruz, *b* is from construction phase 2 of Huaca de los Reyes, *c–e* are from Huaca Herederos Chica, *f* is from construction phase 1 of Huaca de los Reyes and *g–h* are from Huaca Guavalito. Sherds *g–h* were probably decorated using a multi-pronged instrument.

INITIAL PERIOD VERSUS EARLY HORIZON

Up to now, the terms "Initial Period" and "Early Horizon," using the Rowe (1960:627–631) terminology, have been avoided during this discussion of Caballo Muerto, with preference given instead to the more general term "early ceramic." The reason for this avoidance is simple—the distinction between the Initial Period and the Early Horizon is not a clear one. In theory, the distinction seems obvious. Using the Ica

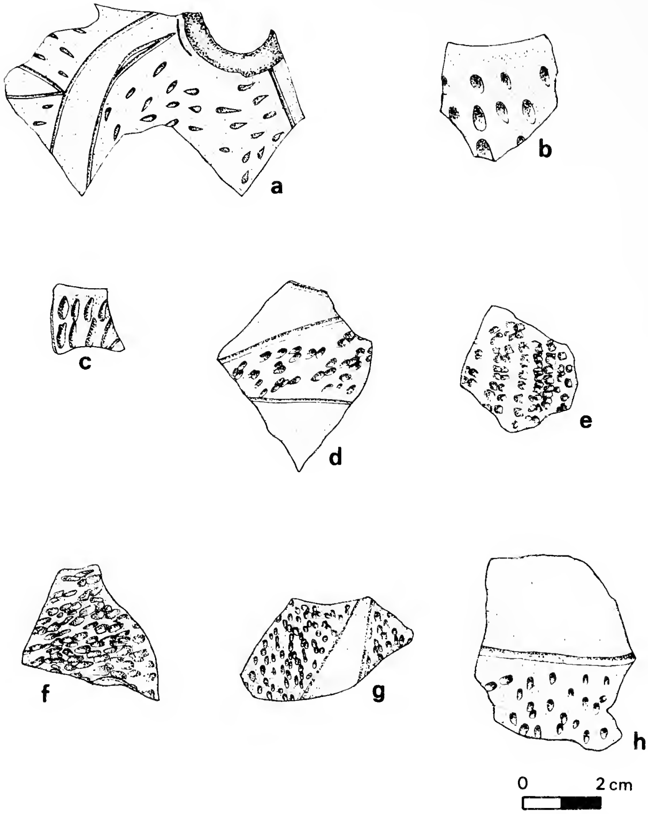

Fig. 9.—Sherds bearing punctation and zoned punctation from Caballo Muerto: *a* and *h* are from construction phase 2 of Huaca de los Reyes, *b* and *d–g* are from Huaca Herederos Chica, and *c* is from the Hall of the Niches.

Valley to set up a master sequence, Rowe (1962*a*:49) designated the Initial Period as the time of the introduction of pottery in Ica. The Early Horizon begins with the first appearance of Chavin influence at Ica. It is characterized by the Chavin style and lasts until polychrome slip painting replaces resin painting in that valley (Rowe, 1960:628).

However, as Lumbreras (1974*a*:49) has pointed out, just because the Chavin cult is predominant in the Early Horizon, this does not mean that contemporary local cultures fold up and disappear. Several areas of Peru, especially southern Peru, were never touched by Chavin influence (Willey, 1951:137) despite the exaggerated claims of Carrion Cachot (1948:166) and Tello (1943:159, 1960:36–41). In the areas of

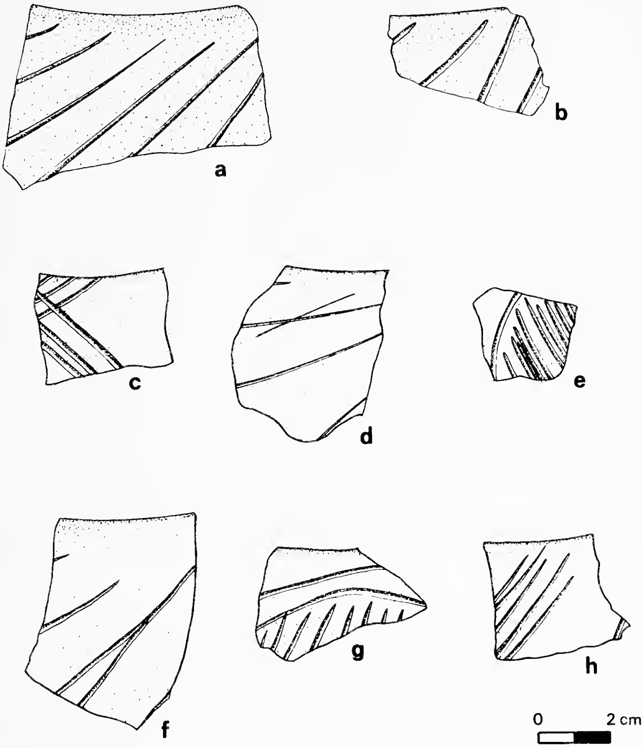

Fig. 10.—Incised sherds from Caballo Muerto: *a–d* and *f–h* are from Huaca Herederos Chica and *e* is from construction phase 2 of Huaca de los Reyes.

postulated Chavin influence, distinctions become blurred, especially with respect to ceramic decoration, because many techniques used during what has been defined as the Early Horizon were also employed in the time range designated Initial Period (Lanning, 1967:101).

First and foremost, it must be remembered that Chavin is essentially an art style, recognizable and distinguishable from other ancient Peruvian art styles. It is when one tries to relate the art style to cultural mechanisms that problems arise. If one adheres to the definition proposed by Willey (1951:138) of the Chavin style as "identical to, or closely resembling the designs of the stone carvings of the type site, Chavin de Huantar," then he is on fairly safe ground. If a stylistically definable Chavin figure, such as a feline, a bird, or a serpent is present, then one can assume that the culture that created such an artifact was in some way in contact with the Chavin phenomenon. Carrying this

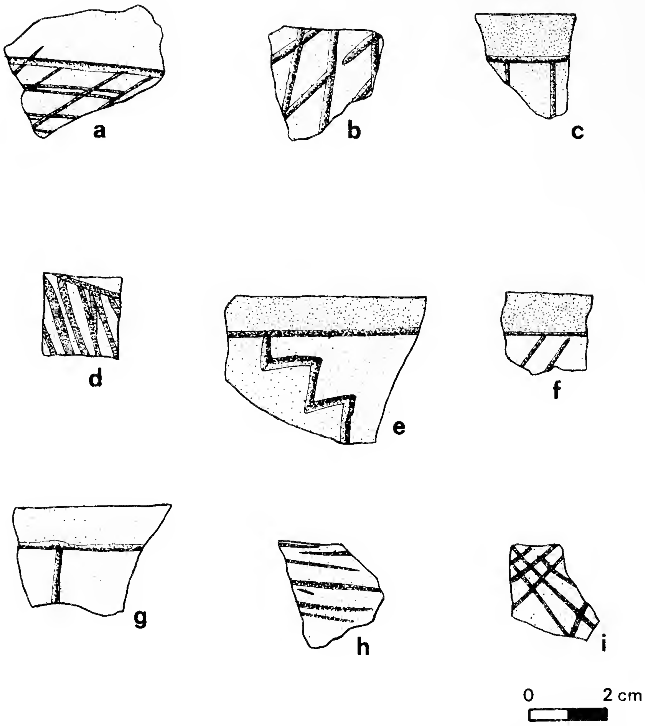

Fig. 11.—Incised and crosshatched decoration from Caballo Muerto: *a–b* and *h–j* are from the Hall of the Niches, *c–f* are from construction phase 2 of Huaca de los Reyes, and *g* is from construction phase 1 of Huaca de los Reyes.

process a step further, artifacts and other materials directly associated with Chavin art are then assumed to be closely connected with the Chavin phenomenon, especially if no local antecedents appear to be present at the site in question. Further, if artifacts associated with definite Chavin style objects are discovered at other sites without true Chavin style associations, then it is often assumed that these contemporary objects that are not stylistically Chavin also mark the spread of the Chavin phenomenon. This has precipitated a search for "fossil index" markers, in the sense used by Adams (1965; Adams and Nissen, 1972) of the Chavin phenomenon—artifacts that one can identify as pertaining exclusively to the spread of the Chavin cult of influence. Theoretically, such "fossil indices" are supposed to be valuable chronological tools, representing a relatively short-lived yet widespread entity or a horizon (Willey, 1951:11; Willey and Phillips, 1958:29–34).

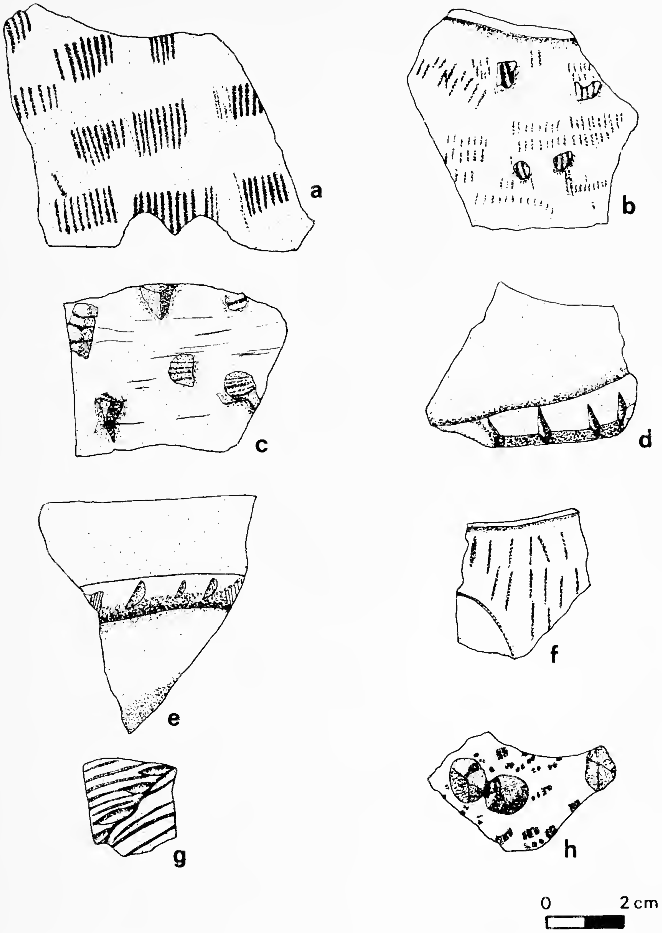

Fig. 12.—Decorated sherds from Caballo Muerto: *a–c* are from Huaca Guavalito, *d* and *h* are from Huaca Herederos Chica, *e–f* are from construction phase 2 of Huaca Curaca, and *g* is from construction phase 1 of Huaca de los Reyes. Sherd *a* is combed decoration, *b* has combing and appliqué bumps, *c* has appliqué bumps, *d–e* have incised raised bands, *f* has zoned slashlike punctations, *g* has an incised raised band as well as incision, and *h* has appliqué bumps and punctation.

Unfortunately, theory, at present, does not correlate well with fact. First, the Chavin phenomenon cannot be strictly called a horizon, because estimates of its duration often range up to 1000 years (Engel, 1966:41; Lumbreras, 1970:41; Mason, 1969:43; Proulx, 1973:6; Rowe,

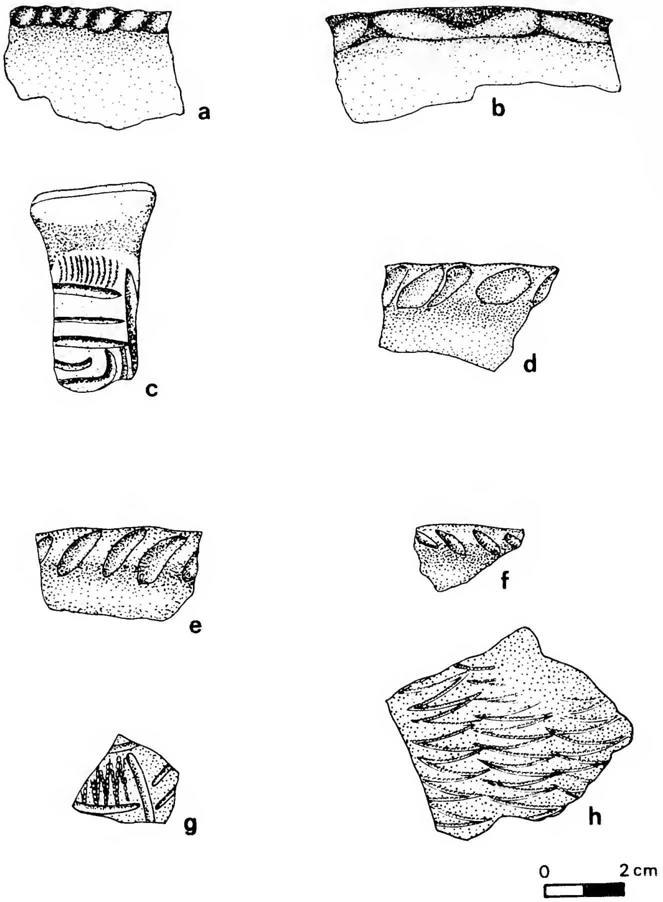

Fig. 13.—Decorated sherds from Caballo Muerto: *a* and *f* are from construction phase 2 of Huaca de los Reyes, *b* and *d* are from Huaca La Cruz, *c* is from construction phase 2 of Huaca Curaca, *e* is from Huaca Herederos Chica, *g* is from Huaca Guavalito, and *h* is from construction phase 2 of Huaca Curaca. Neckless olla sherds *a–b* and *d–f* have incised rim or lip decoration (interiors of sherds are shown), *c* is a bottle spout rim with incised decoration and *g–h* are decorated with dentate rocker sampling.

1967*a*:21, 25; Sawyer, 1968:18–19; Willey, 1971:84–85), and even the most conservative estimate would see it lasting for at least 400 years (Lanning, 1974:76). Second, attempts to find chronological markers other than actual Chavin style designs and motifs have been singularly unsuccessful. This failure is most evident in ceramic decoration.

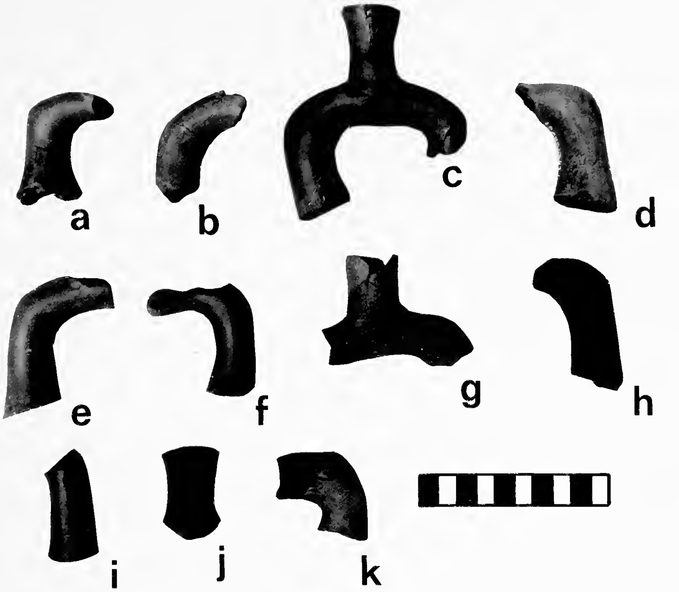

Fig. 14.—Stirrup spout fragments from Caballo Muerto: *a–g, i* and *k* are from Huaca de los Reyes construction phase 2, *h* is from Huaca La Cruz, and *j* is from Huaca de los Reyes construction phase 1.

Ceramic Evidence

Some investigators have designated certain ceramic motifs and modes of decoration as Chavin. One of the most often cited set of Chavin ceramic motifs is the circle, concentric circle, or circle and dot motif (Burger, 1978:336; Fung, 1969:138; Patterson, 1971:33; Proulx, 1973: 23–25; Rosas, 1976:571, 573; Shady, 1976:588; Willey and Corbett, 1954:37, 49), either as stamped or incised decorations. Another commonly cited Chavin motif is plain or dentate rocker-stamping (Collier, 1955:210; Flores, 1960:343; Fung, 1969:139; Matos, 1968:229; Patterson, 1971:32–33). Less cited examples of Chavin ceramic decoration include feline motifs (Matos, 1968:229; Patterson, 1971:33; Shady, 1975:588), pattern burnishing (Proulx, 1973:23; Rowe, 1960:628), and combing (Patterson, 1971:32–33; Rosas, 1976:568, 572).

A review of published literature reveals that each of these "Chavin markers" has been found in pre-Chavin or Initial Period contexts. For example, incised circles, concentric circles, and circle and dot motifs have been found in the highlands (Izumi and Sono, 1963:140, 153; Lathrap, 1974:75; Rosas, 1976:568; Rosas and Shady, 1970:8) and on

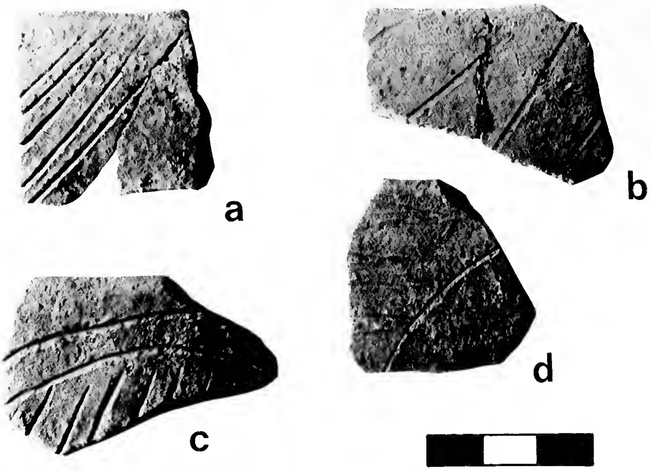

Fig. 15.—Incised neckless olla rims from Huaca Herederos Chica.

the coast Patterson, 1968:423). Stamped circular decoration occurs in Kotosh Kotosh levels at Kotosh (Izumi and Terada, 1972:186–188). Dentate rocker-stamping is pre-Chavin at Chavin de Huantar (Burger, 1978:99–101) and Kotosh (Izumi and Terada, 1972:188–189), and plain rocker-stamping occurs in Initial Period levels both in the highlands (Burger, 1978:101–102; Izumi, 1971:59, 62, 69; Izumi and Sono, 1963:139, 155; Izumi and Terada, 1972:189, 307) and on the coast (Patterson, 1971:32). In addition, feline motifs (Izumi, 1971:59, 69; Kano, 1979:28–38; Rosas, 1976:568; Rosas and Shady, 1970:9; Shady, 1976:588), pattern burnishing (Rosas, 1976:568; Izumi and Terada, 1972:196–198), and combing (Patterson, 1971:32; Rosas, 1976:568; Rosas and Shady, 1970:9) have all been found in pre-Chavin contexts.

All other decorative modes (except square rim castellation) found at Caballo Muerto have been found in Initial Period levels at sites on the coast and in the highlands. These modes include broad-line incision (Burger, 1978:81, 1979:136–137; Fung, 1969:67–69; Izumi and Sono, 1963:139, 153–155; Izumi and Terada, 1972:188–193; Lumbreras, 1974*a*:51–52; Matos, 1968:228–229; Strong and Evans, 1952:289–291); fine-line incision (Fung, 1969:71; Izumi and Terada, 1972:189–196; Larco Hoyle, 1941:81–82; Strong and Evans, 1952:286–289); punctation and zoned punctation (Burger, 1978:87–92; Grieder, 1975:105–106; Izumi, 1971:62–69; Lanning, 1967:86; Reichlen and Reichlen, 1949:154; Rosas and Shady, 1970:9; Strong and Evans, 1952:283–284; Willey, 1971:109); crosshatching (Fung, 1969:86; Patterson, 1971:32; Strong and Evans, 1952:287–288); decorated raised ribs or bands

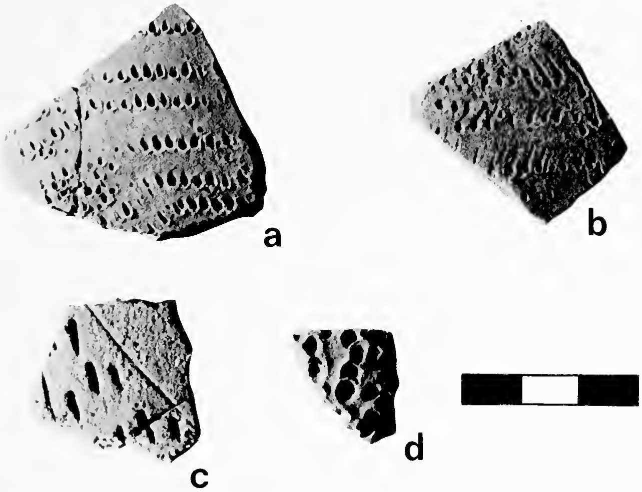

Fig. 16.—Sherds decorated with punctation (*a–b, d*) and zoned punctation (*c*) found at Huaca Herederos Chica.

(Burger, 1978:94–96; Izumi and Terada, 1972:192; Lanning, 1967:86; Rosas, 1976:568; Strong and Evans, 1952:277–282); modeling (Fung, 1969:67–69; Izumi and Sono, 1963:139, 154; Izumi and Terada, 1972: 194; Matos, 1966:515, 1968:229; Rosas and Shady, 1970:9); appliqué bumps (Collier, 1962:413; Lanning, 1967:85; Shady, 1976:582); post-fired paint (Burger, 1978:104; Fung, 1969:69; Izumi and Terada, 1972: 189, 192; Reichlen and Reichlen, 1949:154–155; Wallace, 1962:313); rim lip incision (Shady, 1976:582); and graphite as a filler of incision (Izumi and Terada, 1972:188, 193), in bands on zones (Engel, 1956: 103–104; Izumi and Sono, 1963:155; Lanning, 1967:85–86; Lumbreras, 1974*a*:54; Willey, 1971:109), and as an overall slip (Burger, 1978:103–104; Izumi and Sono, 1963:139, 155; Izumi and Terada, 1972:193).

Though virtually all of the decorative techniques present in the ceramic sample from Caballo Muerto have been recovered from Initial Period contexts in other parts of Peru, these data must be viewed in conjunction with vessel forms and ware types in order to assess the relationship Caballo Muerto had with other areas of Peru. Based on all these characteristics, the ceramics associated with the Group I and Group II mounds of Caballo Muerto, including Huaca de los Reyes, appear to be most closely related to the Early and Middle Guañape ceramics from Huaca Negra in Viru (Strong and Evans, 1952) and to those from Las Haldas south of Casma (Fung, 1969; Grieder, 1975),

Fig. 17.—Rim or lip incision on neckless olla sherds from Caballo Muerto. The interiors of the sherds are shown: *a* is from Huaca Herederos Grande, *b* and *d* are from Huaca La Cruz, and *c* and *e* are from construction phase 2 of Huaca de los Reyes.

two sites generally considered to be representative of the Initial Period (Lumbreras, 1974*a*:51–52; Willey, 1971:109).

Ceramic data suggest that for true time markers of the Chavin phenomenon one must rely on extant Chavin style designs as positive proof. That, however, can also be a mistake. The situation cannot be better exemplified than at Caballo Muerto. At Huaca de los Reyes, Chavin-related friezes are associated with numerous pottery decoration techniques, most of which are present at earlier mounds. Use of graphite in zones and within incision first appears in the Caballo Muerto complex at Huaca de los Reyes. None of the pottery fragments, however, including the graphite ones, exhibit definite Chavin style motifs. If the friezes were not present at Huaca de los Reyes, there would be no evidence that mound was Chavin-related since all of the associated pottery decorative techniques are known from other parts of Peru in pre-Chavin contexts.

Radiocarbon Evidence

The above dilemma points out the current chaotic state of the study of early Andean ceramics. Definitions of just what is "Chavin" and what is "pre-Chavin" seem to vary with each investigator. Absolute dating techniques can help, and an examination of dates from early

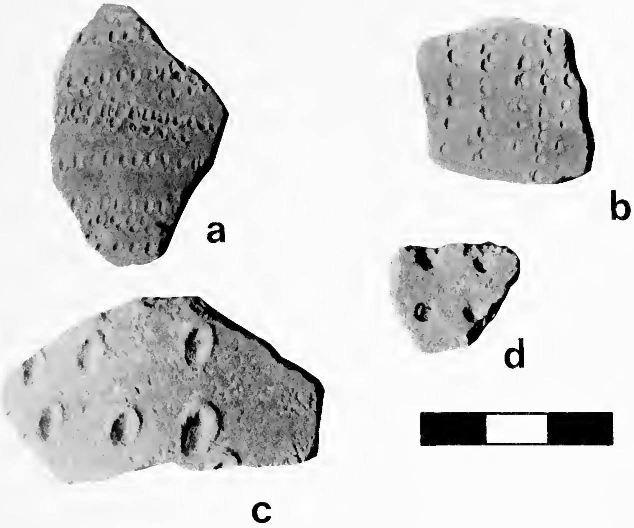

Fig. 18.—Punctated sherds from construction phase 2 of Huaca de los Reyes.

ceramic sites in the Andean area reveals enlightening patterns that are particularly relevant to the dating of the Initial Period and the Early Horizon.

Radiocarbon dates are available from four highland sites, Kotosh, Chavin de Huantar, Shillacoto, and Pacopampa. At Kotosh, the Kotosh Waira-Jirca pottery is dated by radiocarbon dates ranging from 1850 to 1050 B.C., with the investigators assigning a time range of 1500 to 1000 B.C. for the period (Izumi and Terada, 1972:308). The pre-Chavin Kotosh Kotosh period pottery is associated with dates ranging from 1120 to 890 B.C., with an assigned time range of about 1000 to 800 B.C. (Izumi and Terada, 1972:309). For Kotosh Chavin pottery, dates range from 1200 to 870 B.C., with an estimated time range of about 1000 to 300 B.C. (Izumi, 1971:59–62; Izumi and Sono, 1963:154–156; Izumi and Terada, 1972:310).

At Chavin de Hauntar, early dates ranging from 1420 to 940 B.C. have been reported (Amat, 1976:544; Lumbreras, 1970:133), but Burger (1981:596) feels that these dates may have been contaminated by groundwater carbonates. More secure dating obtained by Burger (1979: 154, 1981:594–596) correlates well with the majority of dates obtained by Lumbreras (1972:78). Burger (1981:596) dates the Initial Period or Urabarriu occupation from 850 to 460 B.C. and the last two Early Horizon phases, Chakinani and Janabarriu, as 460 to 390 B.C. and

390 to 200 B.C., respectively. The last phase, Janabarriu, is the one to which Burger (1978:396, 1981:600) ascribes the spread of Chavin influence over a pan-Andean area.

The site of Shillacoto has Waira-jircalike pottery which has a radiocarbon date of 1250 B.C. ± 80 (Izumi and Terada, 1972:308). Finally, at Pacopampa, pre-Chavin pottery is associated with a date of 1835 B.C. ± 100 (Rosas, 1976:568).

On the coast, there is a strikingly different pattern. Relatively few dates have been published for what has been called Chavin or Early Horizon related pottery, but extant dates range from 1090 to 342 B.C. with the majority of the dates in the 800 to 700 B.C. range (Bird, 1951:40; Collier, 1955:25, 1962:413; Fung, 1969:180–186; Ishida et al., 1960:518; Kigoshi et al., 1961:92; Rowe, 1967*a*:27–30). The more abundant dates for what is defined as Initial Period pottery range from 1940 to 570 B.C., with most falling within the 1600 to 1100 B.C. time span (Berger et al., 1965:347; Bird, 1951:40, Burger, 1981:594; Collier, 1955:25; Fung, 1969:180–186; Matos, 1968:230; Patterson, 1968:423; Rowe, 1967*a*:26–30).

Hence, two distinct patterns emerge from the absolute dates available for early ceramic sites in the Andean area. In general, the dates from coastal sites are substantially older than ones from the highlands, even when coastal and sierra sites that supposedly ceramically date to the same time period are compared. There is strong evidence to indicate that what is defined as the Initial Period or pre-Chavin pottery tradition, dominated by the neckless olla, goes back to at least 1800 B.C. on the coast and lasts for 700 years or more. Sites in the highlands assigned to the Initial Period are characterized by an additional variety of vessel shapes and decoration distinct from the coast. The *selva*-related Waira-jirca component at Kotosh and the early pottery of Pacopampa appear to be comparable in date to the coastal Initial Period sites such as Caballo Muerto, Huaca Negra, Las Haldas, Ancon, Garagay and La Florida. Other highland Initial Period components, however, at sites like Kotosh, Chavin de Huantar and Shillacoto date closer to 1000 B.C. or, as at Chavin de Huantar, 200 to 500 years later (Burger, 1981:596–599).

The same distinction between coast and highlands can be made for Chavin-related sites attributed to the Early Horizon. Coastal sites date closer to 1000 B.C., whereas sierra ones date nearer to 500 B.C. Clearly, highland sites attributed to the Initial Period and the Early Horizon date much later than coastal ones considered to be Initial Period and Early Horizon.

With the above review, it is clear that, based on absolute dating, only part of the Waira-jirca phase of Kotosh and the early phase of Pacopampa can be assigned to the Initial Period according to Rowe's

(1960:627–631, 1962*a*:49; Rowe and Menzel, 1967:vi–viii) definition and sequence which places this chronologically between 2100 and 1400 B.C. No other sierra sites are sufficiently early to be correlated with the master sequence of the Ica Valley. Several coastal sites, on the other hand, do date to the Initial Period. If, however, the dates of 1800 to 900 B.C. for the Initial Period according to Lanning (1967:25) are used, then some highland sites do belong in the Initial Period. Thus, the problem becomes one of deciding where to place the dividing line between the Initial Period and the Early Horizon. According to both sequences, sites are present both on the coast and in the highlands that date within the Early Horizon time span. However one looks at the situation, though, the coastal sites consistently predate their highland counterparts within the same general time period.

Reinterpreting the Chavin Phenomenon

In broader terms, how does one interpret this situation? What importance can be placed on the Chavin phenomenon? Was it really a unifying force? Present evidence suggests that it was not. In other words, there has been too much emphasis on relating sites to the Chavin phenomenon without objective analysis. Early civilization of the Peruvian coast was substantially different from that in the highlands, at least as exemplified in ceramics and architecture. Coastal pottery was dominated by the neckless olla tradition which lasted at least 1500 years from 1800 to 300 B.C. if not longer. Often this pottery is directly associated with large corporate labor U-shaped mounds which in turn are frequently associated with sunken circular forecourts. These architectural patterns can be traced back in time to the Cotton Preceramic period (Pozorski and Pozorski, 1979; Moseley, 1975:83; Williams, 1972, 1978–1980).

In the highlands, on the other hand, early pottery is generally later in date, of a finer quality, and bears a great variety of vessel shapes and decoration that are distinct from coastal pottery while showing strong ties to the tropical forest (Lathrap, 1971:73–100). This is especially true at Kotosh (Izumi and Sono, 1963; Izumi and Terada, 1972) and at the recently excavated site of Huaricoto near Huaraz (Burger and Burger, 1980). The one highland site that shows fairly strong ceramic affinities with the coast is Pacopampa (Rosas and Shady, 1970:1–16, 1974:6–32) in the northern highlands.

In terms of monumental architecture, the highlands have a pattern of small mounds and niched rooms that date as early as preceramic times as seen at Kotosh (Izumi and Sono, 1963:40–70, 153–154; Izumi and Terada, 1972:129–176), La Galgada in the upper Santa Valley (Bueno and Grieder, 1979; Grieder and Bueno, 1981:45–48), and Huaricoto (Burger and Burger, 1980:27–28). Chavin de Huantar shows in-

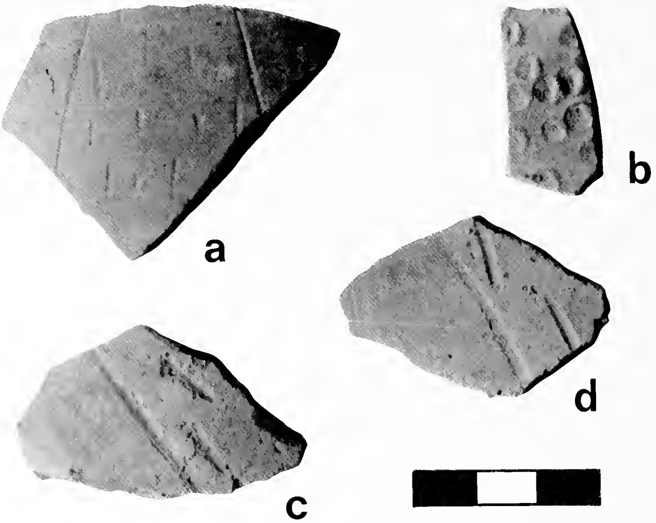

Fig. 19.—Punctated and zone punctated sherds from construction phase 2 of Huaca de los Reyes.

fluences both from the tropical forest and the coast in the form of ceramics and iconography (Burger, 1978:393–402; Lathrap, 1971:73–100). Given the late dates reported by Burger (1979:154–155, 1981: 592–602) which reinforce most of the dates obtained by Lumbreras (1972:78), it is also clear that coastal influence at Chavin de Huantar is reflected in the architecture—specifically the U-shaped mound form and the sunken circular forecourt (Lumbreras, 1971:2, Fig. 2, 1974*b*: 39, 1977:2–14, Laminas I–III).

Interaction occurred between the highlands and the coast, but only in a limited manner and only very late (that is, well into the first millenium B.C.). Chavin de Huantar ceramics contain several coastal elements, even in the earliest phases, and possible Cupisnique trade pieces are present (Burger, 1978:274, 394). On the coast, however, few clearly Chavin-associated highland ceramic traits have been reported, at least at the most famous of the so called "Chavin" sites. Significantly, for example, neither survey and excavation by Tello (1956:82) nor the later work of Collier and Thompson (Thompson, 1964:207) turned up any "Classic Chavin" pottery in the Casma Valley any nearer the coast than Pallka, situated about 40 km inland. Casma is the valley that contains Moxeke, noted for its "Chavin" adobe friezes, and Cerro Sechin, as well as several other reputedly "Chavin" sites. In the neighboring valley of Nepeña, which contains Cerro Blanco and Punkurí,

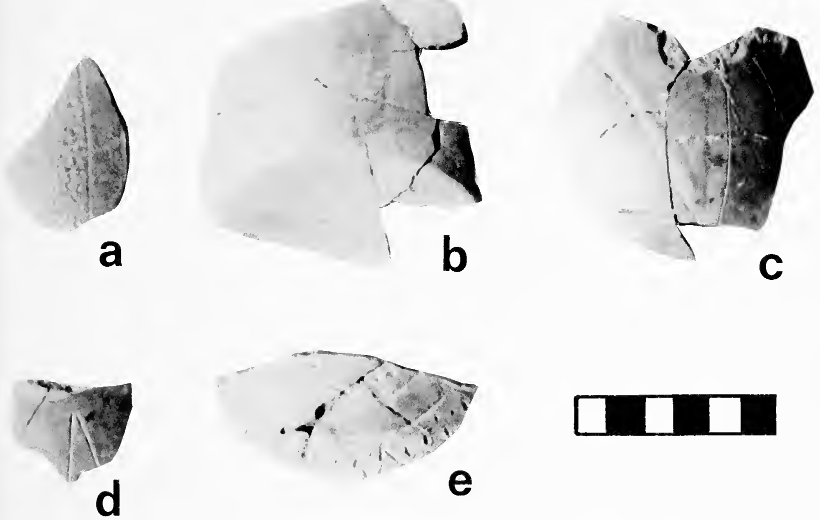

Fig. 20.—Sherds from construction phase 2 of Huaca de los Reyes bearing zones and bands of graphite paint.

both of which are said to have "Chavin" adobe friezes (Roe, 1974:37–38), highland-related pottery is concentrated in the middle and upper reaches of the valley (Daggett, personal communication; Proulx, 1973: 14–29), and no Early Horizon ceramic associations have been documented for the friezes of either Cerro Blanco or Punkurí (Tello, 1943).

However, when investigators speak of highland-coastal interaction during the Early Horizon, the Chavin phenomenon on the coast is invariably said to be represented by the iconography at Moxeke, Punkurí, and Cerro Blanco, occasionally by the anomalous site of Cerro Sechin, and by the Cupisnique pottery of Larco Hoyle from the north coast—all of which are essentially undated and tied only by seriational arguments to the sculptural sequence at Chavin de Huantar (Proulx, 1976:1–5; Rowe, 1962*b*:13, 1967*b*:76; Roe, 1974:26–39, 1978:1–41). Discoveries at Huaca de los Reyes and Garagay near Lima have been considered in this scenario by some authors who cite them as additional coastal examples of Chavin cult influence. Roe (1978:7–8) has recently stated that the Huaca de los Reyes friezes date to late phase D or early phase EF of the Rowe sequence in spite of iconographic (Pozorski, 1975:211–251, 1976:63–92, 112–114, 1980:100–110) and absolute dating evidence for Chavin de Huantar versus Huaca de los Reyes, which make that correlation impossible (Burger, 1981:600; Pozorski,

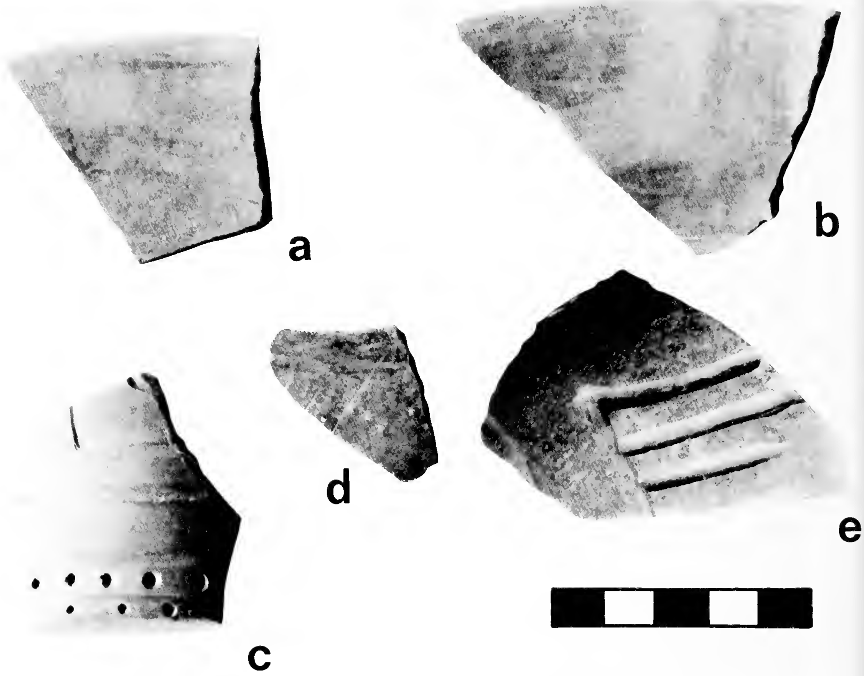

Fig. 21.—Sherds from Huaca Guavalito decorated with graphite: *a–b* are painted with bands of graphite, *c–d* each have an exterior graphite slip, and *e* has a red slip and graphite paint within incised decoration.

1980:108–109). If one accepts Burger's (1978:320, 1981:600) correlation of his Janabarriu phase, the time of the spread of Chavin dominance, with Rowe's phase E and his suggested dates of 390 to 200 B.C., then the radiocarbon dates of about 1300 B.C. from Huaca de los Reyes clearly do not match.

Although Burger (1981:598) accepts the Caballo Muerto dates, he questions them because all were run on *caña brava* (*Gynerium sagittatum*) which might give anomalous results like sugar cane and other grasses. However, Conrad (1974:739–748) had nine *caña brava* samples tested for C^{12}/C^{13} ratios when dating compounds at Chan Chan and found the C-13 average values to be −23.6 ± 0.5%, very close to that for wood and considerably different from the −12% value for sugar cane and other grasses.

Rowe (1962*b*:5–6, 1967*b*:73–74) originally established his Chavin seriation based on the master sequence of the Ica Valley (Menzel et al., 1964). Absolute dates were later assigned to the sequence (Rowe

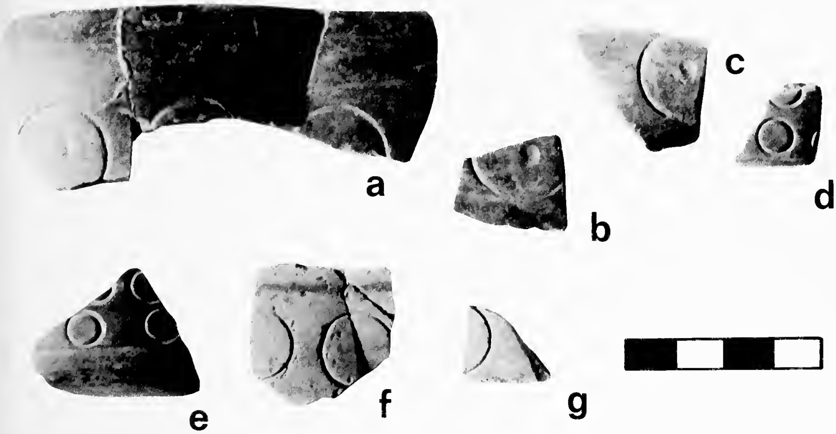

Fig. 22.—Stamped circular decoration on sherds from Huaca Guavalito.

and Menzel, 1967:vi–viii), indicating that the Chavin style and the mechanism that spread the style originated somewhere north of Ica in the late Initial Period. The arrival of the Chavin style in the Ica Valley signalled the start of the Early Horizon. The chart in Rowe and Menzel (1967:vi–vii) indicates that phase AB, the earliest of the Chavin style phases, begins in the Ancash area about 1500 B.C., in the late Initial Period, and is not present until 1400 B.C. in Ica, the beginning of the Early Horizon. This phase is then followed by phases C, D, and EF spaced out over a period of several hundred years. Roe (1974) later extended Rowe's Chavin seriation to include most known Chavin style objects and monuments in Peru. His extension of the original Rowe seriation, however, is biased because 1) he assumes that all Chavin-related elements emanate from Chavin de Huantar, and 2) he uncritically follows the original seriation, which was meant as a preliminary suggestive guide (Rowe, 1967*b*:76), without accounting for associated noniconographic evidence.

Nevertheless, Roe (1974:31, 1978:12–13) as well as Burger (1978: 389–391) have pointed out, at least indirectly, a major weakness of Rowe's original Chavin seriation by reinterpreting the entire Ica sequence as dating no earlier than phase D. This could very well be true because the published radiocarbon dates for Early Horizon phases 3(459 B.C. ± 214) and 9 (451 B.C. ± 110) of the Ocucaje sequence (Rowe, 1967*a*:28–30) are within the range of Burger's (1981:594–596) dating of the Janabarriu phase at Chavin de Huantar which he correlates iconographically with Rowe's phase D (Burger, 1978:389–391). The data from Chavin de Huantar and Ica suggest a possible relationship between the two, but it is clear that neither contributed to the earlier Initial Period developments on the north and central coasts. The proposed absence of Chavin phases AB and C in the Ocucaje sequence of Ica, which was originally used to establish the Chavin sequence (Rowe, 1962*b*:5, 1967*b*:73), brings into question the validity of the Chavin iconographic seriation.

The artifactual, architectural, iconographic, and radiocarbon evidence from Huaca de los Reyes and Caballo Muerto in general are in very good agreement with most of the evidence from coastal Peru for Initial Period times. Looking at the coast as a whole, Caballo Muerto is but one of several centers that arose in the first half of the second millineum B.C. to control irrigation agriculture that was just beginning, but rapidly spreading over most of the north and central coast of (Moseley, 1974; Pozorski, 1976; Pozorski and Pozorski, 1979). Population centers shifted from the coastline, where subsistence in Cotton Preceramic times had emphasized the gathering of marine resources, inland to strategic points within the narrow coastal river valleys to control canal intakes for irrigation agriculture. These corporate labor mound sites are present in every valley on the north and central coast, but a few centers probably became dominant over several valleys. Contrary to Burger's (1981:596–600) assessment, most of these sites contain substantial occupational evidence and are not empty ceremonial centers.

Little, if any, interaction occurred between the coast and highlands from 1800 to 800 B.C., and the interaction accomplished after that time appears to have been mostly one way, from the coast to the highlands. Chavin de Huantar reflects coastal iconography in the form of the human figure (Huaca de los Reyes, Moxeke, Cerro Sechin), the feline (Huaca de los Reyes, Punkurí), and the Ofrendas monster (Garagay). It also reflects coastal architecture in the form of the U-shaped mound and the sunken circular forecourt. Coastal ceramic traits such as stirrup spout vessels are also present at the site.

As Burger (1981:599–600) has demonstrated, when one speaks of the Early Horizon and the spread of Chavin influence, he must realize that the type site of Chavin de Huantar cannot be viewed as a purely "Chavin" site, and and certainly not as the source for all related architectural, iconographic, and ceramic elements. Instead, Chavin de Huantar is a blending of elements from the coast, the highlands, and the tropical forest and was apparently primarily a receiver, not a sender, of what have come to be called "Chavin" traits. This interpretation is quite fitting in view of its intermediate highland location between the coast and the tropical forest (Burger, 1978:400; Silva, 1978:1–25).

Stylistic comparisons of iconography from different regions must take into account associated architectural and artifactual evidence as well as absolute dates. If one attempts to discuss the Chavin phenomenon, then definitions and distinctions between the Initial Period and the Early Horizon must be clarified, refined, and applied to all varieties of archaeological evidence. Anything less would not take into account the present state of knowledge. Conversely, if, as it is now beginning to appear, such a tremendous unifying force or true "horizon" did not exist during the early portion of the central Andean sequence, then more profitable lines of inquiry should be pursued.

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STUDIES ON NEARCTIC *EUCHLOE*. PART 8. DISTRIBUTION, ECOLOGY, AND VARIATION OF *EUCHLOE OLYMPIA* (PIERIDAE) POPULATIONS

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Abstract

The biology, ecology, and geographic variation of the Olympia marble (*Euchloe olympia*), a pierid butterfly, are described and discussed. This species occurs in relatively open native situations with well-drained rocky or sandy substrates where its caterpillar hosts, rock cresses (*Arabis*: Brassicaceae), may be found. The butterfly ranges from Maryland east to Montana and from southern Ontario south to central Texas. Several groups of populations or *isolates* each have distinctive traits relating to their caterpillar host plants, habitat types and adult phenotypes. A statistical analysis of several adult wing characters is presented, and the results are related to possible alternative taxonomic treatments. The subspecific name *rosa* is best treated as a synonym of the nomenotypic species.

Introduction

Euchloe olympia Edwards is a distinctive, single-brooded pierid with a range covering about half of the conterminous United States. Within this range it is usually a highly localized insect with particular habitat requirements.

Although the most recent revisionary treatment considers *E. olympia* undeserving of infraspecific designation (Opler, 1966), other authors

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persist in suggesting such names may be merited (Howe, 1974; Wagner, 1977). Nevertheless, there does exist a certain amount of variation within and between populations that is best treated by referring to aggregates of populations or "isolates."

In this paper we present and discuss the distribution of *Euchloe olympia,* considering several biogeographic isolates. We then consider the ecological attributes and variation shown by these groups of populations.

DISTRIBUTION

The total distribution of *Euchloe olympia* extends from southern Manitoba and southern Ontario south to central Texas and from central Montana, Wyoming, and Colorado east to West Virginia, Virginia, Maryland, and Pennsylvania (Fig. 1).

It can be seen that there are several distinctive clusters or groupings of populations which we will refer to hereinafter as "isolates" (Fig. 1); these are (1) Appalachian isolate, (2) Great Lakes "dune" and "inland" isolates (Wagner, 1977), (3) St. Louis isolate, (4) Texas isolate, (5) Arkansas River isolate, (6) Missouri River isolate, and (7) Front Range isolate.

Appalachian isolate.—This series of *E. olympia* populations extends from extreme southern Pennsylvania south through the mountains of western Maryland, northwestern Virginia, and eastern West Virginia. Colonies in central West Virginia, including Kanawha—*E. olympia's* type locality—are best included with this isolate, although they may be remnants of a once more extensive series of Ohio River drainage populations.

Great Lakes isolates.—This series of populations, which includes colonies of diminutive individuals along lakeshore dunes, inland colonies of larger individuals, and those that appear intermediate, has been described in detail by Wagner (1977). Populations occur in Ontario, Michigan, northern Indiana, northern Illinois, northeastern Iowa, Wisconsin, and Minnesota.

St. Louis isolate.—Near the confluence of the Mississippi and Missouri Rivers occurs a tight constellation of river bluff colonies (Mieners, 1939, 1957).

Texas isolate.—Included here are several Texas populations which occur near the Sabine, Trinity, Brazos, and Colorado rivers, all of which flow into the Gulf of Mexico.

Arkansas River isolate.—This series of populations includes those found along the Arkansas River and its tributaries, including the Canadian River in northern Texas, as well as those found near the Ouachita and White rivers in Arkansas. Populations near the Arkansas in central Colorado are placed with the Front Range isolate.

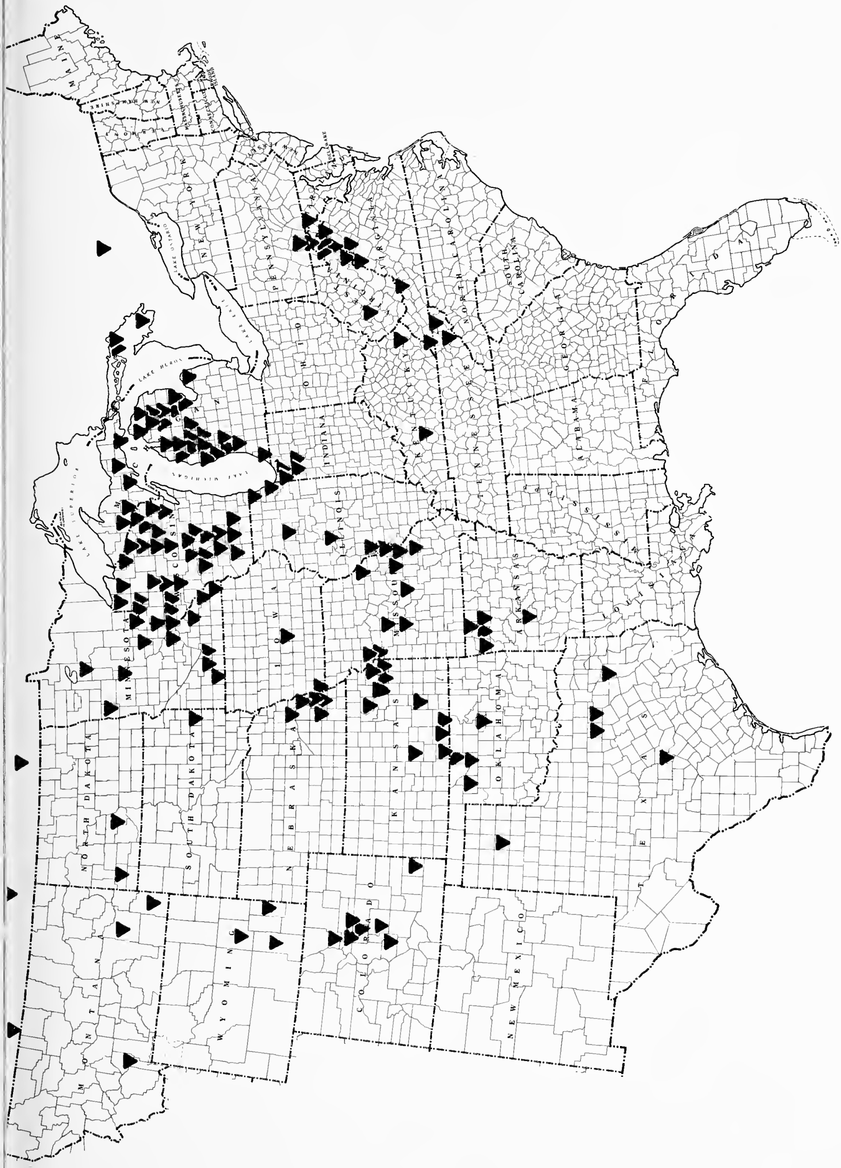

Fig. 1.—Distribution of *Euchloe olympia.*

Missouri River isolate.—All populations along the Missouri River, and its tributaries, except those along the Upper Platte River drainage in central Colorado and Wyoming, are included with this isolate. Also put here is a population found along the Des Moines River in central Iowa.

Front Range isolate.—Populations found in the mountains at the western edge of the plains in central Colorado and Wyoming constitute this isolate.

ECOLOGY

Euchloe olympia is single brooded throughout its range, flying for a brief period in early spring. Wherever it occurs it is among the first emerging butterflies of the year, along with *Incisalia, Anthocharis midea,* the first *Celastrina,* the first *Pieris rapae,* and the first *Erynnis.* At any single locality the average flight period seems to be no more than 20 to 25 days, unusually brief for a butterfly.

The onset of emergence is retarded, on average, about 4.5 days per degree of latitude as one proceeds northward (Fig. 2). At any given latitude, however, the first emergence may vary as much as 20 days or so, depending on elevation, proximity to large water bodies, slope exposure, year to year climatic variation, and other factors. During a typical year *olympia* is on the wing, somewhere, from probably late February, at the southern limit of its range, to early July, at its northern limit or in the Rockies. The latest date of capture known to us is 18 July in Boulder County, Colorado, elevation unknown (Brown et al., 1956).

With one possible exception, all known larval hosts are *Arabis* (Brassicaceae), a primarily western genus. Each isolate seems to differ in habitat type, flight habits, larval food plant, and adult nectar source. As far as these attributes are known for each geographic isolate they are discussed below.

Appalachian isolate.—A unique environment known as the Appalachian shale barrens extends discontinuously from south-central Pennsylvania southwesterly to southern West Virginia and southwestern Virginia (Platt, 1951). This ecological formation, characterized by a number of endemic plant species of western affinities, is closely associated with outcrops of the Devonian Braillier shale formation. A number of Appalachian butterflies occur in close association with these shale barrens, and, of course, *Euchloe olympia* is among them. The others are *Erynnis brizo, Polites mystic, Hesperia sassacus, Hesperia metea, Pyrgus centaureae, Calephelis borealis, Fixsenia ontario, Glaucopsyche lygdamus,* and *Phyciodes pascoensis.*

In the barrens, *E. olympia* occurs in or near open, low pine or pine-oak forests on south or southwest facing rocky shale slopes. It often

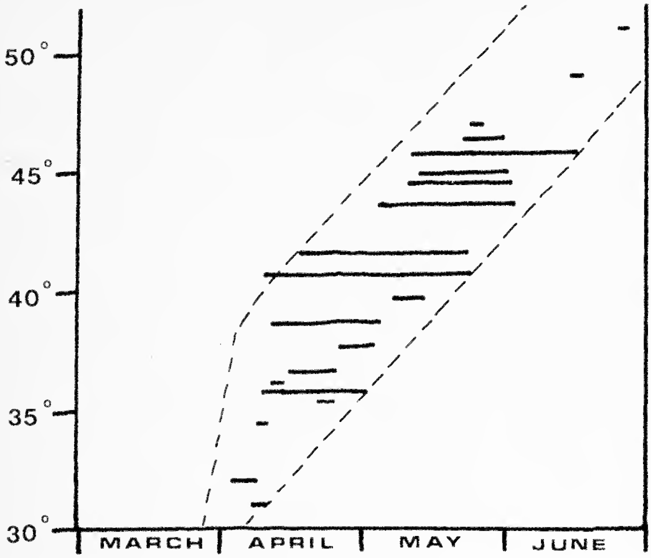

Fig. 2.—Seasonal occurrence of adult *Euchloe olympia* as a function of latitude demonstrating delayed emergence northward.

ventures to the wood edges and is frequently found along traversing roads and trails.

On 27 May 1979, larvae were found by Opler feeding on *Arabis serotina* Steele, a shale barrens endemic, near Sugar Grove, Pendleton County, West Virginia. Other species of *Arabis,* including *A. lyrata* L., occur in shale barrens localities and may be utilized. A record of *Euchloe olympia* larvae feeding on *Sisymbrium* sp. at Coalburgh, West Virginia (Edwards, 1891) is dubious. The host might have been *Arabis glabra.* Clench found adults to nectar at *Phlox subulata.*

Wagner (personal communication) found a population of *Euchloe olympia* residing on a limestone pavement habitat in the White Shoals District, Lee County, southwestern Virginia. Here, where the butterflies have been found from 25 April to 9 May, the habitat is characterized by stunted trees growing on limestone pavement with scattered boulders. Red cedar (*Juniperus virginiana*) is especially prominent. The larval host at this locality is *Arabis laevigata.* It is possible that colonies in central West Virginia and Kentucky may be found in similar situations rather than on typical shale barrens.

Great Lakes dune isolate.—Known only from clusters of colonies in dunes at the upper edge of Lake Huron in Ontario and along the southern end of Lake Michigan in Wisconsin, Illinois, Indiana, and

Michigan is the diminutive dune form of *E. olympia* discussed in detail by Shull (1907) and Wagner (1977).

Shull (1907) describes in great detail the adult flight habits of *E. olympia* at the Indiana dunes. He states that "it flies near the ground, following a rather uncertain course, dancing tremulously (sic!) this way and that." He also describes how *E. olympia* flies into the wind, particularly on the windy days which are so frequent along the lakeshore. Shull found eggs on *Arabis lyrata* at the Indiana dunes and raised larvae to pupation. He described the life history in detail (see also Opler, 1974). In the field, one larva was observed to pupate on the stalks of *Andropogon scoparius* (Michx.) (Poaceae). Nielsen raised larvae found on *Arabis lyrata* at a dune locality in Berrien County, Michigan (Opler, 1974) and *E. olympia* was found associated with this same plant on dunes at Great Bend, Ontario (Wagner, 1977).

At the Indiana dunes location, Shull found adults to alight almost exclusively on the flower clusters of *Arabis lyrata,* which is presumed to be the principal nectar source there. M. C. Nielsen (personal communication) found *E. olympia* in Berrien County, Michigan to fly along the lakeward face of dunes 30 to 50 ft inland from the beach. Here, as at Shull's Indiana locality, *E. olympia* nectared at *Arabis lyrata.*

Great Lakes inland isolates.—Included here are a mixed lot of populations with quite differing ecological features. Populations at inland stations in Michigan, at least those in Allegan, Montcalm, and Roscommon counties, are restricted to prairies, whereas in Ontario at least one population in Garden Township is located on open limestone barrens (Wagner, 1977). Nielsen (personal communication) reports that at several sites in the northern portion of Michigan's lower peninsula *E. olympia* is usually found in openings within scrub oak-jack pine habitat. At one site in Otsego County, he found *E. olympia* occurring in an old pine burn, which had been colonized by mosses, lichens, *Andropogon,* and *Arabis.*

In Minnesota, Masters (personal communication) found *E. olympia* in deciduous woods in Pine and Chisago counties, while reporting it from open hilltops, surrounded by deciduous woods. overlooking the Mississippi River in Goodhue, Houston, and Winona counties, Minnesota.

The usual host for these inland colonies is *Arabis drummondii* Gray. Larvae have been found on this plant in Allegan, Montcalm, and Roscommon counties, Michigan (Opler, 1974; Wagner, 1977), while near Killaloe, Ontario, *Euchole olympia* was observed ovipositing on *Arabis glabra* by Lindsay (1971).

St. Louis isolate.—These colonies are found associated with low, sparse, open forest on the cherty summits of long ridges. There, adults fly low and seem confined to ridgetops (Meiners, 1937, 1939, 1956;

Table 1.—*Three characteristics of populations of* Euchloe olympia.

Isolate	Sex	N	Forewing length (cm)		Forewing apex		Forewing bar	
			Mean	SD	Mean	SD	Mean	SD
Appalachian	♂	18	1.81	0.18	4.4	1.46	0.11	0.02
	♀	20	1.87	0.13	4.9	1.39	0.13	0.02
Michigan (inland)	♂	5	1.84	0.19	4.6	1.14	0.11	0.03
	♀	1	2.06	—	4.0	—	0.15	—
Great Lakes dunes	♂	13	1.72	0.12	4.9	0.95	0.09	0.02
	♀	5	1.70	0.06	5.2	0.45	0.11	0.01
Wisconsin	♂	7	1.74	0.07	3.0	1.00	0.08	0.01
	♀	5	1.80	0.12	3.2	1.30	0.10	0.02
Colorado Front Range	♂	26	1.79	0.08	2.7	0.89	0.10	0.02
	♀	10	1.84	0.12	3.1	1.20	0.13	0.03
Missouri River	♂	31	1.86	0.12	2.5	0.77	0.11	0.02
	♀	8	1.96	0.11	2.8	0.71	0.12	0.02
St. Louis	♂	7	1.96	0.07	4.4	0.98	0.12	0.02
	♀	3	1.91	0.14	4.3	0.58	0.12	0.01
Arkansas River	♂	17	1.89	0.10	2.8	1.30	0.12	0.02
	♀	4	2.03	0.16	3.0	1.15	0.14	0.02
Texas	♂	2	1.93	0.08	2.0	0.00	0.13	0.01
Total	♂	124	1.83	—	3.3	—	0.11	—
	♀	58	1.87	—	3.9	—	0.13	—

Arnhold, 1953), where its larval food plant *Arabis viridis* occurs (Meiners, 1939).

Texas isolate.—Little has been reported concerning this isolate except that it is associated with limestone outcroppings near Dallas (Freeman, 1959).

Arkansas River isolate.—The only ecological data concerning populations that constitute this isolate is that adults are found in bottomland deciduous forest. Such observations have been made in Alfalfa, Payne and Woodward counties, Oklahoma (McCoy, personal communication), as well as in Newton County, Arkansas (Masters, personal communication).

Missouri River isolate.—This isolate covers the largest geographic expanse, and the ecological characteristics of this isolate may be just as wide-ranging. Masters (personal communication) found *E. olympia* on a hilltop in jack pine forest at the Riding Mountains, Manitoba.

Front Range isolate.—Local populations of *Euchloe olympia* in the vicinity of the Colorado Front Range are found on open ridges or low hills in short grass prairie habitat, often not too distant from cottonwood-lined streams (F. M. Brown, personal communication).

Table 2.—*Differences among population of* Euchloe olympia *in mean forewing length. Student's t (degrees freedom),* P $\leq$ *0.05*, $\leq$0.01**, $\leq$0.001.****

Sex	Isolate	Great Lakes dunes	Colorado Front Range	Missouri River	Arkansas River
Males	Appalachians	1.61 (29)	1.00 (42)	−1.10 (47)	1.66 (35)
	Great Lakes dunes		−2.33 (37)*	−3.34 (42)**	−4.32 (28)***
	Colorado Front Range			−2.27 (55)*	−3.42 (41)**
	Missouri River				−1.02 (46)
Females	Appalachians		0.59 (28)	−1.84 (26)	
	Colorado Front Range			−2.33 (16)*	

VARIATION

It is our intent here to analyze three physical characters and their variation between isolates. On this basis, we may comment on the prudence of recognizing any subspecific taxa. The three characters (Table 1) measured were (1) forewing length (base to apex), (2) width of forewing discal black bar, and (3) degree of black infuscation on forewing apex above—judged on a relative scale of 1 to 7 with exemplars as standards as follows: (a) apical area almost unmarked white: a minute black subapical costal spot only; (b) costal spot, subapical (faint) and spot at end of M_3 (faint), apex with at most only a few black scales; (c) costal and M_3 spots strong, slight apical infuscation; (d) costal and M_3 spots strong and with some connecting fuscous between them, apex distinctly infuscate; (e) costal and M_3 spots strong and connected; apical infuscation strong; (f) apical and subapical infuscations strong, slightly fused, (g) apical area almost solidly infuscate: a minute white patch on costa only.

The results of this analysis are shown on Table 1, whereas Student's-t analysis was carried out between paired mean values for isolates with adequate sample sizes (Tables 2, 3, 4).

The sexes were treated separately in these analyses, because females were significantly larger ($t = 2.15$, $P \leq 0.05$), had significantly broader discal bars ($t = 5.15$, $P \leq 0.001$), and had significantly darker apical infuscation ($t = 2.58$, $P \leq 0.05$).

Only the Missouri River-Arkansas River pair did not show significant differences in any character, whereas the Appalachian-Great Lakes dune pair differed significantly only in forewing discal bar width and the Appalachian-Front Range pairing differed significantly only in the degree of apical infuscation. All other pairings differed significantly in at least two of the three characters. The most dissimilar comparisons were between the Great Lakes dune isolate and either the Missouri River or Arkansas River isolates, there being significant differences in the central tendency of all three characters.

Table 3.—*Differences among populations of* Euchloe olympia *in mean forewing apex. Student's t (degrees freedom),* P ≤0.05*, ≤0.01**, ≤0.001.***

Sex	Isolate	Great Lakes dunes	Colorado Front Range	Missouri River	Arkansas River
Males	Appalachians	1.15 (29)	4.89 (42)***	6.00 (47)***	3.47 (35)**
	Great Lakes dunes		7.32 (37)***	8.15 (42)***	5.03 (28)***
	Colorado Front Range			20.77 (55)	−0.33 (41)
	Missouri River				−0.94 (46)
Females	Appalachians		3.40 (28)**	4.04 (26)***	
	Colorado Front Range			0.73 (16)	

Size, which may be at least partially determined by environment, was smallest in more montane, northern, or lakefront isolates, whereas low elevation southern populations had larger individuals.

Degree of apical infuscation, a character asserted to separate subspecies *rosa,* was generally greatest in the eastern-most populations and least in western and southern isolates, although the St. Louis grouping is unusual in having such dark infuscation due to its proximity to the eight prairie isolates. Additionally, the Michigan inland prairie populations, which are similar to the Missouri River and Arkansas River isolates in facies (Wagner, 1977), occur in close proximity to the small, dark dunes isolate.

DISCUSSION

As we have seen with the possible exception of the similar Missouri River and Arkansas River isolates, each of *Euchloe olympia*'s isolates occurs in a unique ecological setting and has its constituent individuals displaying somewhat different phenotypic traits.

As to application of subspecific epithets, one is left with three choices. One could apply a separate subspecies name to each isolate, as might have been done in former times. Alternatively, one might restrict no-

Table 4.—*Differences among populations of* Euchloe olympia *in mean forewing bar. Student's t (degrees freedom),* P ≤0.05*, ≤0.01**, ≤0.001***.

Sex	Isolate	Great Lakes dunes	Colorado Front Range	Missouri River	Arkansas River
Males	Appalachians	2.56 (29)*	1.91 (42)	−0.27 (47)	−1.48 (35)
	Great Lakes dunes		1.05 (37)	−3.56 (42)***	−3.87 (28)***
	Colorado Front Range			−2.86 (55)**	−3.37 (41)**
	Missouri River				−1.23 (46)
Females	Appalachians		0.39 (28)	1.86 (26)	
	Colorado Front Rnage			0.86 (16)	

menotypic *olympia* to isolates with dark apical infuscation, that is, Applachian, Great Lakes dunes, and St. Louis isolates, while applying the subspecific name *rosa* to all lightly marked isolates. Finally, one might choose to apply *no* subspecies names whatsoever. We have chosen the latter course, because we feel the first option would be absurd and the second would group together heterogeneous, polytopic sets of populations which have responded to local environments and may not be each other's closest relatives. Of course, our unofficial isolate terminology may be used in an informal sense to recognize these locally adapted ecophenotypes. We feel that our discourse on the ecological and phenetic variation of *E. olympia* to be of more critical importance than the description of six or seven weakly differentiated subspecies.

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LOCALITY DATA

Abbreviations used.—AMNH, American Museum of Natural History, New York; CAS, California Academy of Sciences, San Francisco; CJM, Clarance J. McCoy, Jr.; CM, Carnegie Museum of Natural History; CNC, Canadian National Collection, Ottawa; *ex*, from, *or* from the collection of; JHM, John H. Masters; *leg.*, collected by; MCN, Mogens C. Nielsen; MNH, Natural History Museum, Washington, D.C.; NWS, Northwestern State College, Alva, Oklahoma; OAS, Oakley A. Shields; OSU, Oklahoma State University, Stillwater; ROK, Roy O. Kendall; SS, Season Summary (News of the Lepidopterists' Society, various years).

CANADA

ALBERTA. Onefour 3. vi.1956 (*leg.* E. E. Sterns, CNC).

MANITOBA. Riding Mountain [town] 24.vi.1967 (*leg.* J. H. Masters, JHM); Brandon (Hanham, 1900); McCreary (per JHM).

ONTARIO. Killaloe [ca. 25 mi SW Pembroke] (SS); "La Cloche" [prob. Grande Cloche Id., Georgian Bay] 28.v.1937 (*leg.* ?, CNC); Strawberry Id., Georgian Bay 10.v.1942 (*leg.* N. J. Durand, CNC).

SASKATCHEWAN. Regina 1885 (*leg.* "N.H.G.," CNC).

UNITED STATES

ARKANSAS. *Carroll Co.:* nr. Eureka Springs 18.iv.1965 (*leg.* J. R. Heitzman, PAO). *Garland Co.:* Hot Springs 5.iv.1932 (*leg.* L. I. Hewes, CAS). *Madison Co.:* Withrow

Springs St. Park (SS). *Newton Co.:* Lost Valley, nr. Ponce iv.1965 (*leg.* J. H. Masters, JHM). *Washington Co.:* Fayetteville (*leg.* L. Paulissen, *per* JHM).

COLORADO. *Arapahoe Co.:* Highline Canal 29.iv.1961 (*leg.* R. Pyle, PAO). *Boulder Co.:* (Brown et al. 1956); Lefthand Canyon 30.v.1957 (*leg.* D. Eff, PAO); Sunshine Canyon 4.v.1962 (*leg.* D. Eff, OAS); Boulder 19.v.1936 (*leg.* T. N. Freeman, CNC); Boulder, 5500 ft, 7.vi.1961 (*leg.* M. R. Mackay, CNC); 4 mi NW Boulder, 6900 ft, 8.vi.1961 (*leg.* J. R. Stainer, CNC). *Denver Co.:* Denver (nfd, CNC). *Douglas Co.:* (Brown et al., 1956). *El Paso Co.:* (Brown et al., 1956). *Fremont Co.:* (Brown et al., 1956). Jefferson Co.: (Brown et al., 1956); Clear Creek Canyon, W. Golden 10.v.1959 (*leg.* D. Eff, OAS); nfd. 8000 ft, 28.v.1961 (*leg.* "D.A.J.," OAS); Lookout Mountain 17.v.1936 (*leg.* L. I. Hewes, CAS). *Prowers Co.:* (Brown et al., 1956). *Note:* In most instances, Brown et al. (1956) give specific localities under the respective counties. These are not repeated here.

ILLINOIS. *Bureau Co.* (nfd, *per* P. J. Conway). *Cook Co.:* Chicago 3.v.1908 (*leg.* A. Kwiat, CM). *Lake Co.:* northeastern part, 17.v.1914, 17.v.1919, 19.v.1923 (all *leg.* H. M. Bower, CM, CNC); Zion (*leg*?, CNC).

INDIANA. Lake Co.: Gary 3.v.1908, 10.v.1910 (both *leg.* A. Kwiat, CM); Whiting (*leg.* ?, *ex* W. H. Edwards, CM). *Porter Co.:* between Clarke Jct. and Pine (Shull, 1907). *Not located:* Miller (s) ("sand dunes," Leussler, 1938), also 6.v.1923 (*leg.* G. M. Dodge, CAS); "N. Ind." (*leg.* ?, *ex* W. H. Edwards, CM [one of these specimens figured, Holland (1931) pl. 67 fig. 28]).

IOWA. *Fremont Co.:* Waubonsie St. Park 10.v.1958 (*leg.* J. A. Ebner, *ex* L. D. Miller, CM). *Polk Co.:* Des Moines (SS).

KANSAS. *Cowley Co.:* nfd, 18,20.iv.1941, 12,17.iv.1942 (*leg.* Stallings and Turner, CAS; also, *ex* ANSP, CM). *Douglas Co.* (Field, 1938). *Greenwood Co.* (Field, 1938). *Harper Co.* (Field 1938). *Johnson Co.:* Camp Towanyak, nr. Tulle Creek, late iii–early iv (*leg.* J. H. Masters, JHM); Shawnee Mission Park 23.iv.1962 (*leg.* J. R. Heitzman, OAS), no date (*leg,* J. H. Masters, JHM): S of Prairie Village 22.iv.1965 (*leg* J. R. Heitzman, PAO); Shawnee 23.iv.1964 (*leg.* J. H. Masters, PAO). *Leavenworth Co.* (Field, 1938). *Pottawotamie Co.* (Field, 1938). *Reno Co.* (Field 1938). *Scott Co.* (Field, 1938). *Shawnee Co.:* Topeka 20, 26.iv.4,5.v.1941 (*leg.* R. H. Whittaker, CNC). *Sumner Co.:* nfd, 14.iv (*leg.* ?, CM); also, nfd (Field, 1938). *Wynadotte Co.:* Quivera Spring, late iii–early iv (*leg.* J. H. Masters, JHM).

KENTUCKY. *Floyd Co.:* Jenny Wiley State Park 26.iv.1969 (C. V. Covell, Jr. and B. L. Monroe). *Green Co.:* Crailhope (C. Cook, 1948).

MARYLAND. *Allegany Co.:* nr. Flintstone, 12.v.1955 (Simmons, 1957); Green Ridge State Forest, ca. 6 mi E Flintstone 9,10.v.1964 (*leg.* L. D. Miller and H. K. Clench, CM), 11.v.1965 (*leg.* Clench, CM).

MICHIGAN. UPPER PENINSULA: *Delta Co.* 16.vi (*per* MCN). *Gogebic Co.:* 5 mi NE Marenisco 2.vi.1967 (*leg.* J. H. Masters, MHM). *Mackinac Co.:* 12.vi (*per* MCN). *Marquette Co.* (*per* MCN). *Schoolcraft Co.* 24.v–2.vi (*per* MCN). LOWER PENINSULA: *Allegan Co.* (*per* MCN). *Arenac Co.* 4–21. v (*per* MCN). *Barrien Co.* 20.iv–v (*per* MCN). *Arenac Co.* 4–21 v (*per* MCN). *Cheboygan Co.* 12–31.v (*per* MCN); Duncan Bay 12.v.1921 (Voss, 1954); Douglas Lake 29v.1939 (Voss, 1954). *Crawford Co.* 11–31.v (*per* MCN). *Emmet Co.* (Moore 1960). *Grand Traverse Co.* 18.v (*per* MCN). *Huron Co.* 14.v (*per* MCN); Sand Point 13.v.1933 (*leg.* W. S. MacAlpine, CNC). *Iosco Co.* 26–30.v (*per* MCN). *Lake Co.* 6–28.v. (*per* MCN). *Montcalm Co.* 7.v–10.vi (*per* MCN). *Montmorency Co.* 24–31.v (*per* MCN). *Newaygo Co.* 7.v–2.vi (*per* MCN). *Oceana Co.* 28.v (*per* MCN). *Ogemaw Co.* 18.v (*per* MCN). *Oscoda Co.* 18–31.v (*per* MCN); Luzerne 31.v.1937, 30.v.1939 (both *leg.* G. W. Rawson, CNC). *Otsego Co.* 17.v–4.vi (*per* MCN). *Presque Isle Co.:* nr. Grand Lake 14.v.1951 (Voss, 1954). *Roscommon Co.* 24–28.v (*per* MCN). *Wexford Co.* 14.v (*per* MCN).

MINNESOTA. *Beltrami Co.* Bemidji 30.v.1967 (Huber, 1967). *Chisago Co.:* Taylors Falls 20.v.1896 (*leg.* H. Skinner, *ex* ANSP, CM), 20.v.1967 (*leg.* J. H. Masters, JHM). *Goodhue Co.:* Redwing (*per* JHM). *Hennepin Co.:* Minneapolis 16.v (*leg.* H. Skinner, *ex* ANSP, CM). *Houston Co.:* 26.v.1940 (Macy and Shepard, 1941); Reno (*per* JHM). *Mille Lacs Co.:* Mille Lacs Lake 14.v.1938 (Macy and Shepard 1941). *Pine Co.:* St. Croix State Park 11,13.v.1965 (Huber, 1965), 16.v.1966) (Huber, 1966; also *per* JHM), 17–24.v.1967 (Huber, 1967). *Washington Co.:* Stillwater 12.v.1934; Lakeland Junction 17.v.1938 (both Macy and Shepard, 1941). *Watonwan Co.:* Butterfield (*leg.* W. Linnscheid, *per* JHM). *Winona Co.:* Dresbach 20.iv.1938 (*leg.* ?, CM; also cf. Arnhold, 1953); Winona (*per* JHM), 20.v.1937 (Macy and Shepard, 1941), 2.vi.1967.

Missouri. *Benton Co.:* Warsaw 26.iv.1962, 24.iv.1966 (*leg.* J. R. Heitzman, DAS, PAO). *Clay Co.:* Liberty (William Jewell Campus) iv (1954–1958, *leg.* J. H. Masters, JHM). *Franklin Co.:* Meramec Highlands 12.iv.1903 (*leg.* ?, CM), cf. also Arnhold (1953), Meiners (1957). *Jackson Co.:* Blue Springs 22.iv.i965, 2.v.1966 (*leg.* J. R. Heitzman, PAO). *Jefferson Co.:* Cedar Hill 17.iv.1938 (*leg.* ?, OAS). *St. Louis Co.:* St. Louis 18.iv.1902, 12.iv.1903 (resp. CM, CAS), "seems to have become extinct at this locality" (Knetzler, 1912); Eureka 13,28.iv.1936 (*leg.* ?, CM *ex* W. E. Sieker); Ranken 16.iv.1936 (*leg.* H. I. O'Bryne, CNC), 26.iv (nfd, CM), cf. also Arnhold (1953), Meiners (1957).

Montana. *Carter Co.:* nfd. 2.vi.1937 (*leg. J. L. Kay, CM). Custer Co.:* Miles City 16.v.1897 (*leg.* H. Skinner, CNC), also (Elrod, 1906). *Gallatin Co.:* Bozeman (Elrod, 1906). *Not located:* Long Pine Hills 2.vi.1937 (*leg.* J. L. Kay, CM); Aldridge (Elrod 1906); "M.C." [=Miles City?] (*leg.* ? [perhaps H. Skinner], *ex* ANSP, CM).

Nebraska. *Cass Co.:* Plattsmouth 13.v (Leussler, 1938). *Dodge Co.:* nfd (Leussler, 1938). *Douglas Co.* Omaha 4.v, 24.v (Leussler, 1938). *Lancaster Co.:* Lincoln 29.iv.1939 (*leg.* W. H. Wagner, CNC). *Otoe Co.:* Nebraska City 10,20.iv.1958 (*leg.* J. A. Ebner, CAS; and *ex* L. D. Miller, CM).

North Dakota. *Morton Co.:* 25.v (Puckering and Post, 1960). *Slope co.:* 24.v, 1.vi (Puckering and Post, 1960).

Oklahoma. *Alfalfa Co.:* Carmen 18.iv.1954 (*leg.* D. L. Shorter). *Major Co.:* Orienta 9.iv.1944 (*leg.* Stallings and Turner, *ex* ANSP, CM). *Payne Co.:* Yale 30.iv.1958 (*leg.* P. McCoy, OSU); Stillwater 12.iv.1941, *leg.* ?, OSU), 2.v.1960 (*leg.* C. J. McCoy, OSU). *Woodward Co.:* Woodward 2.v.1953; Boiling Springs St. Park 8.iv.1954 (both *leg.*, D. L. Shorter, NWS). *Note:* All records, except that for Major Co., furnished by C. J. McCoy, Jr.

Pennsylvania. *Bedford Co.:* 1 mi N Inglesmith [nr. Purcel] 10.v.1964 (*leg.* L. D. Miller and H. K. Clench, CM). *Not located:* "Southwestern Pennsylvania" (Holland 1931; Macy and Shepard, 1941). Original source of information unknown to us. "Pennsylvania" (Klots, 1951; prob. from preceding authors).

South Dakota. *Brookings Co.:* Volga (Truman, 1897).

Texas. "Western Texas" [=vic. Archer Co., *teste* F. M. Brown, letter to Clench 10.vi.1967] *leg.* Boll (Edwards, 1882; types of rosa, CM). *Burnett Co.:* Marble Falls (SS); 8.iv.1965 (*leg.* J. R. Heitzman, per ROK); nfd (larvae, *leg.* R. O. Kendall, per ROK). *Carson Co.:* White Deer 25.iv.1943 (*leg.* H. A. Freeman, CNC); Skellytown (*leg.* H. A. Freeman, *per* ROK). *Dallas Co.:* Dallas (SS); Garland (*leg.* H. A. Freeman, *per* ROK); Irving (*leg.* H. A. Freeman, *per* ROK). *Smith Co.:* 4.iv.1964 (*leg.* C. A. Kendall, *per* ROK.) *Tarrant Co.:* Ft. Worth (SS); 2nd week of March (*per* ROK). *Travis Co.:* Bull Creek (*leg.* Sullivan, *per* ROK). *Tyler Co.:* Tyler St. Park, nr. Tyler 6.iv.1965 (*leg.* J. R. Heitzman, PAO).

Virginia. *Frederick Co.:* W. Cross Jct., 24.iv.1938 (*leg.* A. H. clark, MNH); Whitacre, 9.v.39 (A. H. Clark, MNH); *Lee Co.:* White Shoals distr., 4 mi WSW Jonesville, 25–28.iv. 79,9.v.82 (W. H. Wagner, Jr.).

West Virginia. *Hampshire Co.:* Ice Mountain, 19.iv.38, 7.v.39 (*leg.* A. H. Clark, MNH); Forks of Cacapon, 8.v.39, 26.iv.41 (A. H. Clark, MNH); 7 mi NE Slanesville, 2,3.v and 10.v.1958 (*leg.* J. Bauer, CM); 3.1 mi N Purgitsville 15.iv.1967 (*leg.* H. K. Clench, CM). *Hardy Co.:* 1.8 mi S Baker 16.iv.1967 (*leg.* H. K. Clench, CM). *Kanawha Co.:* Coalburgh 21,22.iv.1890; "Kana" [Kanawha] (*leg.* W. H. Edwards, including the types of *olympia, CM). Mineral Co.:* 4 mi W Burlington 29.iv.1967 (*leg.* H. K. Clench, CM). *Pendleton Co.:* Reddish Knob 27.v.1981 (*leg.* P. A. Opler, MNH).

WISCONSIN. Adams Co.: 13.v.1962 (*ex* W. E. Sieker, CM). *Chippewa Co.:* Lake Wissota, nr. Chippewa Falls (Arnhold, 1953); Chippewa Falls 5.v.1957, 10.v.1958 (*ex* W. E. Sieker, CM). *Dane Co.:* Pine Bluff (*ex* W. E. Sieker, CM). *Marinette Co.:* Crivitz 16.v.1958, 30–31.v.1957, 9.vi.1957 (*leg.* L. Griewisch, *ex* W. E. Sieker, CM). *Marquette Co.:* Westfield 19.v.1934 (*leg.* G. Heid, CAS). *Vilas Co.:* 7 mi W Eagle River 2.vi.1967 (*leg.* J. H. Masters, JHM); 2 mi S Presque Isle 2.vi.1967 (*leg.* J. H. Masters, JHM). *Waushara Co.:* Lake Lucerne [ca. 7 mi N Neshkoro, Marquette Co.] 27,29.v.1967 (*leg.* W. E. Sieker, CM).

WYOMING. *Converse Co.:* vi.1900 (nfd, CM).

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FURTHER RECORDS OF BATS FROM THE CENTRAL AFRICAN REPUBLIC (MAMMALIA: CHIROPTERA)

J. E. Hill[1]

Abstract

These notes supplement the detailed and comprehensive survey of the known bat fauna of the Central African Republic by Schlitter et al. (1982), with records of four further species hitherto unreported from that country.

Introduction

Bats from the Central African Republic have been reviewed in detail by Schlitter et al. (1982). These authors have added numerous species to the hitherto poorly known bat fauna of the Republic and have provided a list of previously recorded species not represented in the collections that they reported, together with a prognosis of others that although not yet recorded from the Republic may well be expected to occur there. However, while their study was in course of publication, a number of bats collected in the Republic by Dr. C. A. Spinage of the Food and Agriculture Organisation of the United Nations was donated to the British Museum (Natural History). For the most part they represent species already recorded by Schlitter et al. but the collection includes four that are new to the reported fauna of the Central African Republic and one other known from there apparently only by one previous record. All come either from the Bamingui-Bangoran National Park or from Bamingui and its environs, in the southern part of the

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Submitted 17 September 1982.

country. This brief account follows Schlitter et al. in treatment; measurements have been made with dial calipers and are in millimetres.

ACCOUNTS OF SPECIES

Family Pteropodidae

Myonycteris torquata (Dobson, 1878)

1878. *Cynonycteris torquata* Dobson, Cat. Chiroptera Brit. Mus. pp. 71, 76, pl. 5, fig. 1. Angola.

Specimen examined (1).—Bamingui-Bangoran National Park, 400 m, 7°55′N, 19°26′E, (1) (1♂).

Remarks.—This species was reported by Vielliard (1974:977) from the "sud de la Republique Centre Africaine," more specifically La Maboké according to Bergmans (1976:195).

Measurements.—Length of forearm, 58.1; condylobasal length, 30.6; alveolar length of maxillary toothrow (C–M^3), 11.8.

Family Hipposideridae

Hipposideros cyclops (Temminck, 1853)

1853. *Phyllorrhina cyclops* Temminck, Esq. Zool. Cote de Guiné, p. 75. River Boutry, Ghana.

Specimen examined (1).—Bamingui River, Bamingui-Bangoran National Park, 400 m, 7°34′N, 19°40′E, (1) (?).

Remarks.—According to Schlitter et al. (1982:153), there is no previous record of *H. cyclops* from the Central African Republic but these authors remarked that among others it is a species that might be expected to occur there. It is known from Senegal and Guinea-Bissau to the southern Sudan and Kenya.

Measurements.—Length of forearm, 68.4; condylobasal length, 24.8; condylocanine length, 24.6; alveolar length of maxillary toothrow (C–M^3), 10.0.

Family Vespertilionidae

Nycticeius schlieffenii (Peters, 1860)

1860. *Nycticejus schlieffenii* Peters, Monatsber. K. Preussischen Akad. Wiss. Berlin, p. 223. Cairo, Egypt.

Specimen examined (1).—Bamingui-Bangoran National Park, 410 m, 7°33′N, 19°58′E, (1) (1♀).

Remarks.—Schlitter et al. (1982:153) remarked of *N. schlieffenii* that it was to be expected in the Central African Republic, although not then recorded from that country. It is otherwise extensively distributed from Mauretania and Ghana to Egypt, the Sudan, Somalia, and southwestern Arabia, thence through much of eastern Africa to Mozambique, South Africa, Botswana, and Namibia.

Measurements.—Length of forearm, 30.2; condylobasal length, 12.3; alveolar length of maxillary toothrow (C–M^3), 4.5.

Family Molossidae

Tadarida* (*Chaerephon*) *ansorgei (Thomas, 1913)

1913. *Nyctinomus ansorgei* Thomas, Ann. Mag. Nat. Hist., ser. 8, 11:318. Malange, northern Angola.

Specimen examined (1).—Foubouloulou, 22 km W of Bamingui, (1) (1♀).

Remarks.—There is no previous record of *T. ansorgei* from the Central African Republic, although the species is known (Eger and Peterson, 1979:1890, fig. 2) to occur in Cameroon, the southern Sudan, and Ethiopia, extending through eastern Zaire, Uganda, and Tanzania to Mozambique, Zimbabwe, and Angola. This specimen agrees with *T. ansorgei* as it is defined by Eger and Peterson (1979:1887) and with the small sample of this species in the collections of the British Museum (Natural History).

Hayman and Hill (1971:65) placed *ansorgei* in the nominate subgenus *Tadarida* (*Tadarida*), an allocation supported by Koopman (1975: 419, 424). More recently, Freeman (1981:109, 150) has transferred *ansorgei* to the group of species included under *Chaerephon,* a change with which Koopman (Freeman, 1981:150, footnote) concurs. Freeman (1981) also considered *Tadarida* and *Chaerephon* generically distinct.

Measurements.—Length of forearm, 45.6; length of second phalange of fourth digit, 10.4; condylobasal length, 18.2; interorbital width, 4.1; height of braincase, 6.5; mastoid width, 11.1; alveolar length of maxillary toothrow (C–M^3), 7.2.

Otomops martiensseni (Matschie, 1897)

1897. *Nyctinomus martiensseni* Matschie, Arch. f. Naturg., 63, sect. 1, p. 84. Magrotto Plantation, near Tanga, Tanzania.

Specimen examined (1).—Bamingui-Bangoran National Park, 400 m, 7°55′N, 19°29′E, (1) (1♀).

Remarks.—This specimen from the Central African Republic represents a considerable westward extension to the northern part of the distribution of this species, which has been known hitherto to extend from Djibouti and Ethiopia through Kenya, northeastern and southern Zaire to Tanzania, Natal, Malawi, Zimbabwe, and Angola; it also occurs on Madagascar.

Measurements.—Length of forearm, 67.6; condylobasal length, 27.0; alveolar length of maxillary toothrow (C–M^3), 10.8.

Other species

Besides the specimens noted above as being of particular interest, the collection made by Dr. Spinage also includes examples of *Epomophorus gambianus, Micropteropus pusillus, Coleura afra, Taphozous mauritianus, Nycteris hispida hispida, Lavia frons affinis, Rhinolopus fumigatus, R. landeri, Hipposideros ruber, H. abae, Pipistrellus nanus, Eptesicus guineensis, E. somalicus, Scotophilus dinganii, S. nigritellus,* and *Tadarida* (*Chaerephon*) *nigeriae.* All of these taxa were reported from the Central African Republic by Schlitter et al. (1982).

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NEW BRACHIOPODS FROM THE GILMORE CITY LIMESTONE (MISSISSIPPIAN) OF NORTH-CENTRAL IOWA

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ABSTRACT

Highly fossiliferous coquinoid lenses within the "*Cyathophyllum* zone" or uppermost Gilmore City Limestone have produced extremely diverse collections of small invertebrates. The brachiopod faunule from these collections consists of at least eighteen species, three of which are new and described herein. Two of the species are the basis for new and unusual genera. *Iowarhynchus mirandum,* new species, is the type species of a new tiny smooth rhynchonellid, and *Gerkispira spinosa,* new species, is the type species of a new impunctate costate spinose spiriferid. *Setigerites facetus,* new species, represents an early occurrence of a typically Visean genus.

INTRODUCTION

The Gilmore City Limestone of north-central Iowa is a very light to medium gray oolitic limestone with some interbedded hard tough gray to blue dolomitic limestone and minor shale. The dolomitic beds and shales occur only in the lower intervals but comprise much of the exposed portion of the formation found in outcrop near the type section at Gilmore City, Pocahontas County, Iowa.

Most of the major invertebrate groups of the Gilmore City Formation of Iowa have been studied to some extent. The crinoids were first described by Laudon (1933), corals by Carlson (1964), conodonts by Anderson (1969), brachiopods by Carter (1972), and gastropods by Harper (1977).

Submitted 22 September 1982.

Table 1.—*List of brachiopods from the upper beds of the Gilmore City Limestone at Hodge's Quarry, Humboldt County, Iowa.*

Rhipidomella sp. (juveniles?)
Hemiplethorhynchus subovatum Carter (3 mature specimens)
Iowarhynchus mirandum, new genus and new species
Schuchertella sp. (juveniles?)
Rugosochonetes sp. (1 specimen)
Avonia sp. (1 specimen)
Setigerites facetus, new species
Pustula sp. (1 specimen)
? Merista sp. (internal morphology unconfirmed)
Cleiothyridina tenuilineata (Rowley)
Composita cf. *C. athabaskensis* Warren (4 valves)
Composita sp. (juveniles?)
Prospira sp. (1 specimen)
Gerkispira spinosa, new genus and new species
Syringothyris sp. (2 incomplete specimens)
Punctospriifer sp. (juveniles?)
Cranaena sp. (2 adult specimens)
Girtyella sp. (3 specimens)

This formation crops out only in north-central Iowa but is reported in subsurface across southwestern Iowa, southern Nebraska, northern and western Kansas. Surface exposures in Iowa are limited to stream banks and limestone quarries, the latter providing the best fossil materials. The quarries in the vicinity of the type section near Gilmore City have produced many of the specimens upon which most of these prior faunal studies were based. My earlier brachiopod paper (1972) was based exclusively on such collections. Almost all of those specimens were recovered from the lower beds of the formation exposed at or near the type section.

The taxa that are the subject of this paper all were collected from the uppermost "zone" or lithologic unit of London (1933), the "*Cyathophyllum* (=*Vesiculophyllum*) zone." This unit is poorly exposed and not fossiliferous in the quarries near Gilmore City, Pocahontas County, but is very well exposed in a relatively new quarry just north of Dakota City, Humbolt County. Originally named Hodge's Quarry, the property is now owned and operated by the P & M Stone Company. This quarry originally consisted of two main pits, east and west. A thin very fossiliferous coquina occurs within the oolitic beds about 35 ft below the top of the formation in the west pit. A very large and diverse collection of invertebrates was assembled from the coquina lenses by A. J. Gerk. Smaller collections made by J. A. Harper of the Pennsylvania Geological Survey and myself, plus the Gerk collections, provided the brachiopod specimens that form the basis for the present study. The east pit was much less fossiliferous but a fine collection of a new productid species was collected from a horizon 22 ft below a distinctive marker bed of orange-brown shale a few feet below the top of the formation. According to Gerk and Levorson (1982:69), the two pits have become merged into a single large quarry in recent years and virtually all of the highly fossiliferous material has been removed. Brachiopods are very saprsely distributed at Hodge's Quarry except for these coquina lenses. The purpose of this paper is to describe several interesting new brachiopods from Hodge's Quarry, including two unusual new genera.

Most of the brachiopods from the coquina lenses of the west pit are very small specimens. There is a mixture of small adults and juveniles that reflect size sorting, probably from wave and current action in a high energy shallow water environment.

Laudon (1933:29) collected six species of brachiopods from the "*Cyathophyllum* zone" at Humboldt, Humboldt County. None of these species can be identified with certainty in the Hodge's Quarry collections.

THE HODGE'S QUARRY FAUNA

At least 18 species of articulate brachiopods occur in the Hodge's Quarry collections. Only two of these occur in the lower horizons or at other localities. *Hemiplethorhynchus subovatum* Carter is common in the lower beds of the formation at Gilmore City and is much less common in Laudon's "*Streptorhynchus* zone." Three specimens were collected at Hodge's quarry by J. A. Harper. *Setigerites facetus,* new species, first occurs in the "*Streptorhynchus* zone" at the quarries near Gilmore City where it is very rare. At Hodge's Quarry it is rare in the lower beds but occurs in large numbers at a single horizon high in the section. Most of the other 16 species (Table 1) are not reported from the lower beds of the formation exposed in Pocahontas County. Many are not identifiable to species level for lack of specimens with adult characters.

BIOSTRATIGRAPHIC RELATIONSHIPS

In my earlier Gilmore City Limestone paper (1972), I concluded that the type Gilmore City brachiopod fauna could not be correlated precisely with either Late Kinderhookian or Early Osagian Faunas in the Mississippi Valley region. This conclusion was essentially in agreement with that of Laudon (1933) who instead readily correlated the Gilmore City crinoids with Lodgepole Limestone crinoid faunas of the Cordilleran Region. Laudon arbitrarily assigned the Gilmore City Limestone to the Late Kinderhookian because it lacked conclusively Osagian crinoid genera. Laudon's crinoids nearly all came from the lower beds of the formation exposed near the type section.

Recently, Harper (1977) also considered the Gilmore City Ls. to be Latest Kinderhookian in its outcrop area. His conclusion was based on his study of the Hodge's Quarry gastropods but he admitted that his judgement was arbitrary and that an Early Osagian correlation was possible. Conodont evidence for precise correlation is scanty (Anderson, 1973). Again, a Late Kinderhookian age is suggested in the absence of Early Osagian taxa. No conodont evidence is available from the "*Cyathophyllum* zone" of Laudon, the highest beds in the formation.

The brachiopods of the "*Cyathophyllum* zone" at Hodge's Quarry for the most part provide little new biostratigraphic information. One possible exception is the small athyridid *Cleiothyridina tenuilineata* (Rowley). This distinctive little species was originally described from the lower Burlington Limestone of Pike County, Missouri. The beds from which the type specimens were recovered are of Early but not Earliest Osagian age. However, this species also occurs in the Chappel Limestone of central Texas and the "middle" Banff Formation of Alberta. The Chappel Limestone specimens occur in beds assignable to the *Gnathodus punctatus* zone of Hass (1959), or roughly to the *Siphonodella cooperi hassi—Gnathodus punctatus* zone of Thompson and Fellows (1970). The Banff specimens of *C. tenuilineata* all occur in the *Siphonodella cooperi hassi—Gnathodus punctatus* zone of Baxter and von Bitter (in press). Wherever recognized, this zone has been considered to be of latest Kinderhookian age. Thus, *C. tenuilineata* occurs only in Late Kinderhookian and Early Osagian strata.

None of the other brachiopod species from Hodge's Quarry offers much assistance in accurately delimiting the age of the "*Cyathophyllum* zone." The available evidence from all groups, such as it is, still suggests a Late Kinderhookian or Early Osagian age for the Gilmore City Limestone. Definitive data pointing to one series or the other are still lacking.

SYSTEMATIC PALEONTOLOGY

Order Strophomenida Öpik
Superfamily Productacea Gray
Family Tolmatchoffiidae Sarycheva
Genus **Setigerites** Girty
Setigerites facetus, new species

Plate 1 (figs. 1–20)

1972. *Buxtonia*? sp. B, Carter, p. 480, pl. 1, fig. 19.

Holotype.—CMNH 34405.

Paratypes.—CMNH 34402–34404, 34406, 34407.

Table 2.—*Measurements of types (in mm) of* Setigerites facetus, *new species.*

CMNH no.	Length	Width	Height	Surface measure
Pedicle valves				
34402	26.3	29.4	16.3	47.0
34403	28.4	28.3	18.6	49.1
34404	29.3	25.2	19.8	52.6
34405	26.8	25.2	17.1	49.0
Brachial valves (natural molds)				
34406	21.0	26.7	—	—
34407	20.7	24.8	—	—

Description.—Average size for genus, outline transversely to longitudinally subovate, lateral profile strongly gibbous; maximum width attained well anterior to hingeline; visceral region subquadrate to convex, brachial valve geniculate, forming moderately thick body cavity; trails moderately produced.

Pedicle valve almost evenly convex in lateral profile, being slightly more convex in region of umbo and visceral disc; venter moderately convex, flattened, or rarely with weak shallow sulcus; flanks dropping steeply to lateral margins; beak small, incurved, slightly overhanging hingeline; anterior margins of largest specimens flaring slightly; radial ornament consisting of elongate spine ridges in umbonal region and irregularly continuous fine costae over remainder of valve that increase by both intercalation and bifurcation, with about 10–13 per cm near anterior margin; concentric ornament consisting of weak irregularly spaced rugae posteriorly, forming weakly reticulate effect on umbo and ears; spine bases irregularly scattered on crests of costae over most of valve; few spines around sides of beak and near hingeline erect and very fine; spine bases on ears and flanks near ears large, not numerous, forming sparse brush in most specimens at cardinal extremities; growth lines very fine, sinuous, irregularly spaced; interior not observed.

Brachial valve with moderately concave visceral disc; trail short, sharply geniculated; ears clearly delineated by convex flexures; dorsum weakly concave, flanks more sharply flexed near margins; pronounced small concave area produced near postero-medial margin by flexures that delimit ears; tiny elongate (protegulal?) node externally marking base of cardinal process; radial ornament consisting of elongated dimples on much of visceral disc, forming furrows between fine discontinuous costae anteriorly; dimples round and large on ears; concentric ornament consisting of numerous weak irregularly spaced sinuous rugae and very fine growth lines; spine bases erect, fine, sparsely scattered on visceral disc and trail.

Brachial valve interior with short stout sessile bilobed cardinal process, dorsally inclined from plane of visceral disc; median septum thick at base of cardinal process, tapering anteriorly, extending forward at least to half length of visceral disc; lateral ridges extending along hingeline almost to ears; other internal details not observed.

Measurements are given in Table 2.

Distinguishing characters.—This species is characterized by its lack of, or poorly developed, flared rim or gutter on the pedicle valve trail, a ventral umbo of moderate breadth, about 12 ribs per centimeter on the ventral trail, the conspicuously dimpled dorsal visceral disc, the


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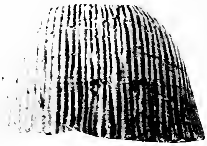
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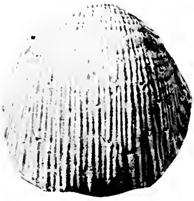
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sparse brush of relatively coarse spines on the ears of the pedicle valve, and very weakly reticulate visceral disc.

Comparisons.—Two species that appear to be similar to this new species are *Dictyoclostus sciotoensis* Hyde, 1953, from the Logan Formation of Ohio, and *Setigerites lichwiniformis* Sarycheva, 1963, from Tournaisian strata of the Kuznets Basin. Both of these species share a similar outline, profile, and ornament with *S. facetus. Dictyoclostus sciotoensis* differs in being larger, its ears are more poorly defined, especially on the visceral disc of the brachial valve, and it has slightly finer costae with more numerous bifurcations on the trail of the pedicle valve. *Setigerites lichwiniformis* can be distinguished by its poorly defined ears on the brachial valve, slightly finer more continuous costae with fewer spine ridges on the umbones, and it has a more dense brush of spines at the cardinal extremities.

Smaller specimens of *Productus jasperensis* Warren, 1932, from the Banff Formation of Alberta are similar to *S. facetus.* They can be differentiated by their broader ventral umbo, more strongly reticulate visceral disc, and dense spine brush on the ears. Mature specimens of *P. jasperensis* are much larger and have a flared marginal rim or gutter.

Setigerites setigerus (Hall) and *S. altonensis* (Norwood and Pratten) are substantially younger species. Both have more continuous costae on the umbones and both have narrower more elongate ventral umbones that substantially overhang the hingeline. In addition, *S. setigerus* has very dense spine brushes on the ears and *S. altonensis* has much finer costae than does *S. facetus,* new species.

Comments.—Assignment of this new species to *Setigerites,* a common Visean genus, is based on general similarity in external form and ornament and close similarity in internal cardinalia. However, there are possibly significant external differences between *S. setigerus* (Hall), the type species, and *S. facetus,* new species. The type species virtually lacks reticulation on the visceral disc in either valve, except near the ears. It possesses a well developed gutter or concave flange around the anterolateral margin, and it has more or less continuous costae that

←

PLATE 1

All figures ×1

Figs. 1–20.—*Setigerites facetus,* new species, 1–16, ventral, lateral, anterior, and posterior views of four large pedicle valves, CM 34403–34406, including the holotype, figs. 9–12; 17–20, ventral and anterior views of two natural molds of brachial valve exteriors, CM 34406, 34407.

All specimens are from Hodge's Quarry, east pit, 22 ft below a thin marker bed of orange-brown shale near the top of the Gilmore City Limestone.

extend virtually to the hingeline in both valves, lacking the elongate spine ridges seen on the visceral disc of *S. facetus.*

Setigerites facetus on the other hand has weak but distinct reticulation on both valves, a gutter has not been observed in any specimen, although the lateral slopes do flare slightly near the margin, and the costae originate from elongate spine bases on the umbo of the pedicle valve and from the complementary ornament of dimples on the brachial valve.

Dictyoclostus sciotoensis Hyde and *Productus jasperensis* Warren, discussed above, are species also assignable to *Setigerites* that possess some or all of these different characters with *S. facetus* and it is possible that these three species are closely related, perhaps representing an early adaptive radiation of this genus into distinctly different environments.

Stratigraphic occurrence.—This species is very rare in the "*Streptorhynchus* zone" of Laudon (1933) in the vicinity of the type section, Pocahontas County, Iowa. At Hodge's Quarry it is rare in the lower beds of both pits, but is common at a single horizon in the east pit about 22 ft below the orange-brown shale marker bed near the top of the formation.

Order Rhynchonellida Kuhn
Superfamily Rhynchonellacea Gray
? Family Pontisiidae Cooper & Grant
Iowarhynchus, new genus

Type species.—*Iowarhynchus mirandum,* new genus and new species.

Species assigned.—Genus monotypic.

Diagnosis.—Very small, smooth, elongate rhynchonellaceans with subcardiiform to guttate outline; sulcus variably present in pedicle valve, rarely in brachial valve; fold lacking; short dental plates present; foramen hypothyridid, slitlike; deltidial plates lacking; dorsal septum lacking; hinge plate often divided but inner hinge plates tending to converge, rarely fused to form undivided hinge plate; crura thin, moderately long, bladelike, falcifer, projecting antero-ventrally.

Comparisons.—Tiny entirely smooth rhynchonellaceans are rare in the stratigraphic record. *Dorsisinus* Sanders is such a genus from the Late Famennian Louisiana Limestone of Missouri. Sanders (1958:53) mistakenly diagnosed *Dorsisinus* as possessing a divided hinge plate and septalium by assuming that his silicified Mississippian species from Mexico was conspecific with the type species, *Centronella louisianensis* Weller. However, *Dorsisinus louisianensis* has an undivided hinge plate, lacks a septalium, and has well developed crural plates that buttress the hinge plate. Both *Dorsisinus* and the unnamed Mexican genus lack a ventral sulcus; instead the venter is arched. The Mexican form does not seem to be related to the Iowa genus of comparable age, but *Dorsisinus* may indeed be a Devonian progenitor of *Iowarhynchus*, new genus.

Other smooth rhynchonellaceans that bear superficial resemblance to *Iowarhynchus* are *Donella* Rotai from the Lower Carboniferous of the Donetz Basin and *Acolosia* Cooper and Grant from the Permian of Texas. *Donella* lacks dental plates, possesses a dorsal septum, and is of enigmatic affinities. Some species of *Acolosia*, especially *A. elliptica* Cooper and Grant, are much more similar both externally and internally to the new Mississippian genus. Externally, *Acolosia elliptica* has a similar outline and profile but differs in having a broader ventral sulcus, a more acute ventral beak, and it never has a dorsal sulcus. Internally, *Acolosia* has fairly wide outer hinge plates and the crura are not as vertically compressed. Interestingly, both *Iowarhynchus* and *Acolosia* lack deltidial plates.

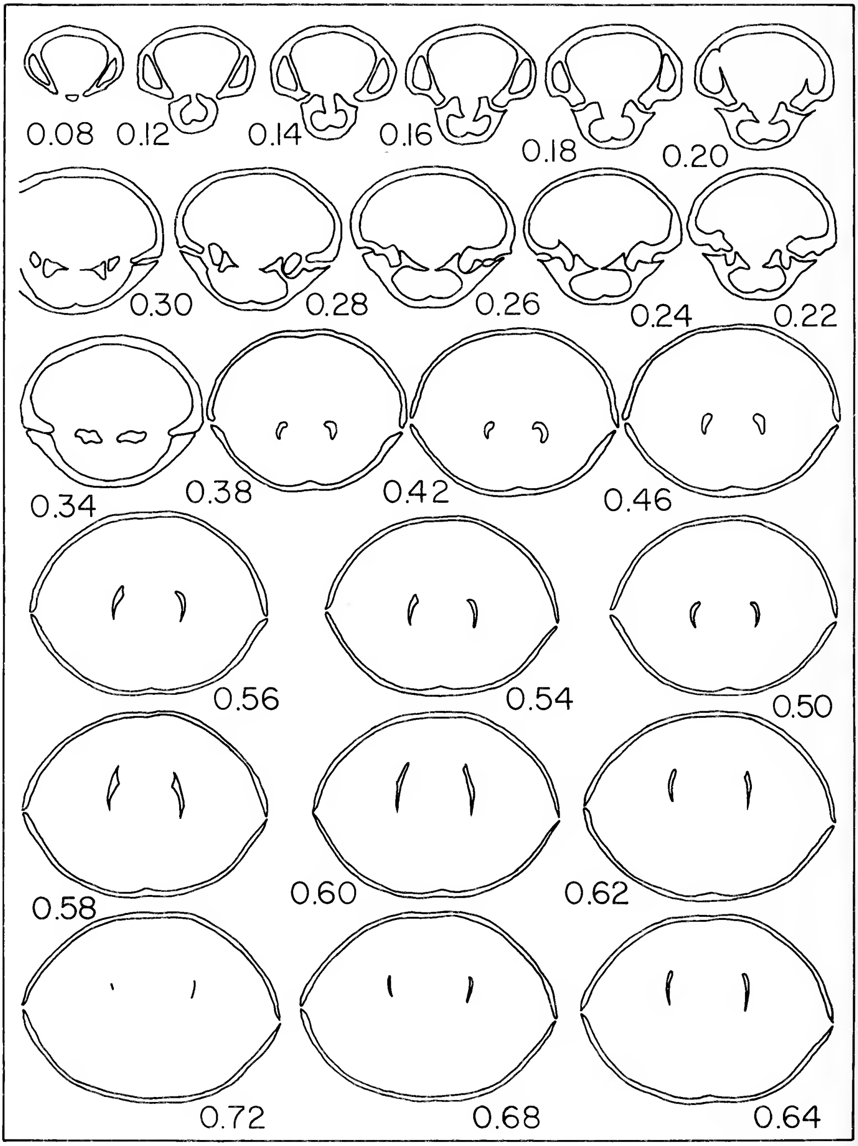
Discussion.—The lack of radial ornamentation and dorsal median septum obviate ready assignment of the new genus to an established Carboniferous rhynchonellacean family. The recently erected Permian Family Pontisiidae of Cooper and Grant (1976:2019) includes the genus *Acolosia* Cooper and Grant discussed above. Most external and internal characters of *Iowarhynchus*, new genus, more or less agree with Cooper and Grant's family diagnosis. However, most of the taxa assigned to the family by Cooper and Grant have radial ornament of some sort except for two species of *Acolosia*. There is also one significant internal difference. Virtually all of the Permian species assigned to the Pontisiidae by Cooper and Grant have recognizable outer hinge plates, whereas in *Iowarhynchus* the crural bases arise directly under the socket ridges, the outer hinge plates being completely suppressed. For these reasons and because of the substantial hiatus in stratigraphic occurrences the new Mississippian genus is assigned to the Pontisiidae tentatively.

Iowarhynchus mirandum, new genus and new species
Plate 2 (figs. 1–44); Figs. 1 and 2

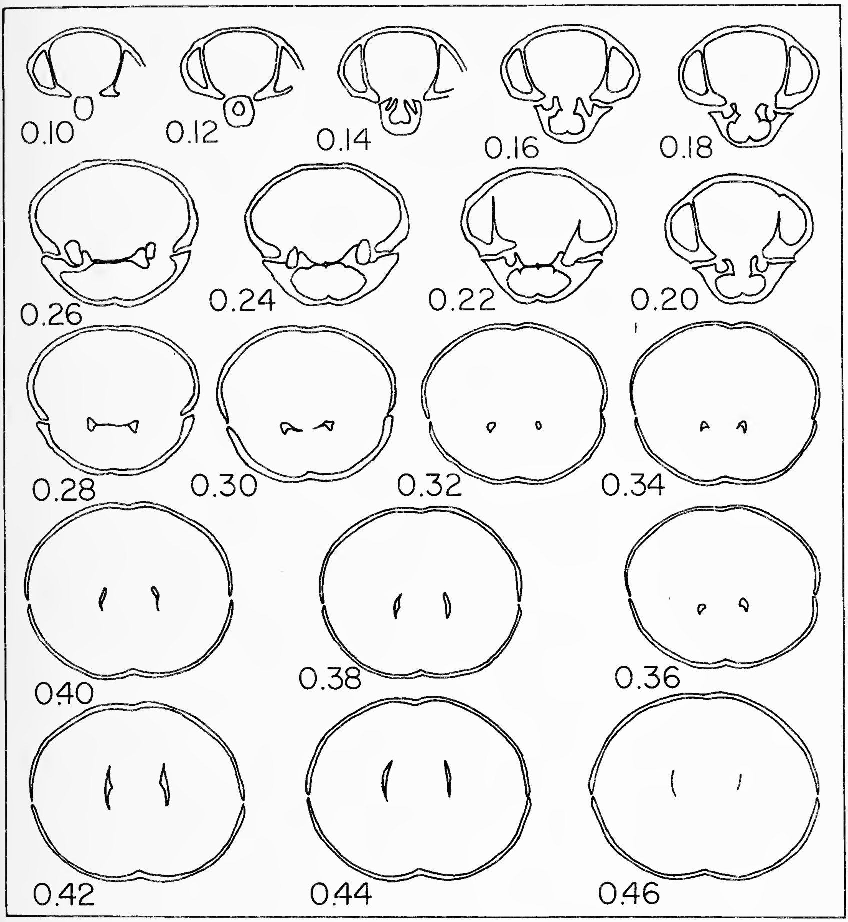
Holotype.—CMNH 34412.
Paratypes.—CMNH 34408–11, 34413–20.

Description.—Very small for the superfamily, subequally biconvex, with longitudinally subovate, subcardiiform, or guttate outline; maximum width attained anterior to midlength; lateral profile lenticular to subovate; anterior commissure uniplicate to rectimarginate; fold never developed; sulcus commonly present in pedicle valve, much less commonly in brachial valve; ornament lacking except for irregularly spaced coarse growth varices and very fine faint irregularly spaced growth lines; shell substance impunctate.

Pedicle valve moderately and evenly convex in profile in most specimens; some mature specimens with sharply deflected growth lamellae at margins producing truncated profile; lateral slopes moderately rounded or sometimes slightly flattened; maximum depth usually



Text-Fig. 1.—Transverse serial sections of *Iowarhynchus mirandum* n. gen. n. sp., CM 34419, ×12. The numbers refer to distance in mm from the ventral beak. This is a mature specimen with a divided hinge plate, externally similar to the holotype, lacking a dorsal sulcus.



Text-Fig. 2.—Transverse serial sections of *Iowarhynchus mirandum* n. gen. n. sp., CM 34420, ×12. The numbers refer to the distance in mm from the ventral beak. This is a mature emarginate specimen with an undivided hinge plate and a sulcus in each valve.

attained near or slightly posterior to mid-length; umbonal region of variable breadth but not inflated in lateral profile; beak small, nearly straight; beak ridges rounded; delthyrium narrow, open, continuous with rounded hypothyridid foramen; sulcus, if present, originating anterior to umbonal region, shallow, rounded; venter usually flatened or weakly convex in specimens lacking sulcus; dental plates short, thin, diverging slightly.

Brachial valve similar in depth and convexity to pedicle valve but with maximum depth slightly anterior to that of opposite valve; umbonal region variably produced, usually low and broad, never strongly inflated; beak inconspicuous; fold lacking, dorsum

Table 3.—*Measurements (in mm) of types of* Iowarhynchus mirandum, *new genus and new species.*

CMNH number	Length	Width	Thickness
34408	4.0	3.3	2.3
34409	3.9	3.5	2.5
34410	3.2	2.5	2.0
34411	2.5	2.0	1.5
34412	4.2	3.4	2.6
34413	4.1	3.4	2.5
34414	4.0	3.0	2.3
34415	3.1	2.4	1.6
34416	4.2	3.2	2.5
34417	3.9	3.0	2.0
34418	2.7	2.1	1.4

usually weakly convex, flattened, or with shallow sulcus, but only very rarely evenly convex; sulcus, when present, very shallow, rounded, originating in dorsal umbonal region as faint medial depression.

Dorsal interior lacking median septum; hingeplate usually divided, often with converging inner hinge plates, rarely with fused single plate; socket ridges high, sturdy, stoutly enclosing teeth; crural bases originating near dorso-medial edges of sockets with outer hinge plates not recognizable; sockets deep and rounded; crura triangular or rodlike in section near hinge plate, becoming comma-like anteriorly, then much flattened or compressed vertically, bladelike, and projecting into ventral valve distally; weak low myophragm present in most specimens.

Measurements are given in Table 3.

Comparisons.—This new species is not closely similar to previously described rhynchonellaceans. Its small size variable sulcus and complete lack of radial ornament are unusual in Mississippian strata, possibly unique. *Dorsisinus louisianensis* (Weller) is a tiny rhynchonellacean from the Louisiana Limestone (Late Famennian) of Missouri that resembles *I. mirandum,* new species, in size and outline. *Dorsisinus louisianensis* differs externally by invariably lacking a sulcus in the

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PLATE 2

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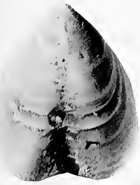
All figures ×6

Figs. 1–44.—*Iowarhynchus mirandum,* new genus and new species, 1–16, ventral, dorsal, anterior, and lateral views of four emarginate specimens with dorsal sulcus, CM 34408–34411; 17–32, ventral, dorsal, anterior, and lateral views of four specimens with ventral sulcus only, CM 34412–34415, including the holotype, figs. 17–20; 33–44, ventral, dorsal, anterior, and lateral views of three rectimarginate specimens lacking a sulcus in either valve, CM 34416–34418.

All specimens are from the thin coquina lenses in the upper 35 ft of the west pit at Hodge's Quarry, Humboldt County, Iowa.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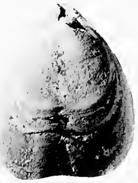
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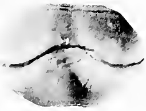
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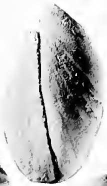
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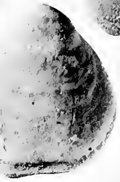
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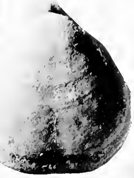
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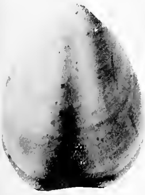
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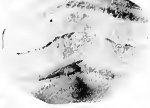
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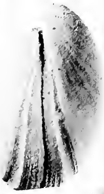
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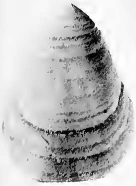
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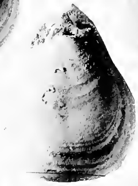
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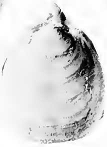
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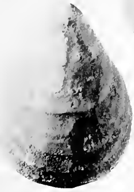
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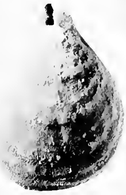
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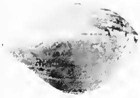
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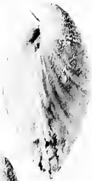
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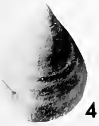
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pedicle valve, it usually has weak radial ribbing, and it has narrow deltidial plates in some specimens. Inside the brachial valve of *D. louisianensis* has substantially different cardinalia.

Stratigraphic occurrence.—Occurs only in the thin coquina lenses of the upper oolitic beds of the Gilmore City Limestone at Hodge's Quarry, west pit. Many of the better type specimens were collected and donated to the Carnegie Museum of Natural History by Arthur J. Gerk of Mason City, Iowa.

Order Spiriferida Waagen
Suborder Spiriferidina Waagen
? Superfamily Reticulariacea Waagen
Family Uncertain
Gerkispira, new genus

Type species.—*Gerkispira spinosa,* new genus and new species.

Species assigned.—Type species only.

Diagnosis.—Small transverse spiriferids with rounded lateral extremities in all growth stages and poorly delimited fold-sulcus; both valves with numerous costae on flanks and fold-sulcus, those on flanks being simple with rare exceptions, and those on fold-sulcus occasionally bifurcating; micro-ornament consisting of numerous fine hollow erect spines on costae and fine growth lines on entire surface; pedicle valve interior with slender dental adminicula; brachial valve interior with small striate cardinal process and short tabellae; shell substance impunctate.

Comparisons.—Impunctate entirely costate spiriferoids with erect hollow spines are rare in the paleontological record. Martynova (1961) described such a genus, *Spinospirifer,* from the Famennian of Kazakhstan. *Spinospirifer* has a capillate lamellose micro-ornament, an unusual nasute fold-sulcus, acute lateral extremities, and thus, does not appear to be related to *Gerkispira,* new genus.

Comments.—The absence of endopunctae in *Gerkispira* is unexpected. The spinose micro-ornament and spiriferoid costation would

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PLATE 3 →

Figs. 1–19.—*Gerkispira spinosa,* new genus and new species, 1,2, enlargements of micro-ornament showing broken spine bases of two typically preserved pedicle valves, CM 34392 (holotype) and CM 34393, ×8; 3, enlargement of an unusually spinose brachial valve, CM 34399, ×5; 4, 5, 15, 16, 18, 19, dorsal, and anterior views of three large branchial valves, CM 34396–34398, ×2; 6, 7, 8, 9, ventral and anterior views of two pedicle valves, CM 34393 and CM 34394, ×2; 10–14, ventral, dorsal, lateral, anterior, and posterior views of the holotype, CM 34392, ×2; 17, enlargement of a small pedicle valve, CM 34395, showing erect hollow spine bases, ×8.

All specimens are from the west pit at Hodge's Quarry, Humboldt County, Iowa.


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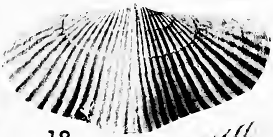
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lead one to expect punctate shell structure. However, no punctae were detected after careful examination of every specimen at hand. Furthermore, other punctate taxa from the same collection, such as *Cranaena* sp., *Punctospirifer* sp., and *Rhipidomella* sp., have well preserved punctae. It seems unlikely that the shell substances of *Gerkispira,* new genus, has been altered.

This new genus is not closely similar to any previously described genus and its familial affinities are uncertain. If one ignores the spinose ornament it would be most similar to members of the Choristitidinae by virtue of its rounded lateral extremities, numerous costae, poorly differentiated fold-sulcus, and short tabellae. On the other hand spinose ornamentation has not, to my knowledge, been reported in impunctate Carboniferous Spiriferacea. The spinose non-capillate micro-ornament, well rounded lateral extremities, poorly delimited fold-sulcus, lack of true spiriferid denticulation (with taleolae in the secondary layer of the interarea), and presence of short tabellae in the brachial valve suggest reticulariacean affinities. However, strongly ribbed reticulariaceans are very rare. Two Triassic genera, *Mentzeliopsis* Trechmann, and *Spiriferinoides* Tokuyama, appear to be reticulariaceans with strongly costate flanks. Both possess hollow spines but they differ from *Gerkispira* n. gen. in having a bald fold-sulcus and imbricate growth lamellae externally, and both have a ventral median septum internally. Although the strongly transverse outline, entirely costate macro-ornament, and erect spines are not reticulariacean characters, *Gerkispira* might be best assigned to the Reticulariacea for the reasons cited above.

Gerkispira spinosa, new genus and new species
Plate 3 (figs. 1–19); Fig. 3

Holotype.—CMNH 34392.
Paratypes.—CMNH 39393–39401.

Description.—Smaller than average for superfamily, subequally biconvex, transverse, wider than long in all but earliest growth stages; outline spiriferoid; greatest width posterior to mid-length; lateral extremities rounded in all growth stages; fold-sulcus moderately developed, rounded, not well delimited from flanks; anterior commissure uniplicate; ornament consisting of numerous costae, irregularly spaced growth varices, fine rounded spine bases usually on crests of costae, and fine regularly and closely spaced growth lines; flanks with about 9 to 15 mostly simple costae, usually about 11 to 13, sulcus with about 5 to 9 costae, with bifurcation usually restricted to sulcus-bounding costae and median costa in posterior portion of valve; fold with about 7 to 12 costae,

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Text-Fig. 3.—Transverse serial sections of *Gerkispira spinosa* n. gen. n. sp. The numbers refer to the distance in mm from the ventral and dorsal beaks, respectively. A) a pedicle valve, CM 34400. B) a brachial valve, CM 34401, showing the short tabellae.

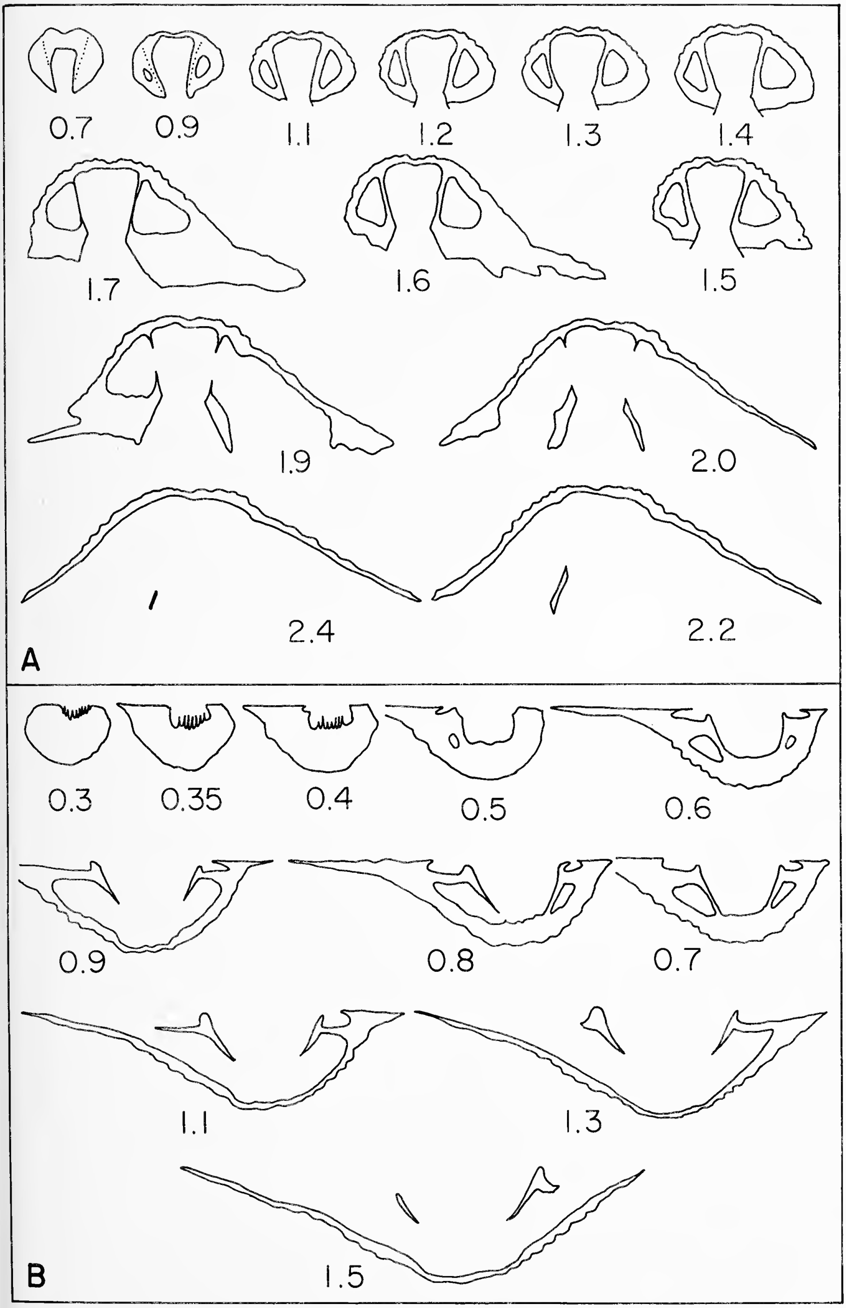
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Table 4.—*Measurements (in mm) of* Gerkispira spinosa, *new genus and new species.*

CMNH no.	Length	Hinge width	Maximum width	Thickness	Rib count
Holotype					
34392	11.1	16.0	19.1	8.6	34
Pedicle valve paratypes					
34393	+8.4	8.5	±14.0	±4.0	28
34394	8.4	10.5	12.8	3.9	±32
34395	+5.0	—	+7.0	2.3	23
Brachial valve paratypes					
34396	11.6	17.1	21.0	5.5	33
34397	9.3	14.0	16.9	4.0	32
34398	8.8	±15.0	17.7	3.8	34
34399	8.5	—	±15.2	3.8	26

usually 11 to 12, bifurcation usually restricted to median and one or two lateral sulcal costae; total rib count ranging from about 27 to 39 per valve, usually about 32 to 34 in larger specimens; intercostal furrows of moderate depth, rounded; erect hollow spine bases arranged in radial rows on costae, very rarely occurring in intercostal furrows, highly variable in density, appearing in earliest discernible growth stages; shell substance thin, impunctate.

Pedicle valve moderately inflated, slightly thicker than brachial valve, forming low equilateral triangle in posterior profile; maximum thickness attained in umbonal region, just anterior to hingeline; umbonal region moderately developed; flanks slightly convex medially, sloping evenly to antero-lateral margins; cardinal extremities slightly compressed and rounded; beak small, wide, projecting posteriorly only slightly beyond dorsal umbo; beak ridges subangular but only moderately well defined; interarea low, acutely triangular, slightly procline, moderately concave, weakly vertically grooved in primary shell layer; hingeline not denticulate; delthyrium about as high as wide, with short outward-flaring stegidial plates; sulcus originating near beak, remaining narrow and shallow in posterior half, becoming wider and rounded anteriorly but remaining shallow; sulcus poorly delimited from flanks, with well rounded shoulders; sulcus-bounding costae in umbonal region commonly bifurcating and becoming incorporated with sulcal slopes anteriorly; moderate tongue produced; costae near cardinal extremities very faint; bifurcations of lateral costae extremely rare, especially anterior to umbonal region; origination of secondary sulcal costae sometimes by intercalation.

Pedicle valve interior with strong dental flanges and thin dental adminicula of moderate length; subdelthyrial plate lacking; teeth small; muscle field weakly impressed; other details not discernible in transverse section.

Brachial valve moderately to strongly convex, nearly as thick as opposite valve, with maximum thickness attained at about mid-length of valve; umbonal region moderately swollen, flanks evenly curving to lateral margins, but cardinal extremities slightly compressed; beak small but well produced for this superfamily, projecting posteriorly to slightly overhang delthyrial chamber; dorsal interarea low, slightly concave, acutely triangular, orthocline to slightly anacline; fold originating anterior to umbonal region, remaining low and rounded throughout, poorly differentiated from flanks except near anterior margin; ornament similar to that of pedicle valve.

Brachial valve interior with small cardinal process composed of at least eight vertical plates; inner socket ridges fused dorsomedially with crural bases, forming short tabellae; muscle impressions obscure, no median ridge posteriorly; brachial details not observed.

Measurements are given in Table 4.

Stratigraphic occurrence.—This species is based on a single collection of 93 specimens taken from the upper oolitic beds, about 35 feet below the top of the formation, in the west pit at Hodge's Quarry, near Dakota City, Humboldt County, Iowa, SW¼, SW¼, Sec. 32, T. 92 N., R. 28 W. All of the better specimens were collected and donated to the Carnegie Museum of Natural History by Arthur J. Gerk of Mason City, Iowa. The genus is named for Mr. Gerk in appreciation of his outstanding contribution.

ACKNOWLEDGMENTS

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PHENETIC RELATIONSHIPS WITHIN THE CICONIIDAE (AVES)

D. SCOTT WOOD
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ABSTRACT

The major skeletal elements of all 17 species of storks were analyzed using techniques from multivariate statistics to assess the phenetic affinities within the avian family Ciconiidae. The common-part transformation and the use of taxonomic distances clustered by the unweighted pair-group method with arithmetic averages gave significantly more stable phenetic arrangements than other methods used. My results are very similar to the classification of Kahl (1979*b*) at the generic level with the exception that *Jabiru* is more similar to *Ephippiorhynchus* than would be indicated from Kahl's classification. Also, Kahl's placement of these two genera in the tribe Leptoptilini is not supported by results based on skeletal data; these genera are phenetically similar to the *Ciconia* species.

INTRODUCTION

The cosmopolitan avian family Ciconiidae is composed of the 17 species of storks (Table 1, nomenclature from Kahl 1971*a*, 1972*a*). By 1901, there was agreement as to the membership of the family except for the Shoebill (*Balaeniceps*), which most authors considered to be in a separate family (for example, Beddard, 1886, 1896, 1901; Garrod, 1875, 1877, 1878; Parker, 1860; Weldon, 1883) and is currently recognized as such (Kahl, 1979*a*). The classification of Peters (1931, Fig. 1A) summarized the systematic findings with the 17 species allocated to 11 genera in two subfamilies. Prior to Peters' classification, virtually all studies involving storks either focused on the relationships of the Ciconiidae as a whole to other birds (or vice versa) rather than on relationships within the family or were concerned with describing a

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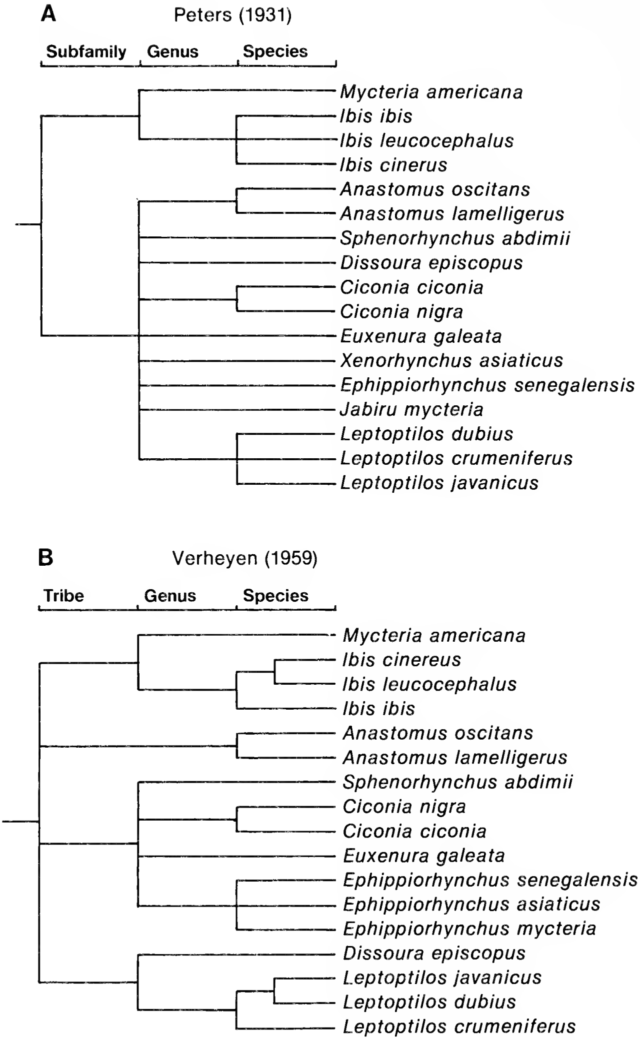


Fig. 1.—Dendrograms representing (A) the classification of Peters (1931) and (B) the relationships postulated by Verheyen (1959).

new feature of some particular species. More recent morphological studies also have focused on the relationships of the family to other birds (for example, Cottam, 1957, Ligon, 1967). With the exception of Verheyen (1959), there has been no comprehensive investigation of

Table 1.—*Taxa and number of specimens used in this study (nomenclature from Kahl, 1972a).*

Name	No. specimens	Geographic range (Kahl, 1979*b*)
Mycteria americana American Wood Stork	5	Southern United States to Paraguay
Mycteria cinerea Milky Stork	2	Cambodia to Java
Mycteria ibis Yellowbilled Stork	6	Africa, from Senegal to Sudan; south to Natal
Mycteria leucocephala Painted Stork	5	India and Sri Lanka to Vietnam
Anastomus oscitans Asian Openbill Stork	5	India and Sri Lanka to Vietnam
Anastomus lamelligerus African Openbill Stork	4	Africa, from Senegal to Sudan; south to Transvaal
Ciconia nigra Black Stork	4	Much of Palearctic; South Africa
Ciconia abdimii Abdim's Stork	5	Africa, from Senegal to Uganda and Yemen
Ciconia episcopus Woolynecked Stork	5	India and Sri Lanka to Borneo and the Philippines
Ciconia maguari Maguari Stork	5	Colombia to Argentina
Ciconia ciconia White Stork	6	Europe to Turkistan; Cape Province; Eastern Siberia
Ephippiorhynchus asiaticus Blacknecked Stork	5	India and Sri Lanka to northeastern Australia
Ephippiorhynchus senegalensis Saddlebill Stork	5	Africa, from Senegal to Sudan; south to Transvaal
Jabiru mycteria Jabiru Stork	5	Mexico to Argentina
Leptoptilos javanicus Lesser Adjutant Stork	5	Eastern India to Borneo
Leptoptilos dubius Greater Adjutant Stork	5	Northeastern India to Vietnam
Leptoptilos crumeniferus Marabou Stork	6	Africa, from Senegal to Sudan; south to Natal

the comparative morphology of members of the Ciconiidae, although Fürbringer (1888), Garrod (1873), and Vanden Berge (1970) included representatives of the family in their comparative studies of muscles.

Verheyen (1959) examined a wide range of characters in an attempt

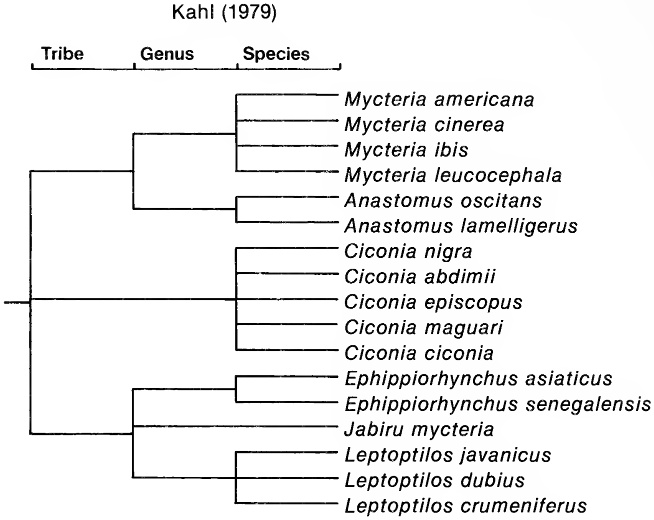


Fig. 2.—Dendrogram representing the classification of Kahl (1979*b*).

to clarify the relationships within the order Ciconiiformes (*sensu* Wetmore, 1960) and included all but one species of stork (*Anastomus oscitans*) in his analysis. He proposed a classification for this family (Fig. 1B) that differed in several important respects from that of Peters (1931). In the process, he only reduced the number of genera to nine, referring the genera *Jabiru* and *Xenorhynchus* of Peters to *Ephippiorhynchus* and placing the genus *Dissoura* in the Leptoptilini, one of the four tribes he recognized.

Kahl (1966, 1971*a*, 1972*a*, 1972*b*, 1972*c*, 1972*d*, 1972*e*, 1973) compared the ritualized courtship behavior of all 17 storks and considerably improved our knowledge of the intrafamilial relationships. His classification (Kahl, 1979*b*) is shown in Fig. 2. Kahl also made important departures from both Peters' (1931) and Verheyen's (1959) classifications, reducing the number of genera to six and allocating these genera to three tribes. Significantly, he combined several genera into *Ciconia*, merged *Ibis* into *Mycteria* and placed *Anastomus* and *Mycteria* in a separate tribe. He also associated *Jabiru* and *Ephippiorhynchus* with *Leptoptilos*, although not on behavioral grounds (Kahl, 1973).

As part of a larger study involving the relationships of the Ciconiidae, I investigated the phenetic associations within the family as implied by the structure of a number of different skeletal elements. I also use

Table 2.—*Bones used to infer phenetic relationships among the Storks; numbers of points and characters defined on each bone.*

Bone	Number of		
	Points	Linear measurements	Angles
Ossa cranii, ossa faciei	16	39	51
Axis[1]	8	18	24
Humerus	17	36	57
Clavicula[1]	10	15	18
Coracoideum[1]	10	16	21
Sternum	9	21	33
Synsacrum, os coxae	11	21	30
Tibiotarsus[1]	12	20	24
Tarsometatarsus	15	29	39

[1] Used only in preliminary analyses.

my empirical results to evaluate the efficacy of the phenetic methods chosen, some of which have received little critical attention.

MATERIALS AND METHODS

Skeletons of the 17 species were obtained (Table 1). Because of the paucity of material, I measured the first five or six specimens encountered, as listed in Appendix I, regardless of origin (unless a specimen was damaged); for some species fewer than five specimens were available. I chose characters by: (1) comparing among a reference series of ciconiiforms in the University of Oklahoma collections; (2) rejecting skeletal elements for which I could discern only small variation over the series; (3) identifying points on each of the remaining bones in such a way that for any individual I could identify the point homologous to that of the reference series; (4) choosing interpoint distances that would, when measured, describe variation visible to my eye. The interpoint distances were also chosen so that they formed the sides of triangles; in this way I could calculate the angles subtended by the sides of the triangles and thus have a relatively size-independent measure of the shape of the bone. Using this procedure I chose 107 points spread over nine bones or bone complexes. Fig. 3 shows the points chosen for each of the bones. From this network I selected 215 measurements; these delimited 99 triangles giving 297 angular characters (Table 2). Descriptions of the points, characters and angles are listed in Appendix II; nomenclature is taken from Baumel et al. (1979) and Bock and McEvey (1969). The data for each bone were analyzed separately; in addition, I analyzed the total data set (as defined below).

Computations were performed on the IBM 370-158 at the University of Oklahoma. Some analysis was done using FORTRAN routines but most employed the packages NT-SYS (Rohlf et al., 1979) and SAS (Barr et al., 1979). The three-dimensional models were plotted using the program GRAFPAC developed by F. J. Rohlf.

Each species was represented by the means of each character over all individuals. Missing values were estimated using regression; of the approximately 12,000 measurements used in this study, only 9 were coded as missing.

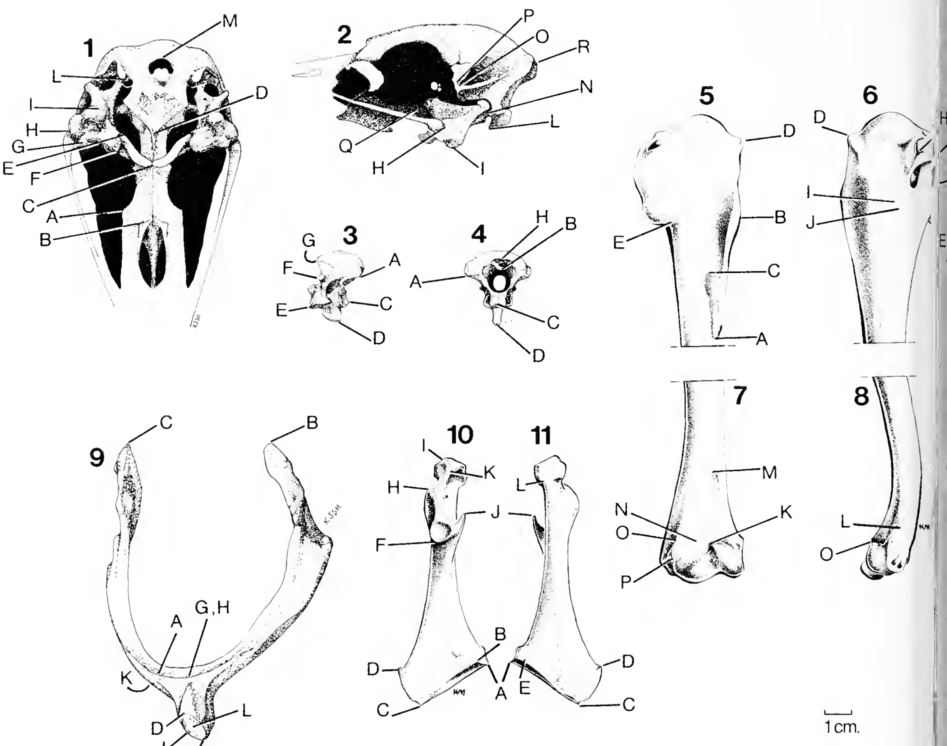
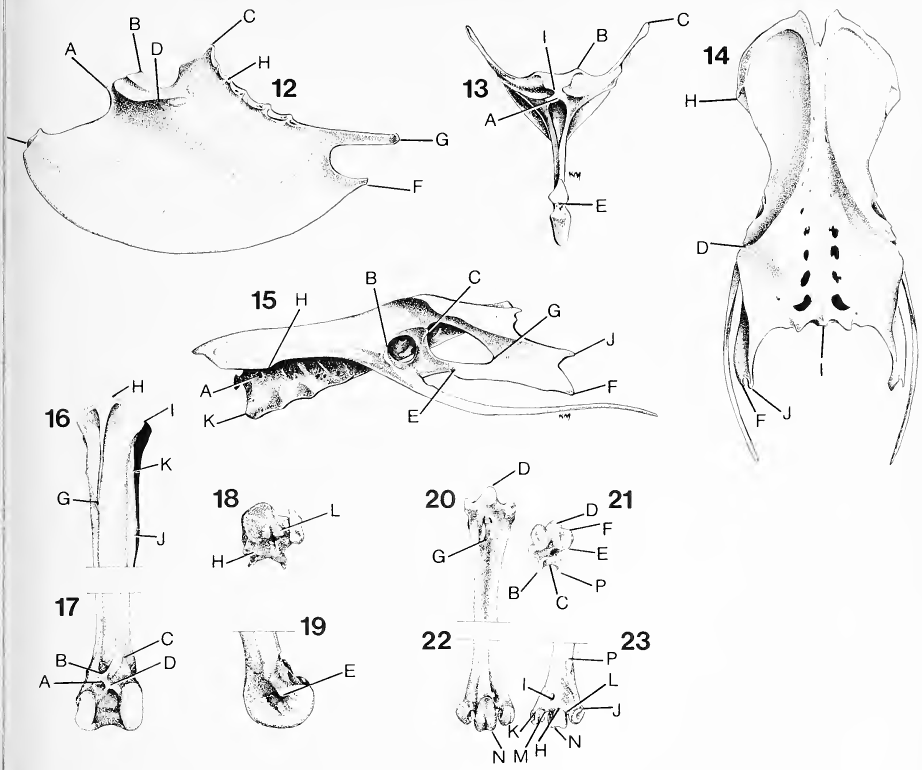


Fig. 3.—Representative skeletal elements of the storks showing the points defined in this study. The characters defined from these points are listed in Appendix II. The specimens illustrated are *Leptoptilos* sp. (UOMZ 7722, views 1–4), *Ciconia ciconia* (CM S-1813, views 5–8, 10–15), *Jabiru mycteria* (UOMZ 6794, view 9), and *Mycteria americana* (UOMZ 7720, views 16–23). The following bones and views are illustrated: (1) skull and palate, ventral view; (2) skull and palate, left lateral view; (3) axis, right lateral view; (4) axis, caudal view; (5) left humerus, proximal portion, cranial view; (6) left humerus, proximal portion, caudal view; (7) left humerus, distal portion, cranial view; (8) left

Angles were calculated in radians in the following way: let A, B, and C be the sides of the triangle (the measured characters) and X be the angle opposite A. Then $X = 2*\arctan(R/(S - A))$ where $S = (A + B + C)/2$ and $R = \sqrt{(S - A)*(S - B)*(S - C)}/\sqrt{S}$. The angles were calculated for all individuals and means were computed to represent each species. Where, due to measurement error, angles could not be calculated (the sum of the lengths of two sides of a triangle was less than the third), the angles were estimated by comparing the relative lengths of the sides and then assigning values representing angles of a very obtuse triangle of similar proportions.

Size (at least its linear effects) is considered by many workers to be a poor indicator of taxonomic relationships (Sneath and Sokal, 1973). For many taxonomic studies using



humerus, distal portion, dorsal view; (9) clavicula, right dorsolateral view; (10) left coracoideum, dorsal view; (11) left coracoideum, ventral view; (12) sternum, left lateral view; (13) sternum, cranial view; (14) synsacrum, dorsal view; (15) synsacrum, left lateral view; (16) left tibiotarsus, proximal portion, dorsal view; (17) left tibiotarsus, distal portion, dorsal view; (18) left tibiotarsus, proximal end; (19) left tibiotarsus, distal portion, medial view; (20) left tarsometatarsus, proximal portion, dorsal view; (21) left tarsometatarsus, proximal end; (22) left tarsometatarsus, distal portion, dorsal view; (23) left tarsometatarsus, distal portion, plantar view.

continuous characters, size has thus been considered a problem; using untransformed data, large (or small) species cluster together regardless of shape (see discussion in Sneath and Sokal, 1973:169–174). The problem of size has two facets: (1) the definition of size; and (2) how to remove or reduce its effects. Sneath and Sokal (1973) suggested that if in an ordination the first axis has mostly positive loadings then this axis represents a size axis. They proposed removing the effect by collapsing the ordination by that dimension and using the remaining axes. Alternatively, they suggested removing a measure of size through the use of ratios, a common and widespread practice.

More recently Atchley et al. (1976), Atchley and Anderson (1978) and Atchley (1978) have pointed out some potential dangers of using ratios. They suggested using regression analysis to remove the effects of size (or some other variable). I expected size to have a considerable influence on the magnitude of the raw measurements since the family includes some of the largest of flying birds as well as a few of only moderate size (range in height 76 cm–152 cm; Harrison, 1978). Principal component I (based on a matrix of correlations among the characters from the total data set as defined below) did not represent size since the high loadings were restricted to a specific set of characters and were not all positive. However, clusters of species derived from the raw data (using the unweighted pair-group method with arithmetic averages; UPGMA) appeared to reflect a large size influence, that is, all large species clustered together.

I operationally defined size as the mean of three length characters corresponding to the lengths of the tarsometatarsus, tibiotarsus and ischium (TA-DN, TI-EL, SY-CJ; see Appendix II). To check that this variable reflected size, I clustered the species according to size by eye and compared these groups to the UPGMA clusters formed using the size variable only. The results were concordant and were also very similar to clusters derived from the raw data. I then regressed each variable against the size variable to obtain the regression estimate, subtracted the estimate from the original value and used the residual as the character state.

Explicitly, this procedure is as follows: let Y be a vector of measurements for a given character over all species. Let X be the size vector over all species. The estimate of Y_i $(=\hat{Y}_i)$ can be found from the equation $\hat{Y} = \alpha + \beta X$, where $\alpha = \bar{Y} - \beta \bar{X}$ and $\beta = r_{(Y,X)} {*} (s_Y / s_X)$. The quantity $r_{(Y,X)}$ is the correlation between the variables Y and X; s_Y and s_X are the standard deviations of these variables. The residual, R, is found from $R_i = Y_i - Y_i$. These residuals are uncorrelated with X (size). Size accounted for between 60% and 90% of the variance of the data for the various bones. The angular data provided a second transformation to reduce the effects of size; tests indicate the correlation with the size variable to be much reduced.

For another transformation I removed the "common part" from each of the data sets. This idea is described and developed more fully in Wood (1983*a*). Briefly, the variable representing a particular stork (the vector of measurements on that stork) can be thought of as having two parts: (1) a part predictable by regression from some reference variable (some bird other than a stork) and (2) a part not predictable from the reference variable. If the reference variable is chosen to estimate the essence of the stork family as closely as possible, then I will refer to the first component as the common part. The second part I will call the clustering part; the variance accounted for by the latter concerns differences between the various storks as well as variation due to measurement error.

The clustering part is of most use when evaluating relationships within a group. The common part can be removed in a manner analogous to the procedure outlined above for removing size if an estimate of the common part can be found. In phenetic studies, a species (or several species) that is very similar to the members of the group under study can be used to estimate the common part; the more similar the outside species is, the better will be the estimate. For this study I used two species to estimate the common part—*Balaeniceps rex* and *Scopus umbretta.* They are osteologically very similar to the storks and several authors have suggested they are related to the storks (for example, Mitchell, 1913; Parker, 1860; Peters, 1931; Wetmore, 1960). The regression equation used in this case is: $\hat{Y}_i = \alpha + \beta_1 X_1 + \beta_2 X_2$, where $\hat{Y}_i$ is the estimate of all variables for species *i*, X_1 and X_2 are the vectors of character measurements for *Scopus* and *Balaeniceps* and α and β are as above (β_1 and β_2 correspond to *Scopus* and *Balaeniceps,* respectively). Between 80% and 90% of the variance was removed from the various data sets by this procedure. A separate estimate of the common part was also calculated from four other species (one pelican, one cormorant, and two New World vultures). Average taxonomic distances (Sneath and Sokal, 1973) were calculated between all storks for each set of estimates for each bone. The average matrix correlation between estimates (over all bones) was 0.91 indicating that the transformation (removal of the common part) is robust to the choice of estimator for the common part.

The use of means obscures variability within each species and, consequently, the overlap in phenetic space. If substantial overlap exists, there may be insufficient information present in a particular matrix to discern the relationships among the elements (taxa). Partitions from such a data set should give less consistent taxonomic results than partitions taken from a case showing much less overlap because in the first case the variation is more nearly random with respect to the taxa. For all of the transformations (size removed, angles, common part), I subjected each of the data sets to a multiple discriminant function analysis (using PROC DISCRIM of SAS). My interest was in the resolution afforded by the data: how many individuals were misclassified? If the resolution was poor (that is, poor discrimination among species resulting in many misclassifications, particularly if they were misclassified to species thought on other grounds to be relatively dissimilar or unrelated) then I judged that using means would be likely to compound errors and give discordant results. Of the nine bones originally used (Table 2), five showed sufficient resolution to be useful in subsequent analyses (the remaining four produce far less consistent results). Thus, the remainder of the analyses were restricted to the following: skull, humerus, sternum, synsacrum, and tarsometatarsus. One reason for the poor resolution resulting from use of the other bones is that the original measurements were devised to describe variation over all ciconiiforms (*sensu* Wetmore, 1960); the elements not used further (axis, clavicula, coracoideum, and tibiotarsus) are very uniform within the Ciconiidae but show considerable variation over the several families of the Ciconiiformes.

All subsequent analyses (except as noted) were performed on each of the 18 data sets—six partitions (skull = SK, humerus = HU, sternum = ST, synsacrum = SY, tarsometatarsus = TA, all characters from these five bones = ALL) with three transformations for each (size removed by regression = SIZE, size effect reduced by using angles = ANGLES, common part removed = COMMON). A given data matrix is named by concatenating the transformation code with the partition code (for example SIZE-SK, ANGLES-SY). The following analyses were performed after standardization of the data: (1) a phenogram summarized the results of a UPGMA cluster analysis on a matrix of average taxonomic distances. (2) Factor analysis using a matrix of correlations among taxa (Q-type) was performed with a secondary factor structure matrix obtained by oblique rotation using the functionplane technique of Katz and Rohlf (1974). Communalities were estimated using the maximum of the absolute values of the elements for each variable in the correlation matrix and all factors with eigenvalues greater than 1.0 were retained. The secondary structure matrix was interpreted as a taxon by character matrix and used to produce inter-taxon correlations as the similarity measure. These were subjected to a UPGMA cluster analysis and the results summarized in a phenogram. This procedure seeks to identify patterns of common variation (clusters of taxa) and emphasize these by rotating the axes to be coincident with the clusters. An oblique rotation was used because there is no *a priori* reason to expect clusters of biological organisms to be orthogonal. The analysis reconstitutes the among-taxa correlation matrix but emphasizes the similarities between members of a cluster because the components of variance unique to a given taxon are discarded. Thus, the phenograms closely resemble phenograms produced by UPGMA clustering of the original inter-taxon correlation matrix except that the clusters are better defined and phenograms based on different partitions of the data are slightly more consistent (i.e., have a higher average matrix correlation among results).

(3) Projections of the taxa on axes from a principal components analysis (the number of components was determined by the number of eigenvalues greater than 1.0) were subjected to a cluster analysis using the adaptive hierarchical clustering scheme (AHCS) of Rohlf (1970); these results were summarized in a phenogram. AHCS can find elongated clusters in multidimensional space rather than only the hyperspheroidal clusters searched for by most clustering algorithms (including UPGMA). The degree of elongation sought is controlled by a parameter of the program (set to 1.0 for this study). The technique

uses inter-taxon distances for the similarity measure and so may give results similar to UPGMA clustering of these distances, particularly if elongated clusters do not exist. Because of computer limitation, AHCS was not run on the combined (ALL) data sets. (4) Non-metric multidimensional scaling (MDS) was used to reduce the dimensionality of the data to three. The species were plotted on these axes using GRAFPAC to produce three-dimensional (3-D) models; these give better visual representation of the distances among taxa than is usually possible using phenograms. (5) Minimum-spanning trees for taxa (Prim networks) were derived from average distance matrices and superimposed on the 3-D models. (6) Matrix correlations were calculated between all pairs of phenograms and between a phenogram and its basic similarity matrix (cophenetic correlations).

Codes for the three phenogram-producing analyses are: DIST (UPGMA clustering of distances), AHCS (AHCS clustering of distances) and CORR (Q-type factor analysis). Phenograms, basic similarity matrices and other results were named by concatenating these codes with the codes for transformation and partition (e.g., COMMON-SK-DIST, SIZE-ALL-CORR). A dendrogram of phenograms was created by applying UPGMA to the matrix of correlations among phenograms (after changing the sign on the matrix correlations between distance analyses and correlation analyses). Further discussion of these techniques may be found in Sneath and Sokal (1973) or in the documentation to NT-SYS (Rohlf et al., 1979).

RESULTS AND DISCUSSION

Fifty-one phenograms were constructed to represent the similarities among the storks. Fig. 4 is a dendrogram of these phenograms based on correlations between all pairs of cophenetic matrices. The cophenetic correlation of this dendrogram is 0.693, an indication of some distortion in the original associations. Figs. 5–7 show phenograms representative of the major clusters present in the dendrogram (using an arbitrary level of 0.4); additional phenograms are shown in Figs. 8–10 and in Wood (1982, 1983*b*).

Fig. 5A depicts the phenogram for ANGLES-HU-DIST, a representative of one of the two largest clusters in Fig. 4. Except for *Anastomus oscitans,* which is well separated from the other species, the clusters correspond closely to the genera of Kahl (1979*b,* Fig. 2). In addition to *A. lamelligerus* being associated with *Ciconia, Jabiru* clusters with the *Ciconia* species. This is one of only four phenograms to support Kahl's placement of *Ephippiorhynchus* with *Leptoptilos* (the others are ANGLES-HU-AHCS, COMMON-HU-CORR and COMMON-SK-CORR). The cophenetic correlation is 0.737 due to distortion among the major branches of the phenogram.

The phenogram of COMMON-SK-AHCS (Fig. 5B) is a representative of the other large cluster in Fig. 4. The structure of this phenogram matches the structure of Kahl's (1979*b*) classification (Fig. 2) closely with the exceptions that *Anastomus* and *Ephippiorhynchus* are associated with *Ciconia,* and *Jabiru* clusters with *Mycteria.*

In the phenogram for COMMON-ALL-CORR (Fig. 6A), the species cluster very tightly, a phenomenon generally true of the CORR analyses because of the emphasis placed on close similarities by the factor an-

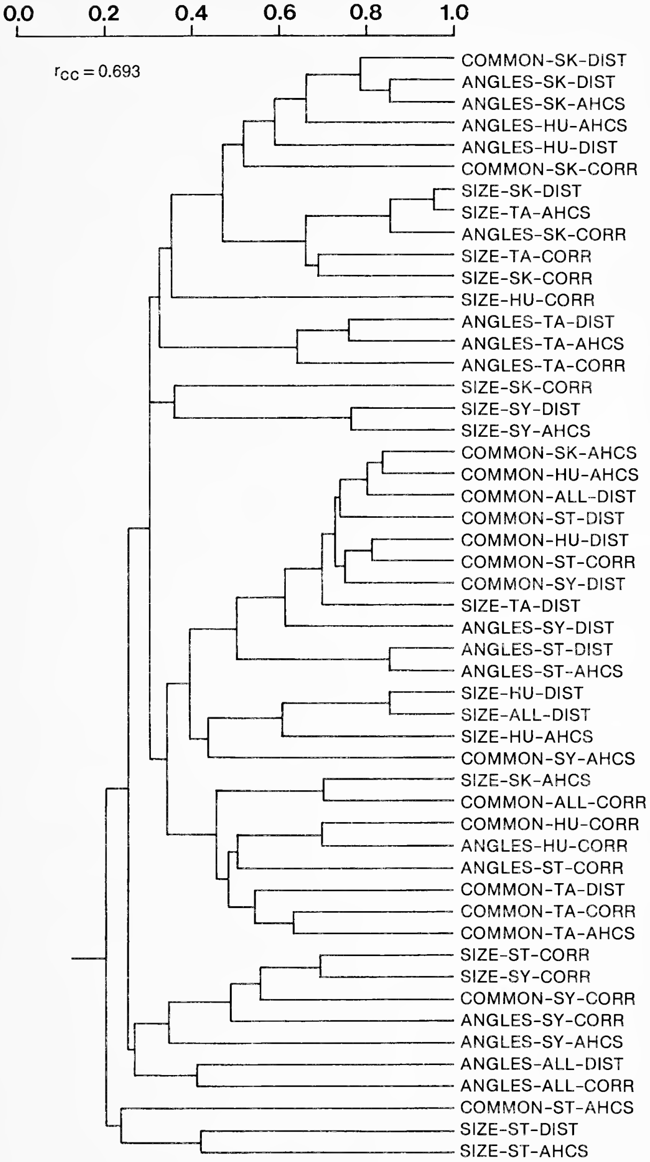


Fig. 4.—Dendrogram of phenograms derived from a UPGMA analysis of all possible matrix comparisons between the cophenetic matrices for the 51 phenograms of this study (scale is in correlation units).

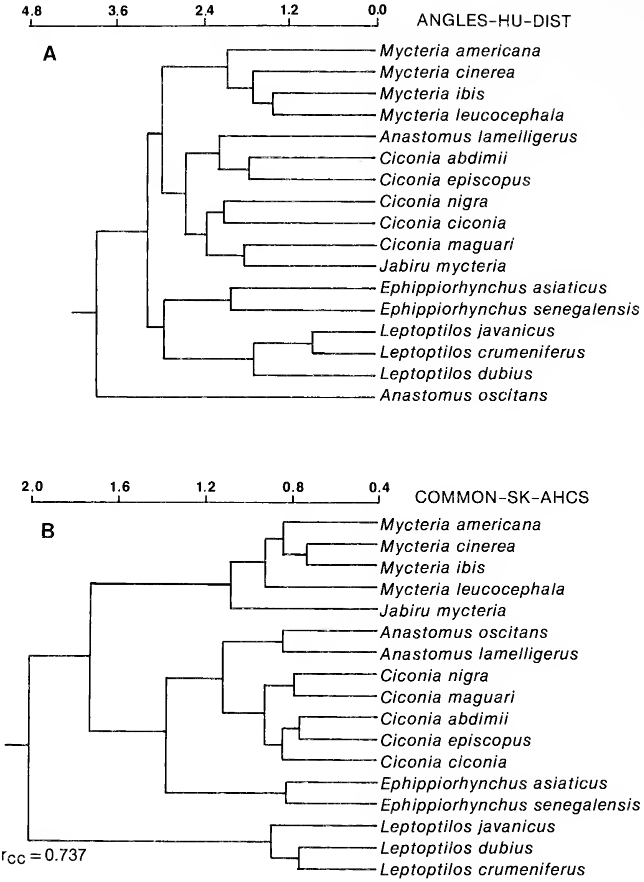


Fig. 5.—Phenograms representative of the major clusters of the dendrogram of phenograms: (A) derived from UPGMA clustering of taxonomic distances based on angular characters of the humerus; (B) derived from an AHCS analysis of taxonomic distances based on the COMMON transformation of skull characters. Scales of both phenograms are in units of average taxonomic distance.

alytic procedure used. The composition of the clusters is similar to that found in the previous examples with the exception of *Ciconia* which is split among two groups. *Jabiru* is most similar to *Ephippiorhynchus* and *Ciconia,* whereas *Leptoptilos* is closer to *Mycteria.* The cophenetic correlation of 0.893 indicates relatively little distortion in the phenogram.

The phenograms in Figs. 6B, 7A and 7B are representatives of relatively small clusters of the dendrogram of phenograms (Fig. 4). The

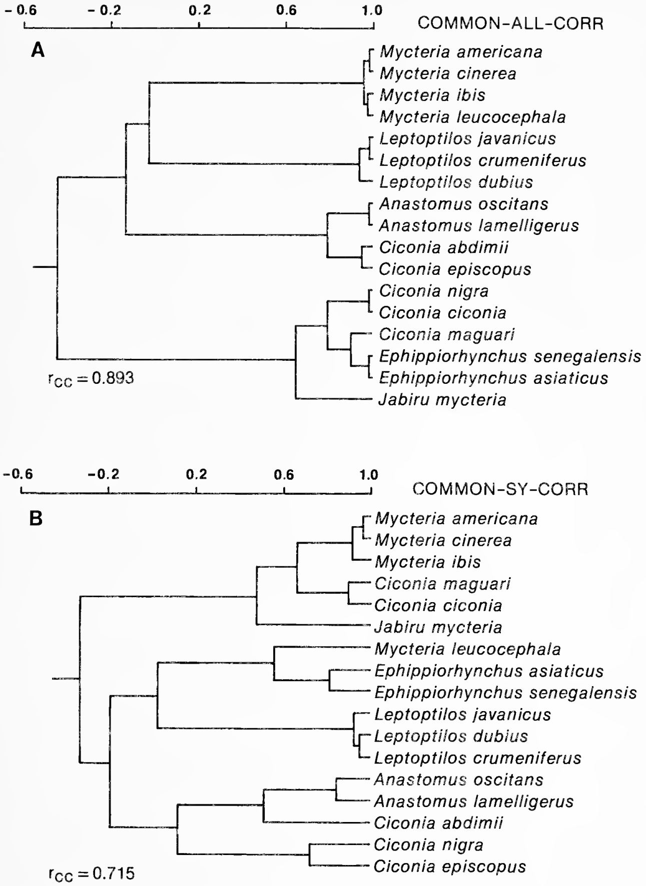


Fig. 6.—Phenograms representative of the major clusters of the dendrogram of phenograms. Both are derived from UPGMA clustering of correlations taken from a Q-type factor analysis of characters transformed using the COMMON transformation: (A) based on all characters; (B) based on synsacral characters. Scales of both are in correlation units.

phenogram for COMMON-SY-CORR (Fig. 6B) shows several clusters that are similar to Kahl's genera but both *Mycteria* and *Ciconia* are split. *Mycteria leucocephala* clusters with *Ephippiorhynchus* and *C. abdimii* is associated with *Anastomus.* The cophenetic correlation (0.715) is relatively low; the relationships of the storks implied by the phenogram are somewhat distorted from the basic similarities. *Mycteria* and *Anastomus* cluster together in the phenogram SIZE-ALL-DIST (Fig. 7A). Four of the five species of *Ciconia* also cluster together but

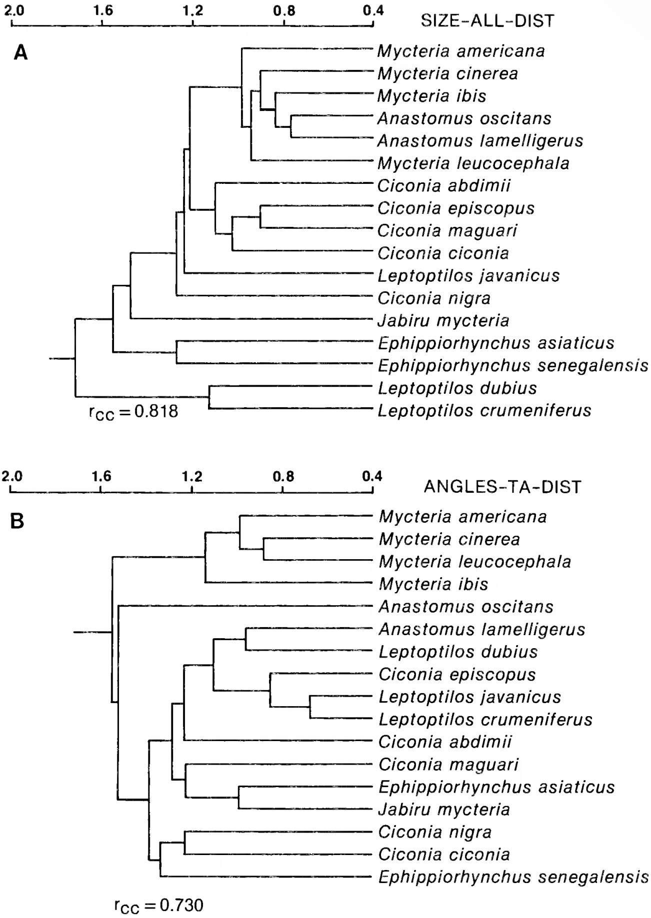


Fig. 7.—Phenograms representative of the major clusters of the dendrogram of phenograms: (A) derived from UPGMA clustering of taxonomic distances based on the SIZE transformation of all characters; (B) derived from UPGMA clustering of taxonomic distances based on angular characters of the tarsometatarsus. Scales of both are in average taxonomic distance units.

Leptoptilos javanicus is separated from its congeners. Some distortion is present (cophenetic correlation of 0.818). The phenogram ANGLES-TA-DIST (Fig. 7B) represents a cluster in Fig. 4 composed of the three analyses using the data set ANGLES-TA. These three phenograms are the only results concordant with Verheyen's (1959) suggestion that *Ciconia episcopus* is closely related to *Leptoptilos.* Only the *Mycteria* cluster resembles the groups proposed by Kahl (1979*b,* Fig. 2). The cophenetic correlation of 0.730 is relatively low for this study.

Clearly, there are considerable differences between some phenograms (the range of matrix correlations is −0.10 to 0.95). These differences are not only between transformations and analyses but also between data sets for a given transformation and analysis.

Rohlf and Sokal (1981) pointed out that methods that produce more stable classifications (other factors being equal) would be preferred over those that produce less stable classifications. They also noted that stability, by itself, is not a good criterion since perfect stability can be achieved by making the results independent of the data. However, this criterion can be useful when comparing methods chosen for reasons other than stability (for example, to emphasize a particular aspect of the data).

Rohlf and Sokal (1980, 1981) have discussed several definitions of stability, of which robustness of a classificatory procedure to changes in character sets (congruence of resultant classifications) is applicable here. They defined congruence as "agreement of separate classifications arrived at by the same algorithms and based on the same set of operational taxonomic units but on different sets of characters" (Rohlf and Sokal, 1981). The sets of characters should not represent different classes of characters because such an evaluation of stability would be confounded with an evaluation of the non-specificity hypothesis (Rohlf and Sokal, 1980). Matrix correlations are a useful measure of the relative congruence of classifications although this measure may not be optimal for evaluating absolute levels of concordance (Rohlf, 1982).

The partitions of the characters used in this study provide an opportunity to evaluate the stability of the methods employed. Both the transformations of the data as well as the analyses applied to these data are evaluated with respect to the stability of the resulting classifications. Table 3 lists the average matrix correlations among phenograms over all partitions (five bones) for all transformations and analyses considered. Ranges and standard deviations are included. Within each transformation and analysis (for example, ANGLES-DIST) the 10 correlations used to calculate the mean are not independent since they represent all possible comparisons among the five partitions. However, at least four comparisons are independent and the degrees of freedom in all significance tests are adjusted accordingly. Significant heterogeneity exists among the means listed in Table 3 (analysis of variance, $F = 3.35$, $F_{0.5[4,36]} < 2.69$). If the means are ranked, no significant differences exist between adjacent means. However, the analysis COMMON-DIST has a significantly higher mean than any analysis except COMMON-AHCS ($t = 2.71$, $t_{0.5[8]} = 1.86$ [one tailed] between COM-

Table 3.—*Statistics on matrix correlations between all pairs of cophenetic matrices derived from each of the five data partitions. Each treatment of the data is analyzed separately; for each analysis the number of possible intercorrelations is 10.*

Analysis	Mean	Standard deviation	Range
COMMON-DIST	.352	.182	.805–.291
COMMON-AHCS	.407	.193	.833–.177
COMMON-CORR	.353	.100	.471–.190
SIZE-DIST	.312	.145	.520–.051
SIZE-AHCS	.275	.151	.568–.107
SIZE-CORR	.339	.171	.679–.102
ANGLES-DIST	.303	.192	.597–.102
ANGLES-AHCS	.187	.209	.667–−.007
ANGLES-CORR	.291	.108	.475–.151

MON-DIST and COMMON-CORR). If the analyses are pooled so that the differences between transformations can be evaluated, then the COMMON transformation gives significantly more congruent results (that is, a higher mean) than does SIZE ($t = 2.274$, $t_{0.5[16]} = 1.746$ [one tailed]). The ANGLE transformation gives results with lower average congruence than SIZE. These findings are supported by a more detailed analysis of a subset of the data which is presented elsewhere (Wood, 1983*a*).

The mean matrix correlation among partitions is very low for both the SIZE and ANGLE transformations (Table 3). These transformations were chosen to emphasize the shape of the skeletal elements used as the source of information about relationships among the storks. Shape was defined in two different ways—in the SIZE transformation shape was the residual variance remaining from a statistical removal of a size estimate; in the ANGLE transformation shape was defined as the angles subtended by pairs of measurements on the bones. The emphasis on shape (or the de-emphasis of size) has been commonly used in phenetic studies because the single characteristic "size" often has such a pervasive influence as to mask the information about relationships present in the other characters used in the study. However, the classifications I have derived from the size transformations show rather low stability (as measured by matrix correlations) regardless of the analysis employed.

In contrast to findings of some other investigators (for example, Schnell, 1970; Robins and Schnell, 1971; Hellack, 1976) but similar to my earlier results on cranes (Wood, 1979), distances gave the most stable (consistent) results. However, this may be more an effect of the transformation than of other considerations since the transformations

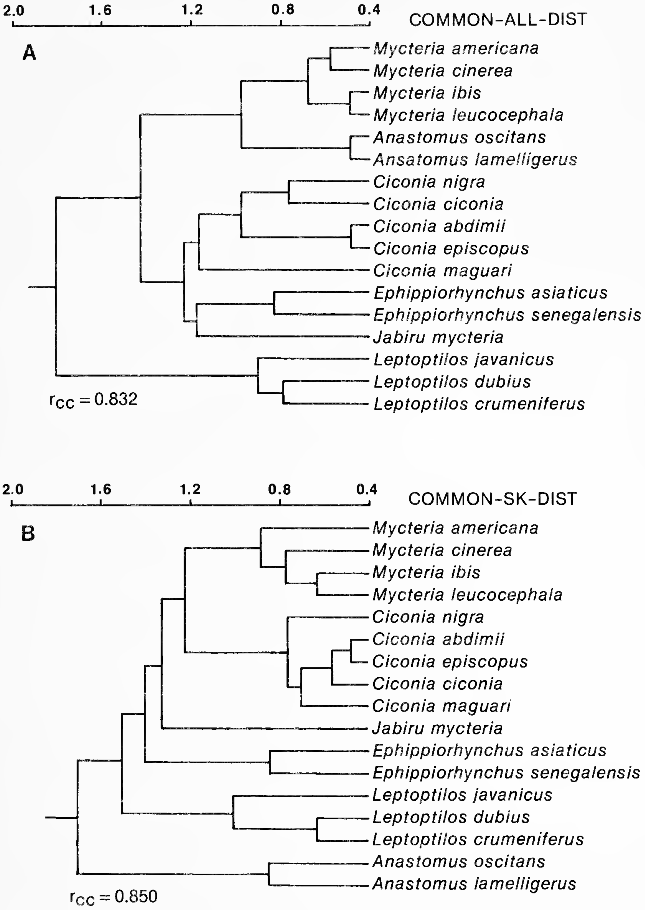


Fig. 8.—Phenograms derived from UPGMA clustering of average taxonomic distances based on the COMMON transformation of the data: (A) all characters; (B) skull characters. Scales of both are in units of average taxonomic distance.

used by the investigators cited above were quite different from those used here.

Both analyses (UPGMA and AHCS) of distances among the taxa using the COMMON transformation produced results that were more stable than the CORR analysis but only the UPGMA (DIST) was significantly higher. The DIST (UPGMA) and AHCS analyses are very similar except that AHCS can also find clusters that are not hyperspheroidal. If the clusters are elongated then AHCS should better detect them and, hence, give more stable results. This is not the case here

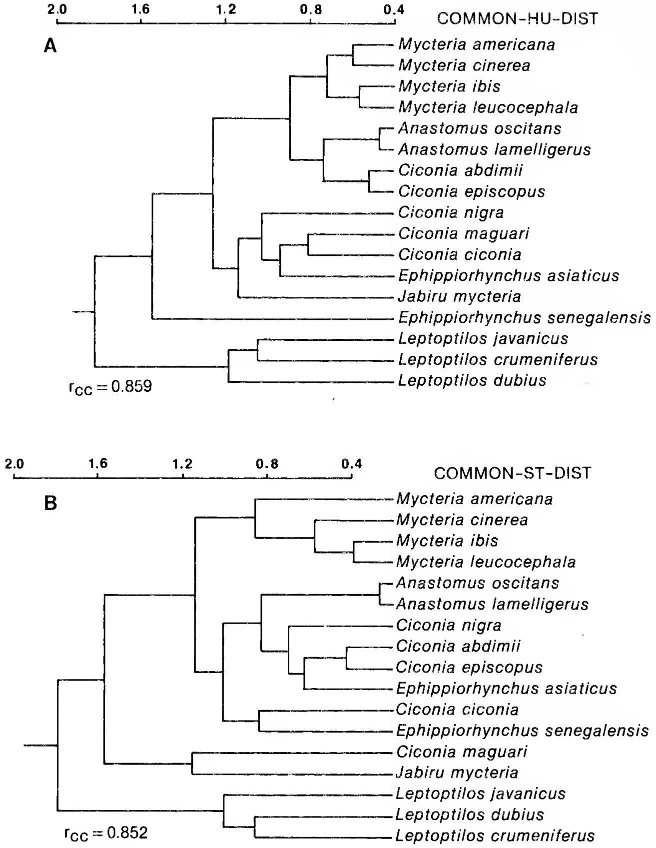


Fig. 9.—Phenograms derived from UPGMA clustering of average taxonomic distances based on the COMMON transformation of the data: (A) characters of the humerus; (B) characters of the sternum. Scales of both are in units of average taxonomic distance.

although the difference in stability (measured by matrix correlation) is not significant. Inspection of the 3-D models (Figs. 11–16; these represent the interspecific distances very closely) reveals little elongation of clusters.

Thus, for the purpose of revealing phenetic structure consistent over different sets of characters, the transformation and analysis COMMON-DIST is most effective. Figs. 8–10 show the phenograms from the six partitions (five bones plus the combined data) for this transformation and analysis. All except COMMON-SY-DIST are relatively good representations of the basic similarity matrices (cophenetic cor-

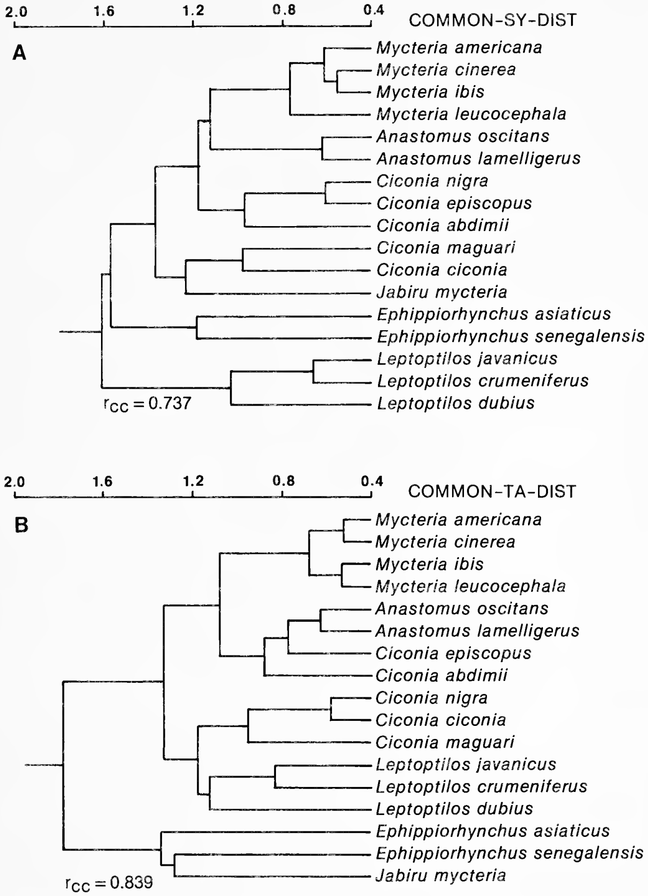


Fig. 10.—Phenograms derived from UPGMA clustering of average taxonomic distances based on the COMMON transformation of the data: (A) synsacrum characters; (B) tarsometatarsus characters. Scales of both are in units of average taxonomic distance.

relations greater than 0.830). The cophenetic correlation for COMMON-SY-DIST is 0.737, indicating distortion in the phenogram. Figs. 11–16 show the 3-D models derived from MDS analyses of the COMMON transformed data sets. These give more accurate representations of the dissimilarities (distances) among the storks than the phenograms but are much more difficult to interpret as hierarchically nested sets of clusters (classifications in the usual sense). The minimum spanning networks superimposed on the models give further information on the close affinities of the storks.

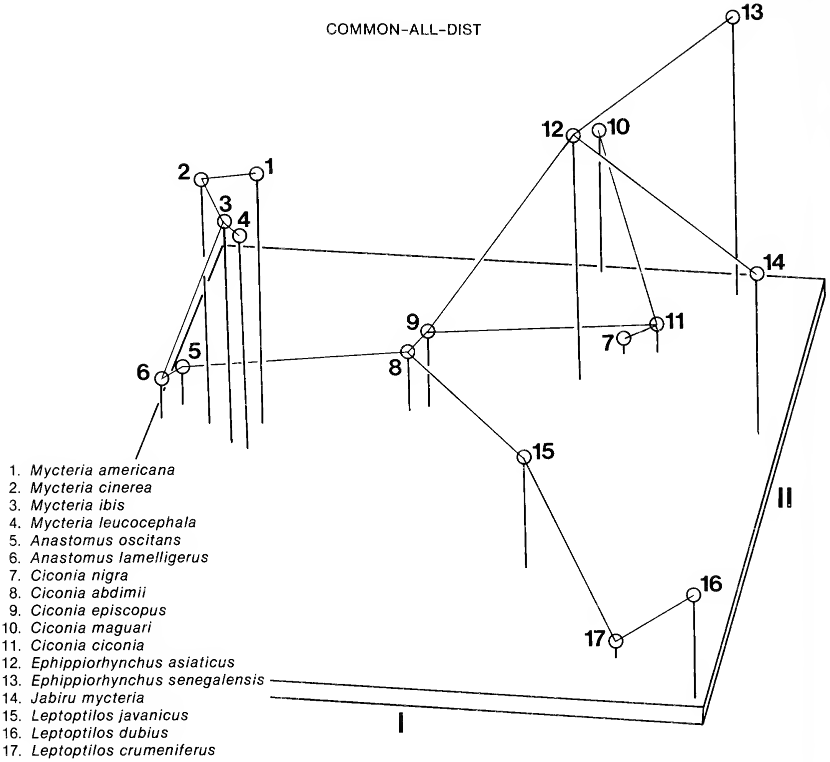


Fig. 11.—Three-dimensional model showing arrangement of storks in phenetic space based on a multidimensional scaling analysis of all characters transformed using the COMMON procedure. A minimum spanning network derived from taxonomic distances calculated from the transformed data is superimposed on the model.

The six phenograms of Figs. 8–10 have many clusters in common (the average matrix correlation between them is 0.531). In particular, some of the genera proposed by Kahl (1972*a*, 1979*b*) appear consistently as clusters. The four species placed by Kahl in the genus *Mycteria* cluster together in all analyses, as do the two species of *Anastomus* and the three of *Leptoptilos*. Within the *Mycteria* association, *M. ibis* and *M. leucocephala* are a mutually close pair in all analyses except COMMON-SY-DIST (Fig. 10A). In the latter, *M. ibis* is the species most similar to *M. leucocephala* but not vice versa (see Fig. 15). *Mycteria americana* and *M. cinerea* form a mutually close pair in three of the analyses (COMMON-ALL-DIST, Fig. 8A; COMMON-HU-DIST, Fig. 9A; and COMMON-TA-DIST, Fig. 10B) but in the remaining three,

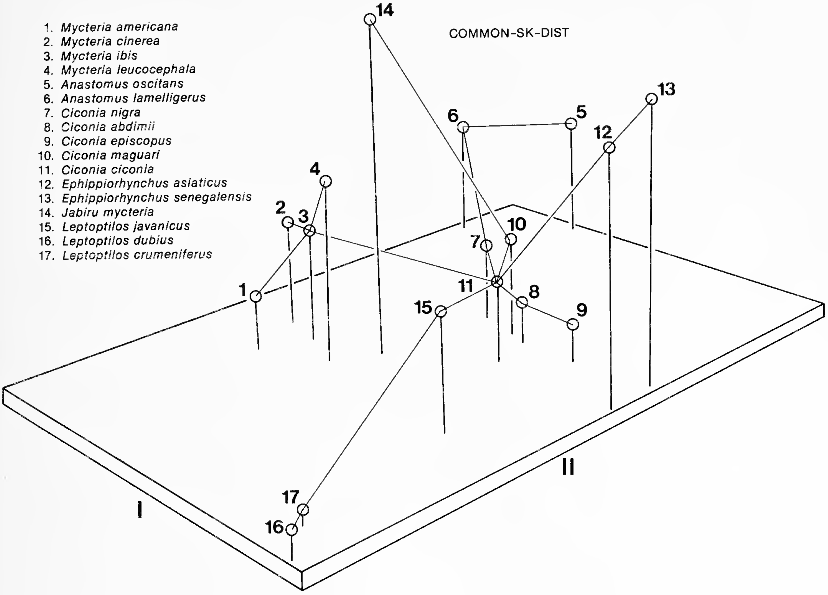


Fig. 12.—Three-dimensional model depicting an arrangement of storks in phenetic space based on a multidimensional scaling analysis of skull characters transformed using the COMMON procedure. A minimum spanning network derived from taxonomic distances calculated from the transformed data is superimposed on the model.

M. americana is represented as the most divergent of the group. This latter arrangement is not new; *M. americana* has traditionally been separated generically from the other wood storks (Fig. 1A).

The two species of *Ephippiorhynchus* cluster less consistently, being a mutually close pair in only three of the phenograms (Figs. 8A, B and 10A). However, *E. senegalensis* is more similar to *E. asiaticus* than to any other species in analyses of both the humerus and sternum (Figs. 13–14). For the tarsometatarsus data, *E. senegalensis* is nearly as similar to *E. asiaticus* as is *Jabiru* (Fig. 16).

The relationships of the species placed by Kahl into the genus *Ciconia* are less consistently portrayed. In only two phenograms (Fig. 8A and 8B) are all five species clustered together to the exclusion of the other storks. However, some close similarities are most consistently found: *C. abdimii* and *C. episcopus* group together in all analyses and in four cases are mutually close pairs; *C. nigra, C. maguari,* and *C. ciconia* are present in the same cluster in four analyses. Table 4 summarizes the nearest neighbors (along the minimum spanning network in the

Table 4.—*Nearest neighbor in phenetic space (average taxonomic distances) for members of the genus* Ciconia *for each data partition; SK = skull, HU = humerus, ST = sternum, SY = synsacrum, TA = tarsometatarsus, ALL = all characters.*

Reference species	*Ciconia*					Other (see text)
	nigra	*abdimii*	*episcopus*	*maguari*	*ciconia*	
Ciconia						
nigra			ST, SY		SK, HU, TA, ALL	
abdimii			SK, HU, ST, SY, TA, ALL			
episcopus	SY	SK, HU, ST, ALL				TA
maguari					SK, HU, ST, SY, TA, ALL	
ciconia	HU, TA, ALL	SK		SY		ST

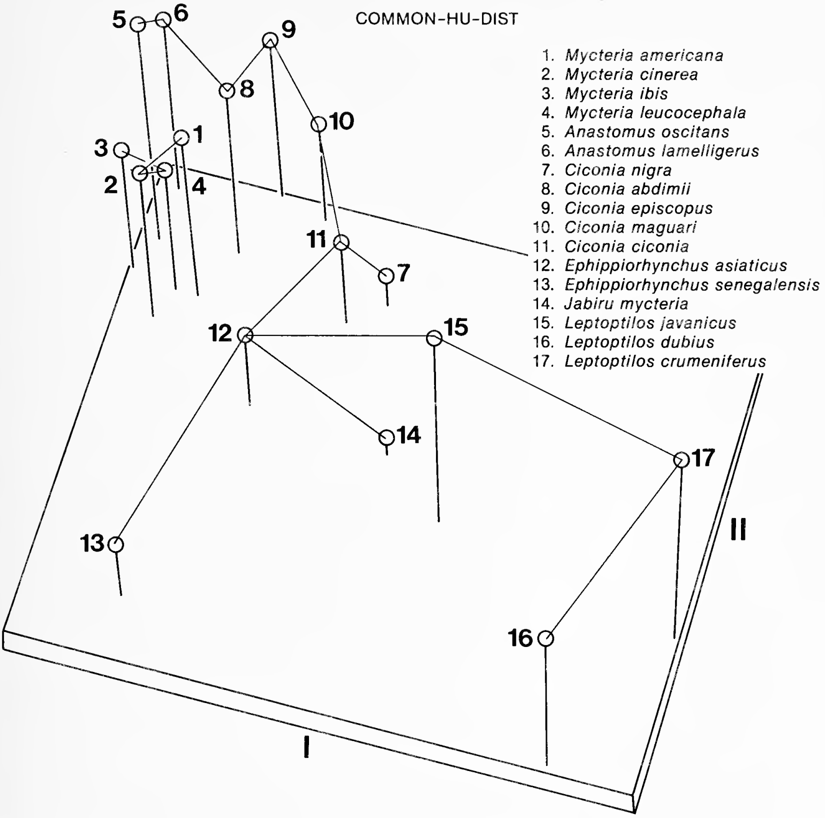


Fig. 13.—Three-dimensional model showing arrangement of storks in phenetic space based on a multidimensional scaling analysis of humerus characters transformed using the COMMON procedure. A minimum spanning network derived from taxonomic distances calculated from the transformed data is superimposed on the model.

multidimensional character space) of each of the *Ciconia* species for each data set. For two species, the results are the same regardless of data set—the most similar species to *C. abdimii* is always *C. episcopus* and the most similar to *C. maguari* is in every case *C. ciconia.* The converse is not true; that is, *C. maguari* is not always the most similar species to *C. ciconia.* In fact, in only one of the six analyses (synsacrum) is this true. However, in all but two of 30 cases the nearest (most similar) species to a member of the genus *Ciconia* is a congener (*C. episcopus* is most similar to *Anastomus oscitans* in the sternal analysis and *C. ciconia* is most similar to *Ephippiorhynchus asiaticus* in the

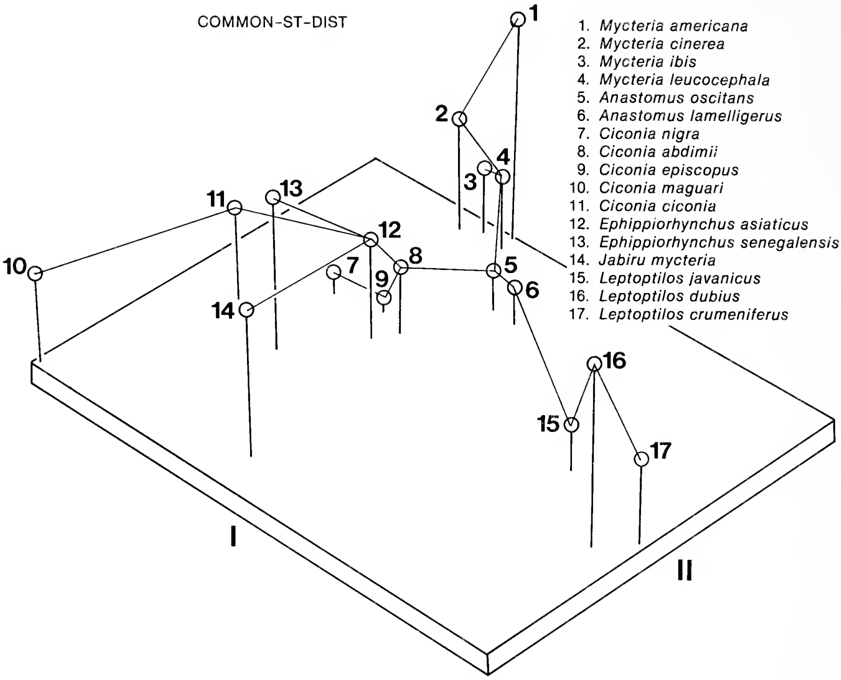


Fig. 14.—Three-dimensional model showing arrangement of storks in phenetic space based on a multidimensional scaling analysis of sternum characters transformed using the COMMON procedure. A minimum spanning network derived from taxonomic distances calculated from the transformed data is superimposed on the model.

analysis of tarsometatarsal data; see Figs. 14 and 16). *C. nigra* is intermediate between the two pairs of species discussed above; *C. ciconia* is most similar to it in four analyses (and vice versa in three of those) and *C. episcopus* is most similar to it in the remaining two (sternal and synsacral data). These results suggest that for summarizing the phenetic relationships among the *Ciconia* species using a phenogram, COMMON-ALL-DIST (Fig. 8A) is the best consensus. *C. maguari* should be shown more similar to *C. ciconia* and *C. nigra* than is depicted. The 3-D model for this analysis (Fig. 11) gives a good graphic summary of the phenetic relationships of the *Ciconia* species.

The relationships of *Jabiru* are less consistent than for other storks. In the phenograms it is associated with *Ephippiorhynchus* in COMMON-ALL-DIST (Fig. 8A) and COMMON-TA-DIST (Fig. 10B), and with *Ciconia ciconia* and/or *C. maguari* in COMMON-HU-DIST (Fig. 9A), COMMON-ST-DIST (Fig. 9B) and COMMON-SY-DIST (Fig.

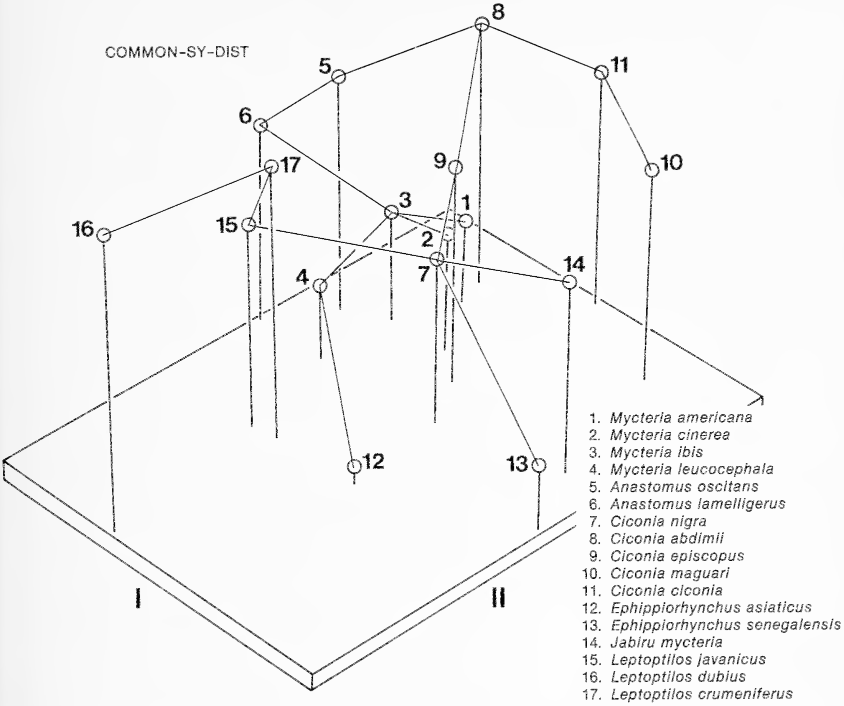


Fig. 15.—Three-dimensional model showing arrangement of storks in phenetic space based on a multidimensional scaling analysis of synsacrum characters transformed using the COMMON procedure. A minimum spanning network derived from taxonomic distances calculated from the transformed data is superimposed on the model.

10A); it is very different from other storks when only the skull is considered (see Figs. 8B, 12). However, in the analyses using data from either the humerus of sternum, the species most similar to *Jabiru* is *Ephippiorhynchus asiaticus* (Figs. 13, 14). *Jabiru* thus shows closest similarities to *Ephippiorhynchus* but is also clearly related to some members of the *Ciconia* group.

The relationships among the groups discussed above (corresponding to the genera of Kahl) also show some consistent features. *Leptoptilos* is divergent from other groups in five of the six analyses, COMMON-TA-DIST (Fig. 10B) being the exception, and in all but COMMON-SK-DIST (Fig. 8B) is the most divergent group. In this latter exception (Fig. 8B), *Anastomus* is the most divergent but because the two storks of this genus have such highly modified bills and associated skull structures adapted to a particular feeding method (Kahl, 1971*b*), it is not

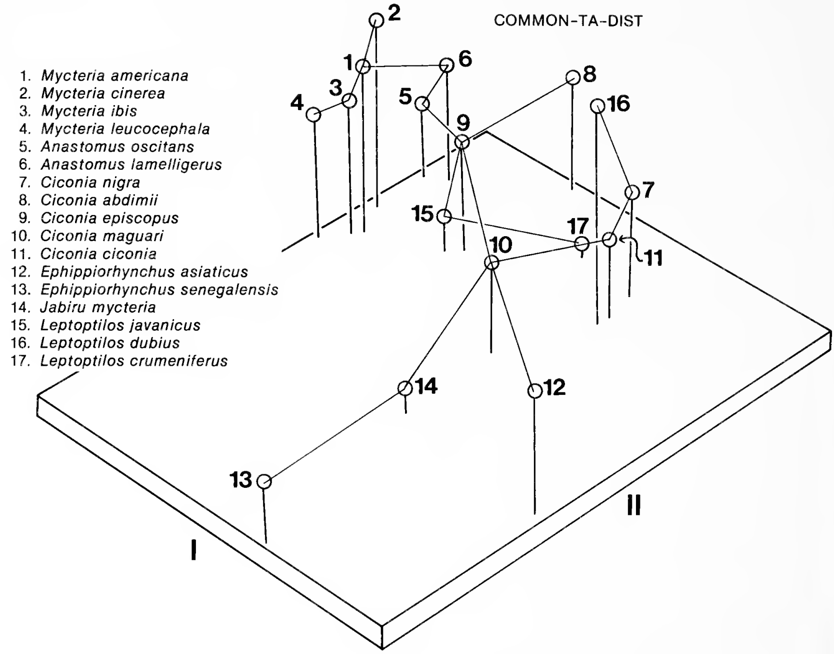


Fig. 16.—Three-dimensional model showing arrangement of storks in phenetic space based on a multidimensional scaling analysis of tarsometatarsus characters transformed using the COMMON procedure. A minimum spanning network derived from taxonomic distances calculated from the transformed data is superimposed on the model.

surprising that an analysis of skull characters shows them to be quite divergent. In four of the other five analyses, *Anastomus* is closely linked with *Mycteria*; in the fifth (COMMON-ST-DIST, Fig. 9B), the association is much less close but, as can be seen from the corresponding 3-D model (Fig. 14), *Mycteria* is more similar to *Anastomus* than to any other genus or group. Members of the *Ephippiorhynchus-Jabiru* group are associated with the *Ciconia* species in three of the phenograms (Figs. 8A, 9) but in every 3-D model this group (or a majority of the group) is linked in the minimum spanning network to *Ciconia* species.

SUMMARY OF PHENETIC RESULTS

A major use of summaries of relationships is to predict the character states of characters outside those used in the study. Phenetic methods are designed explicitly to maximize this predictiveness. They are not designed, as are cladistic methods, to produce estimates of phylogeny.

However, if in the evolution of the characteristics of the group under study there is little homoplasy (convergence, parallelism) and rates of divergence are approximately equal in all lineages, the phenetic and cladistic summaries will be very similar.

I used phenograms and 3-D models as summaries of the phenetic relationships among the storks. A further form of summary is a hierarchic classification of names such as used in the Linnaean system. Phenograms can easily be transformed into such classifications since both are composed of hierarchically nested sets. The 3-D models do not correspond directly to such classifications but often exhibit greater accuracy in portraying the phenetic relationships. Each of the considerable number of phenograms and 3-D models constructed in this study emphasizes a different aspect of the phenetic relationships. Clearly, if the characters whose states are to be predicted all relate to a specific portion of the animal, then a summary emphasizing that part is likely to be most useful. For example, predictions of the similarities in feeding habits and apparatus of the storks would likely be most accurately obtained from a phenogram, 3-D model, or classification emphasizing characteristics of the head region of the skeleton. However, for a general statement, a summary representing the similarity over all characters is most appropriate provided it shows little distortion of the consensus of relationships implied by the different partitions of the data.

Both the technique employed to examine the relationships and the character set used affect the results produced. For the data analyzed in this paper, the COMMON transformation is clearly preferred as is the use of average distance as a similarity measure. UPGMA is appropriate because there is little evidence for elongated clusters among the storks. The phenogram resulting from this analysis on all characters is COMMON-ALL-DIST (Fig. 8A). This appears to represent the consensus of relationships well with the exception that *Ciconia maguari* should be shown more similar to *C. ciconia* and *C. nigra*. A better summary but one that is more difficult to compare with previous classifications (the most common form of summary of relationships) is given by the 3-D model for this analysis (Fig. 11).

My results are very similar to the relationships implied by Kahl's (1979*b*) classification (Fig. 2) except that *Jabiru* is more similar to *Ephippiorhynchus* than would be predicted from Kahl's summary. Also, Kahl's placement of these two genera in the tribe Leptoptilini is not supported by results based on skeletal data; these genera are phenetically similar to the *Ciconia* species. Specific taxonomic recommendations and further discussion of the relationships among the storks is in Wood (1983*b*).

ACKNOWLEDGMENTS

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APPENDIX I

Specimens used in this study. The following abbreviations for museums are used: AMNH, American Museum of Natural History, New York, New York; FM, Field Museum of Natural History, Chicago, Illinois; KU, Museum of Natural History, University of Kansas, Lawrence, Kansas; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley, California; NMNH, National Museum of Natural History, Smithsonian Institution, Washington, D.C.; OU, Stovall Museum of Science and History, University of Oklahoma, Norman, Oklahoma; UMMZ, Museum of Zoology, University of Michigan, Ann Arbor, Michigan; YPM, Peabody Museum, Yale University, New Haven, Connecticut

Mycteria americana—AMNH 605, 9856; KU 30867; NMNH 19532; OU 7720.
Mycteria cinerea—NMNH 345229, 430169.
Mycteria ibis—AMNH 2626; FM 104694; KU 70791; NMNH 431651; UMMZ 215038; YPM 7526.
Mycteria leucocephala—NMNH 432506, 432507; UMMZ 153055, 154507; YPM 406.
Anastomus oscitans—NMNH 488759, 489353, 553234; UMMZ 216572, 216573.
Anastomus lamelligerus—MVZ 133407; NMNH 291418, 291419, 291420.
Ciconia nigra—MCZ 6997; NMNH 19784, 291560; YPM 4350.
Ciconia abdimii—AMNH 4860; NMNH 430455, 430456, 430528; YPM 7588.
Ciconia episcopus—AMNH 3553, 1370, 4952; NMNH 225807, 226001.
Ciconia maguari—NMNH 19940; OU 10611; UMMZ 156986, 156987, 158608.
Ciconia ciconia—AMNH 1723, 1724, 2286; NMNH 343156, 430168; UMMZ 151110.
Ephippiorhynchus asiaticus—AMNH 1729, 2083, 3891; NMNH 19694, 346193.
Ephippiorhynchus senegalensis—AMNH 2433, 2903; FM 104380; UMMZ 211561, 211562.
Jabiru mycteria—NMNH 343465; OU 6794, 10612, 14386; UMMZ 154788.
Leptoptilos javanicus—AMNH 2721, 4392, 5059; NMNH 223897; UMMZ 218204.
Leptoptilos dubius—AMNH 4023; FM 104387; NMNH 225988, 429220; YPM 409.
Leptoptilos crumeniferus—AMNH 1731, 5862; NMNH 488129; OU 14385; UMMZ 210451, 218203.
Balaeniceps rex—AMNH 5935, 8817; NMNH 344963, 345070; UMMZ 215884.
Scopus umbretta—NMNH 18898; UMMZ 154762, 158164, 185419, 158435.

Appendix II

Descriptions of the points, linear measurements and angular characters used in this study. The letters identifying the points correspond to those labeled on Fig. 3. Nomenclature follows Baumel et al. (1979) and Bock and McEvey (1969). The linear measurements are inter-point distances; they are listed as pairs of letters corresponding to the described points. References to these measurements use a combination of the two letter code for the bone and the two letters for the points (for example, SK-CR, TA-JP). The interconnections between any three points form a triangle; angles subtended by the sides of these triangles are used as angular characters. Specific angles are named using the letters of the three points forming the triangle with the point at the vertex of the angle listed second (that is, character AEB is the angle subtended by lines connecting point A with point E and point B with point E). As with the linear measurements, references to the characters include the code for the bone (for example, AX-BCH, HU-KMN). Since all angles for each triangle are used as angular characters, only the triangles are listed.

Ossa cranii, ossa faciei—SK

Points

A. Os palatinum; lamella caudolateralis; caudolateralmost point
B. Os palatinum; crista ventralis; caudoventralmost point
C. Os palatinum; margo ventralis articularis pterygoideum; medialmost point
D. Lamina basisphenoidalis; processus medialis; rostralmost point
E. Os pterygoideum; facies articularis guadratum; medialmost point
F. Os quadratum; condylus medius; rostralmost point
G. Os quadratum; condylus medius; lateralmost point
H. Os quadratum; cotyla quadratojugalis; caudoventralmost point
I. Os quadratum; condylus caudalis; ventralmost point
L. Ala occipitalis; processus exoccipitalis; medioventralmost point
M. Foramen magnum; margo dorsalis; medial point
N. Processus suprameaticus; ventralmost point
O. Processus zygomaticus; rostralmost point
P. Processus postorbitalis; ventralmost point
Q. Processus orbitalis quadrati; medialmost point
R. Os parietalis; margo caudalis articularis supraoccipitalis; medialmost point

Linear measurements

AB AC BC CD CE CH CM CN CR DE DH DI DL DM DN EF
EG EH EN FG FH FI FM GH HI HL HN HO HQ IL IN LM
MR NP NR OP OQ OR PR

Triangles

ABC CDE CDH CDN CMR DLH DLI DLM EFG EGH ENH FHN FHI
HIN HOQ NPR OPR

Axis—AX

Points

A. Processus articularis caudalis; facies articularis; caudolateralmost point
B. Arcus axis; caudomedialmost point
C. Corpus axis; facies articularis caudalis; ventromedialmost point
D. Corpus axis; processus ventralis; ventralmost point
E. Corpus axis; facies articularis atlantica; ventralmost point
F. Processus articularis cranialis; facies articularis; cranialmost point
G. Arcus axis; craniomedialmost point
H. Area ligamentum elastici caudalis; dorsalmost point

Linear measurements

AB AC AD AE AF BC BD BE BG BH CD CE CG CH DE EF EG FG

Triangles

ABC ABD AEF BCE BCG BCH CDE EFG

Humerus—HU

Points

A. Impressio m. pectoralis pars profundus; distalmost point
B. Crista pectoralis; cranialmost point
C. Impressio m. pectoralis pars profundus; proximalmost point
D. Tuberculum dorsale; dorsalmost point
E. Junctura intumescentia, margo ventralis
F. Impressio m. scapulohumeralis caudalis; distalmost point
G. Impressio m. biceps brachii; proximalmost point
H. Tuberculum ventrale; dorsolateralmost point
I. Impressio m. latissimus dorsi caudalis; proximalmost point
J. Impressio m. latissimus dorsi caudalis; distalmost point
K. Condylus dorsalis; cranioventralmost point
L. Impressio m. supinator; proximalmost point
M. Fossa m. brachialis; proximalmost point
N. Fossa m. brachialis; distalmost point
O. Tuberculum supracondylare ventrale
P. Epicondylus ventralis; ventralmost point
Q. Epicondylus dorsalis; caudodistalmost point

Linear measurements

AB AC AD AE BC BD BE BI CE DE DF DH DI DJ EF EH FG FH FI GH IJ KL KM KN KO KP KQ LM LN LQ MN MO NO NP OP OQ

Triangles

ABC ABE ACE ADE BDI BED DEF DEH DIF DIJ FGH KLM KLQ KMN KMO KOP KOQ LMN NOP

Clavicula—FU

Points

A. Synostosis interclaviculare; point sinister to craniodorsalmost point; points A and I are on smae plana paramediana
B. Processus acromialis; caudodorsalmost point; sinister
C. Processus acromialis; caudodorsalmost point; dexter
D. Apophysis furculae; facies articularis apex carinae sterna; dorsalmost point
E. Apophysis furculae; facies articularis apex carinae sterna; ventralmost point
G. Synostosis interclaviculare; craniodorsalmost point
H. Same as point G (in the Ciconiidae)
I. Apophysis furculae; facies articularis apex carinae sterna; lateralmost point
K. Point to give maximum thickness of extremitas sternalis claviculae at point A
L. Apophysis furculae; facies articularis apex carinae sterna; midpoint

Linear measurements

AB AC AD AE AG AH AI AK AL BC DE GH GL IK IL

Triangles

ABC ADE AGH AGL AIK AIL

Coracoideum—CO

Points

A. Angulus medialis; medialmost point
B. Facies articularis sternalis; lateralmost point
C. Processus lateralis; dorsolateralmost point
D. Facies articularis sternalis; crista ventralis; craniolateralmost point
E. Facies articularis sternalis; crista dorsalis; caudalmost point
F. Junctura facies articularis humeralis, cotyla scapularis; ventralmost point
H. Facies articularis humeralis; dorsalmost point
I. Impressio ligamentum acrocoracohumeralis; dorsolateralmost point
J. Processus procoracoideus; dorsalmost point
K. Facies articularis clavicularis; caudalmost point
L. Processus acrocoracoideus; tuberculum brachialis

Linear measurements

AB AC AD AJ BC BD BJ FH FI FJ HI HJ HL JK JL KL

Triangles

ABC ABD ABJ FHI FHJ JHL JLK

Sternum—ST

Points

A. Spina externa; cranialmost point
B. Spina interna sinister; dorsalmost point
C. Processus craniolateralis; craniolateralmost point
D. Tuberculum labri ventralis (junctura labrum ventralis, lineae intermusculare); sinister
E. Apex carinae; facies articularis; ventralmost point
F. Margo caudalis; median point
G. Trabecula lateralis sinister; caudolateralmost point
H. Process costalis 2 sinister; facies articularis; midpoint
I. Facies articularis coracoideus dexter; medialmost point

Linear measurements

AB AC AD AE BC BD BE BH BI CD CE CF CH DE DF DG
DH DI EF EH FG

Triangles

ABD ABE ACD BCD BDE BDI BEH CDH DCF DFG ECF

Synsacrum, os coxae—SY

Points (all sinister or median)

A. Fovea costalis for caudalmost costa vertebralis
B. Fossa acetabuli; margo cranialis; cranialmost point
C. Antitrochanter; caudalmost point
D. Processus lateralis crista iliaca; lateralmost point
E. Foramen obturatum; margo caudalis; caudodorsalmost point
F. Processus terminalis ischii; caudalmost point
G. Foramen ilioischiadicum; caudalmost point
H. Ala preacetabularis ilii; lateralmost point
I. Extremitas caudalis synsacri; middorsal point
J. Processus dorsolateralis ilii; caudalmost point
K. Extremitas cranialis synsacri; ventromedialmost point

Linear measurements

AC AF AH AK BC BD BE CD CE CF CG CI CJ CK DE EF EG EJ FI HK IK

Triangles

ACF AHK BCE BDE CDE CEF CEG CEJ CFI CIK

Tibiotarsus—TI

Points

A. Pons supratendineus; margo proximalis
B. Pons supratendineus; margo distalis
C. Impressio lateralis ligamentum transversum; distalmost point
D. Tuberculum intercondylare; cranialmost point
E. Epicondylus medialis; medialmost point
F. Sulcus cartilaginis tibialis; proximomedialmost point
G. Impressio m. gastrocnemius medialis; distalmost point
H. Crista cnemialis cranialis; proximalmost point
I. Crista cnemialis lateralis; lateralmost point
J. Foramen interosseum distale; proximalmost point
K. Foramen interosseum proximale; distalmost point
L. Area interarticularis; proximalmost point

Linear measurements

AB AD BC BD BE BF CD EF EL GH GI GJ GK HI HJ HL IK IL JK JL

Triangles

ABD BCD BEF GHI GIK GJK HLI HLJ

Tarsometatarsus—TA

Points

A. Crista medialis hypotarsi; margo plantaris; proximalmost point
B. Crista lateralis hypotarsi; margo plantaris; proximalmost point
C. Sulcus hypotarsi; facies plantaris; proximomedialmost point
D. Eminentia intercondylaris; proximalmost point
E. Cotyla medialis; margo lateralis; plantolateralmost point
F. Cotyla medialis; margo dorsalis; dorsalmost point
G. Sulcus extensorius; midpoint between margo distalis impressiones retinaculi extensorii
H. Trochlea metatarsi III; facies plantaris; proximalmost point
I. Foramen vasculare distale; facies plantaris; margo distale
J. Trochlea metatarsi IV; margo lateralis; proximalmost point
K. Trochlea metatarsi II; margo medialis; proximalmost point
L. Trochlea metatarsi IV; margo medialis; proximalmost point
M. Trochlea metatarsi II; margo lateralis; proximalmost point
N. Trochlea metatarsi III; condylus lateralis; distalmost point
P. Fossa metatarsi I; margo proximalis; proximalmost point

Linear measurements

AB AC AE BC BE CD CE CF DF DG DN FG HI HJ HK HP IK IM IP JK JL JN JP KM KN LM LN LP MN

Triangles

ABC ABE ACE CDF DFH HIK HIP HJK HJP IMK JKN JLP LMN

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SYSTEMATICS OF *LIOPHIS REGINAE* AND *L. WILLIAMSI* (SERPENTES, COLUBRIDAE), WITH A DESCRIPTION OF A NEW SPECIES

James R. Dixon[1]

Abstract

The currently recognized species *Liophis zweifeli* is reduced to a subspecies of *L. reginae* and *L. oligolepis* is shown to be a junior synonym of *L. reginae semilineata.* Geographic variation in *L. reginae* is discussed in relation to major physiographic zones and the relationship of *L. reginae* to *L. epinephelus* is briefly discussed. *Liophis williamsi* is redefined, but its relationship to *L. reginae* is unclear. *Liophis andinus,* sp. nov., is described from the Cochabamba area, Bolivia.

Introduction

The species discussed herein have cis-Andean South American distributions. *Liophis williamsi* and a new species described herein occur in widely separated, middle elevation Andean locations. Whereas *L. reginae* also occurs at middle elevations, it is a species primarily of lowlands, from Colombia to Argentina. *Liophis reginae* has the widest distribution of any South American *Liophis.*

Liophis reginae has seven names associated with it that are principally based on variant color patterns. The descriptions of *violaceus* (Lacepede, 1789), *graphicus* (Shaw, 1802), *semilineata* (Wagler, 1824), *reginae macrostoma* (Amaral, 1935), *reginae maculicauda* (Hoge, 1954), and *zweifeli* (Roze, 1959) are based on color morphs, whereas *reginae*

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(Linnaeus, 1758) and *oligolepis* (Boulenger, 1905) are based on both quantitative and color pattern characters. *Liophis williamsi* has a single color pattern morph that is repeated in one population of *L. epinephelus* from Peru. *Liophis andinus* exhibits color pattern variation similar to that of *L. reginae.*

Liophis reginae is closely related to *L. epinephelus.* The latter species is discussed elsewhere (Dixon, 1983), but for the purpose of comparison with *reginae,* the following points obtain: the two species are similar in most characters in some parts of their ranges (Fig. 1A, B, C, and Table 1), but they are primarily allopatric, *epinephelus* being, in general, trans-Andean and *reginae* cis-Andean. The two species are parapatric along the eastern slope of the Ecuadoran Andes, principally in the upper Rio Pastaza and the upper Rio Santiago basins at about 1800 m. Where they are parapatric, their color patterns are not identical. *Liophis reginae* has a posterior lateral black stripe that occurs as a narrow border between scale rows three and four, whereas in *L. epinephelus* the stripe covers most of the third, from one-third to all of the fourth, and occasionally part of the fifth scale row.

SYSTEMATIC ACCOUNT

Liophis reginae (Linnaeus)

Distribution.—Liophis reginae is restricted to cis-Andean South America, where it occurs in every country except Chile and Uruguay. Its distribution extends from southern Brazil and northern Argentina to Trinidad and Venezuela (Fig. 2).

Lectotype.—The original description of *Coluber reginae* by Linnaeus (1758) gave the number of ventrals as 137 and subcaudals as 70. According to Andersson (1899), the Drottingholmense Museum (Museum Regis Adolphi Friderici I) has a jar labeled *C. reginae* that contains two young specimens of *L. reginae* (ventrals 137, 141; subcaudals 76, 81, respectively) and one young specimen of *Liophis lineatus.* Andersson (1899) thought that the latter specimen had been put among the young *L. reginae* by mistake because at first glance they appear similar. Andersson suggested that these were the specimens upon which Linnaeus based his description and by inference, the specimen with 137 ventrals should be the lectotype. Based upon the number of ventrals and subcaudals given by Andersson, there are two possible geographical areas from which the specimens may have come: the central coast zone of Brazil or the Suriname/Guyana area. The latter region is more likely because many of Linnaeus' South American specimens came from Suriname through the various directors of the East India Company (Holm, 1957). I accept Andersson's (1899) lectotype designation, and suggest the restriction of the type-locality to "Suriname."

Table 1.—*Variation in* Liophis reginae *and* L. epinephelus *for ventrals, caudals, and tail/total length ratios. Am. = middle and western Amazon, exclusive of Perú; Para = eastern Amazon; Mt. = Mato Grosso; NE = northeastern states; RJ = Rio de Janeiro region; SP = São Paulo region; Par/Argen. = Paraguay/Argentina sample. N = number in sample; M = mean; SE = standard error.*

Taxa and geographic origin	Ventrals				Subcaudals				Tail/total length ratio (%) (Adults only)			
	N	Range	M	SE	N	Range	M	SE	N	Range	M	SE
L. reginae												
Suriname	27	131–145	137.9	0.7	21	63–78	72.9	0.8	12	27.1–30.5	28.3	0.3
Guyana	22	129–147	138.7	0.8	13	68–80	75.1	1.1	9	25.5–30.5	27.7	0.6
Trinidad	12	137–146	142.6	0.7	7	77–83	80.0	0.8	5	24.4–30.0	28.4	1.0
Venezuela	31	132–148	142.3	0.6	23	69–88	79.9	1.2	21	24.1–31.0	28.1	0.3
Colombia	8	137–147	144.3	1.2	5	65–76	68.2	2.0	4	23.3–27.4	24.9	0.9
Ecuador	79	133–150	141.1	0.4	48	56–77	68.7	0.5	47	2.17–28.8	26.2	0.2
Peru	227	137–161	145.5	0.2	174	55–78	65.2	0.3	103	20.2–28.3	24.3	0.2
Am. Brazil	26	138–155	146.5	1.1	16	60–80	65.1	1.4	5	21.2–29.7	25.3	1.5
Para, Brazil	34	138–155	145.9	0.6	25	62–76	68.3	0.9	17	23.2–26.8	25.0	0.3
Bolivia	45	138–155	146.9	0.6	34	57–79	70.4	0.9	19	20.6–28.0	25.0	0.4
Mt. Brazil	29	145–160	149.8	0.8	21	70–85	74.3	1.6	12	21.3–29.7	25.3	0.6
NE Brazil	16	143–153	148.0	0.9	11	67–81	74.3	1.5	0	— — —	—	—
RJ Brazil	11	136–150	143.4	1.5	11	63–81	68.5	2.1	7	23.2–28.7	26.2	0.7
SP. Brazil	19	150–158	152.8	0.5	13	75–89	82.2	1.4	8	27.3–30.7	28.1	0.4
Par/Argen	10	150–159	152.4	0.8	9	77–91	80.9	1.4	7	23.3–28.7	26.7	0.6
L. e. juvenalis	51	139–152	145.0	0.4	45	51–62	56.0	0.4	25	18.9–25.2	21.5	0.2
L. e. pseudocobella	50	135–158	146.6	0.6	46	45–57	51.2	0.4	14	17.1–20.9	19.2	0.3
L. e. epinephelus	103	128–152	138.4	0.4	100	49–72	61.4	0.4	74	19.0–26.0	23.1	0.2
L. e. albiventris	93	141–165	150.7	0.5	83	52–70	60.3	0.5	63	19.1–24.2	22.0	0.2
L. e. fraseri	43	143–164	153.8	1.3	43	51–75	66.6	0.8	17	18.5–26.6	23.7	0.6
L. e. lamonae	48	141–157	149.7	0.7	41	51–67	59.2	0.7	22	20.2–24.1	22.2	0.2
L. e. opisthotaenia	32	142–152	147.0	0.5	29	53–78	64.7	0.9	17	20.2–25.6	23.6	0.3
L. e. bimaculatus	41	162–191	174.9	1.0	34	44–80	63.2	1.0	17	18.9–24.0	21.3	0.3

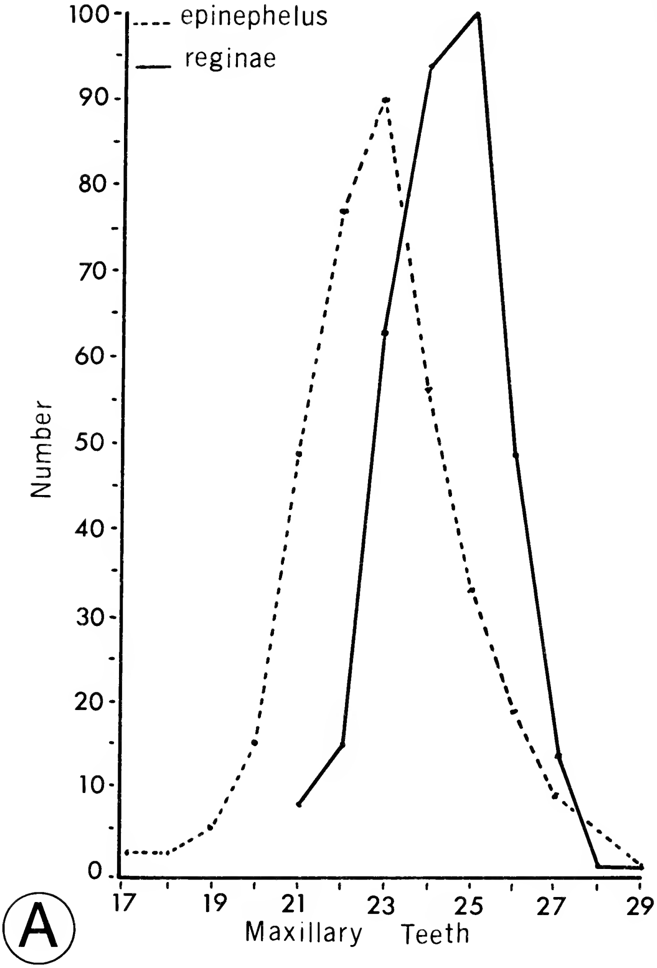

Fig. 1.—Comparison of *Liophis reginae* and *L. epinephalus* in: A) numbers of maxillary teeth.

Variation in color pattern.—The color pattern of 80% of the specimens examined of *L. reginae* consists of an olive to grayish green dorsum, with faint to well-marked dorsolateral diagonal black streaks or spots on the anterior one-third of the body. A thin black lateral line begins on the border of scale rows three and four on the posterior one-fourth of the body and continues to the tip of the tail. Occasionally, this line may be present only above the vent or slightly in front of it

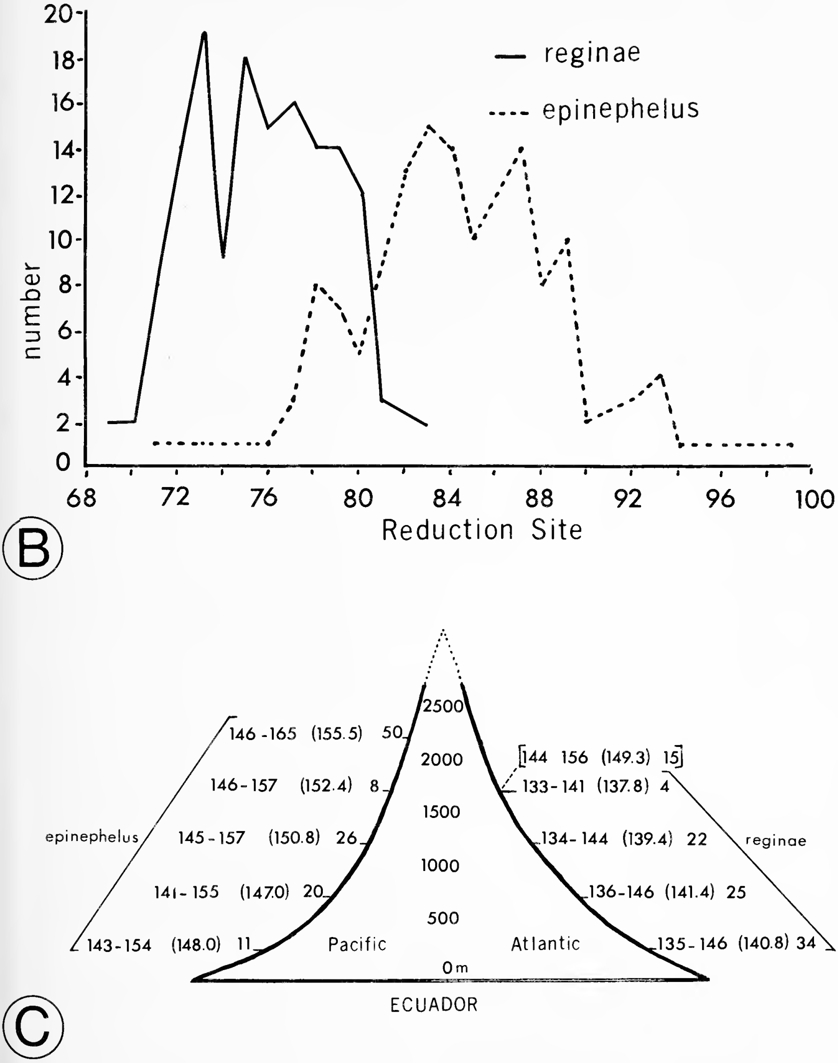

Fig. 1 (cont.)—Comparison of *Liophis reginae* and *L. epinephalus* in: B) comparison of the site of the reduction from 17 scale rows to 15; C) range and mean numbers (in parentheses, followed by sample size) of ventrals at various elevations along the Pacific and Atlantic versants of the Ecuadorean Andes (single set of numbers, in brackets on the right in 1C, represent the only population of *L. epinephelus* that appears to be parapatric with *L. reginae*).

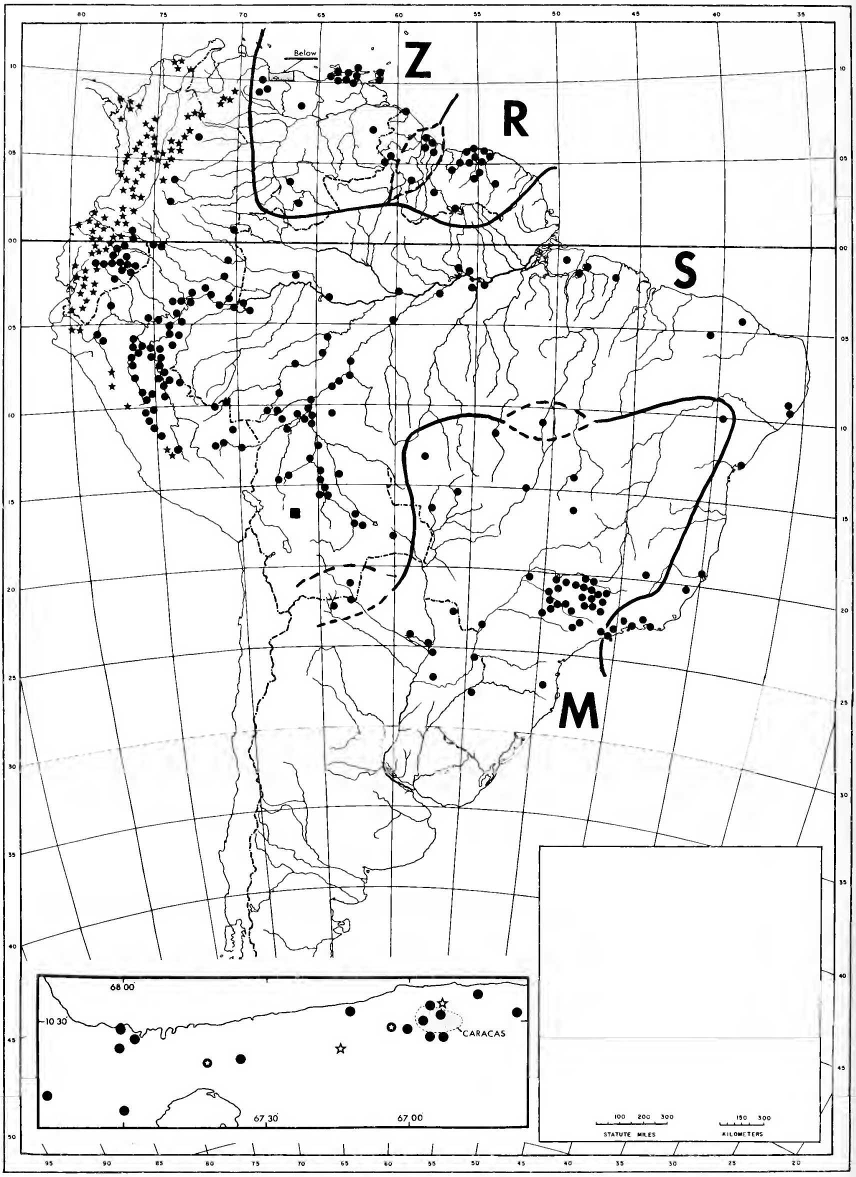

Fig. 2.—The distribution of *Liophis reginae, L. epinephelus, L. williamsi,* and *L. andinus* in South America. Circular dots represent the distribution of *L. reginae,* black stars represent *epinephelus,* and the square represents *L. andinus.* The insert shows the distribution of *L. williamsi* (open star) and sympatric localities of *williamsi* and *reginae*

thence continuing to the tip of the tail. The venter is checkered yellow and black in 95% of individuals and the subcaudal area is white. The ventral surface of some females in some populations is immaculate white (rare in males).

A sample of 100 individuals of *L. reginae* from Iquitos, Perú, contains at least three discrete patterns. One pattern is distinctly "salt and pepper" with each scale reddish anteriorly, greenish medially, and black posteriorly. Another pattern has the first and second scale rows pale green or yellowish green. The anterior part of the body is bright red and the posterior part dull green, with a black lateral stripe on the borders of the third and fourth scale rows continuing to the tip of the tail. The third pattern is the one previously described for about 80% of individuals. A combined form, with elements of all three patterns, can occasionally be found in a single individual.

The Peruvian sample seems to have the highest number (18%) of individuals with immaculate venters. Three hundred and two of 395 individuals have 17-17-15 scale rows and checkered venters. Sixty-nine males from Perú with 17-17-15 scale rows have checkered venters—none were immaculate white. The holotype of *L. oligolepis* Boulenger (Fig. 3D) is the only available male with the combination of 15-15-15 scale rows and a white venter. Of 107 Peruvian females with 17-17-15 scale rows, four have white venters and 103 are checkered; of 53 Peruvian females with 15-15-15 scale rows, 35 have white venters and 15 are checkered. These data suggest that scale row reductions and ventral color in Peruvian *reginae* is sex-linked in females, and only rarely so in males.

The subcaudal area is usually white, yellow, or salmon. However, specimens from the population in central Brazil and northwestern Argentina tend to have a few black spots on the outer edges of the subcaudals. In preservative, these spots appear as black smudges.

Geographic association of patterns seems to be discordant on the north and west sides of the Amazon Basin. The "salt and pepper" pattern is common in the coastal Andes of Venezuela (Fig. 3C), part of the Tepui region of the Guiana Shield, Trinidad, and extreme northern Guyana. However, this same pattern is present in the eastern middle slopes of the Andes of central Perú and continues southward into Bolivia. The pattern also shows up as an occasional variant in the mid-Amazon Basin, Iquitos area of Perú, and extreme western Venezuela.

(circle/white star) and localities of *reginae* (black circles). The heavy black lines denote the approximate boundaries of the subspecies of *L. reginae* (Z = *zweifeli*; R = *reginae*; S = *semilineata*; M = *macrostoma*). Dashed lines around circular dots represents zones of intergradation.

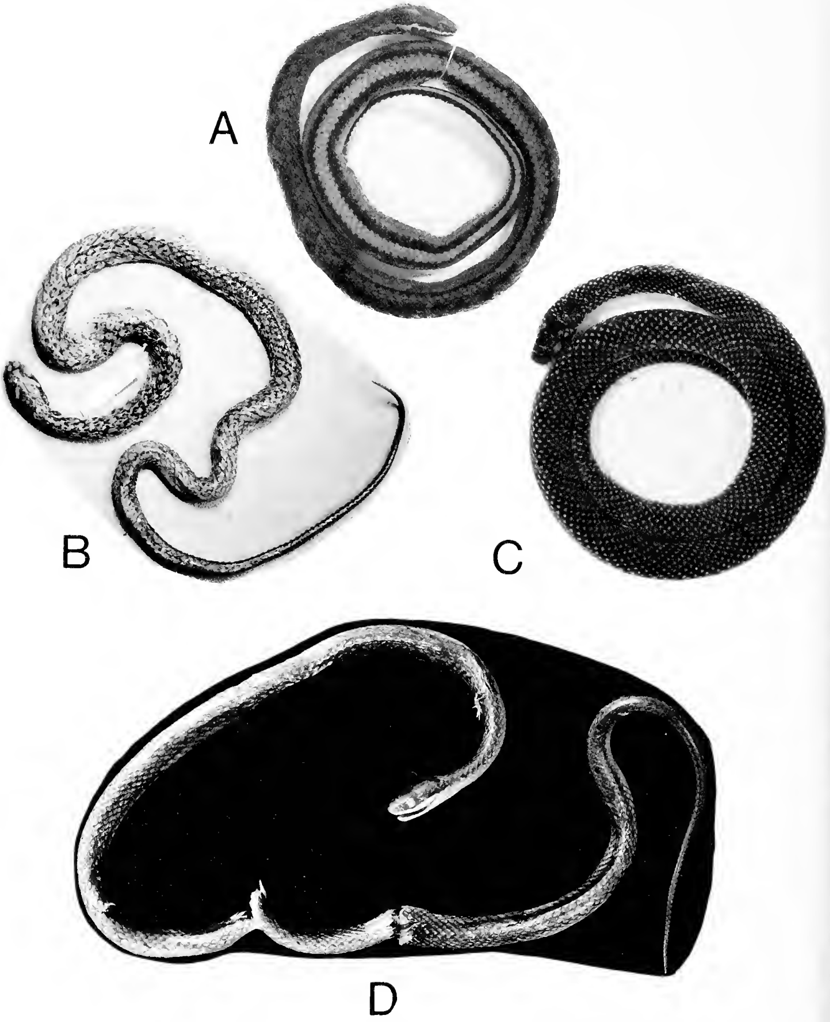

Fig. 3.—A) paratype of *Liophis williamsi* (MBUCV 3044), Rancho Grande, Venezuela. B) Holotype of *Liophis graphicus* (BMNH 1946.1.5.73), "America," represents *L. reginae reginae.* C) Holotype of *Liophis zweifeli* (MBUCV 95), Rancho Grande, Venezuela, represents *L. reginae zweifeli.* D) Holotype of *Liophis oligolepis* (BMNH 1946.1.4.66), Igape-Assu, Brazil, represents *L. reginae semilineata.*

The light-side, brightly colored pattern (Fig. 3B) is frequently seen in the lowlands of central and southeastern Perú, but more commonly in the Guianas (southern Guyana, Suriname, and French Guiana). The latter pattern is supplemented with dorsolateral light flecking and/or dark spotting in Suriname and southern part of Guyana.

The typical pattern of an olive green dorsum with faint dorsolateral black streaks anteriorly and a thin, black lateral line posteriorly is prevalent throughout Amazonian South America in lowland situations, including the Amazon tributaries that extend into central portions of Brazil. The same pattern, but with a paler hue, is present in the Paraná drainage of Paraguay. Specimens from the Brazilian states of São Paulo and Paraná tend to have denser dorsolateral spotting anteriorly, brighter colors, and the subcaudals more often smudged with black.

A single female specimen of *L. reginae* from Tobago (USNM 228069) has an atypical color pattern. It resembles the pattern of *L. epinephelus lamonae* (*sensu stricto,* Dixon, 1983) from the middle elevations of eastern Colombia. The dorsal pattern (at 100th ventral) consists of the first and second scale rows olive green; third scale row olive green with a large black smudge in the middle of the scale; fourth scale row tan (cream in life?) with the lower edge black; fifth scale row tan with the upper one-third with greenish black flecks; sixth to tenth scale rows olive green. The ventrals and subcaudals are immaculate cream. The absence of black marks on the ventrals that are typical of most *L. reginae,* may be sex-linked as indicated for females with immaculate ventrals from the Amazon Basin (this paper). The dorsolateral tan stripe is the most striking difference between the patterns of the specimens from Tobago and *L. reginae* from Trinidad (the latter lack this stripe).

Other characters of the Tobago specimen follow: 27 maxillary teeth, 17-17-15 scale rows, 143 ventrals, 77 subcaudals, 8-8 subcaudals, 8-8 supralabials, 9-10 infralabials, 4+5 supralabials entering orbit, 1+2 temporals, 1-1 preoculars, 2-2 postoculars, divided anal plate, 482 mm in total length, 120 mm tail length; 0.270 tail/total length ratio. All of the latter characters are typical for most samples of mainland and Trinidadian *L. reginae* (see Tables 1 and 2). Hardy (1982) has commented on this specimen and presented a photograph.

Scutellation variation.—The number of head scales varies little between and among samples of *L. reginae* from throughout its geographic range. The distribution of the numbers of head scales (Table 2) of *L. reginae* is typical for most species of *Liophis.*

A comparison of the usually sexually dimorphic characters (ventrals and caudals) between males and females of *L. reginae* from Amazonian Perú (sample of 67 ♂♂ and 174 ♀♀) reveals no significant differences in mean numbers. Therefore, sexes were combined for analyses of these characters in sample by sample comparisons. An examination of the average number of ventrals throughout the cis-Andean distribution of *L. reginae* (Fig. 4) shows that the Amazonian population (samples 7–

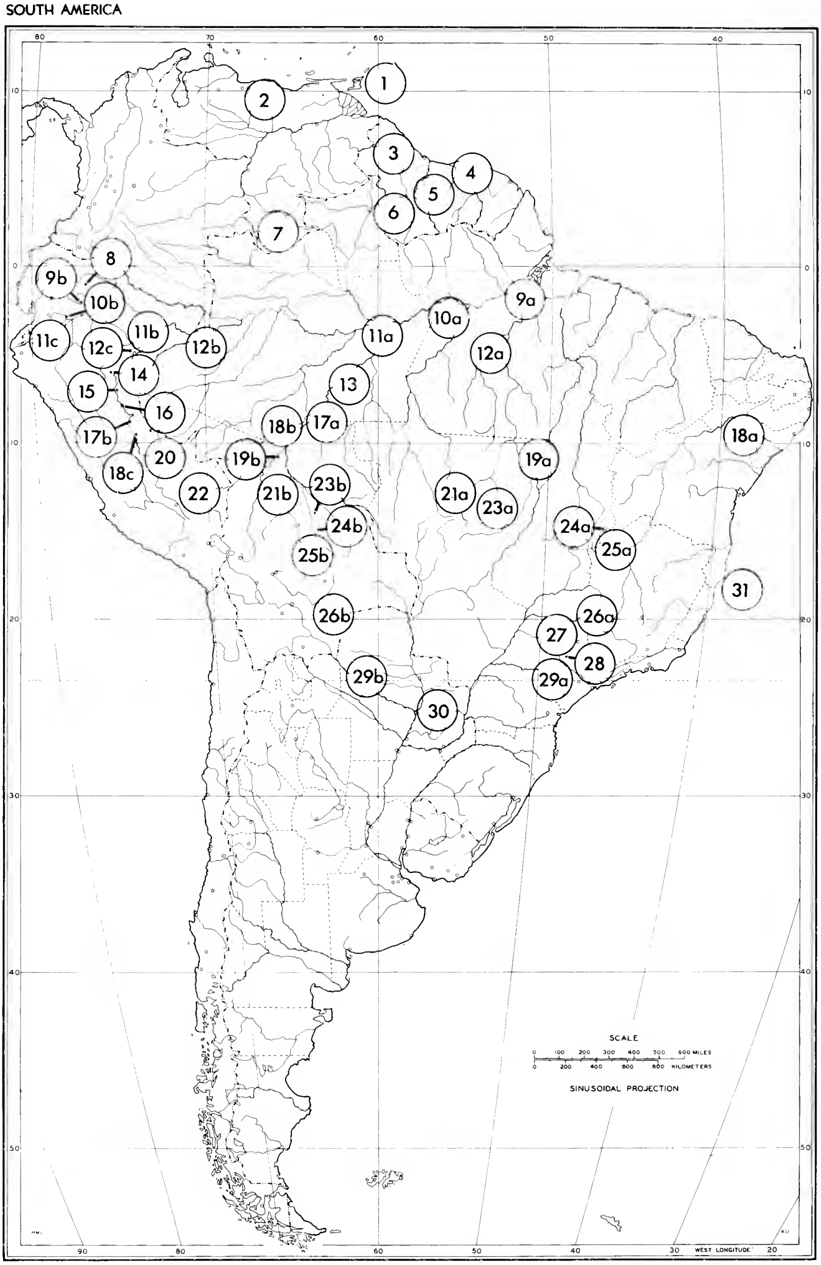

Fig. 4.—A) Geographic locations of samples of *L. reginae,* arranged by latitude from North to South, and by longitude from East to West.

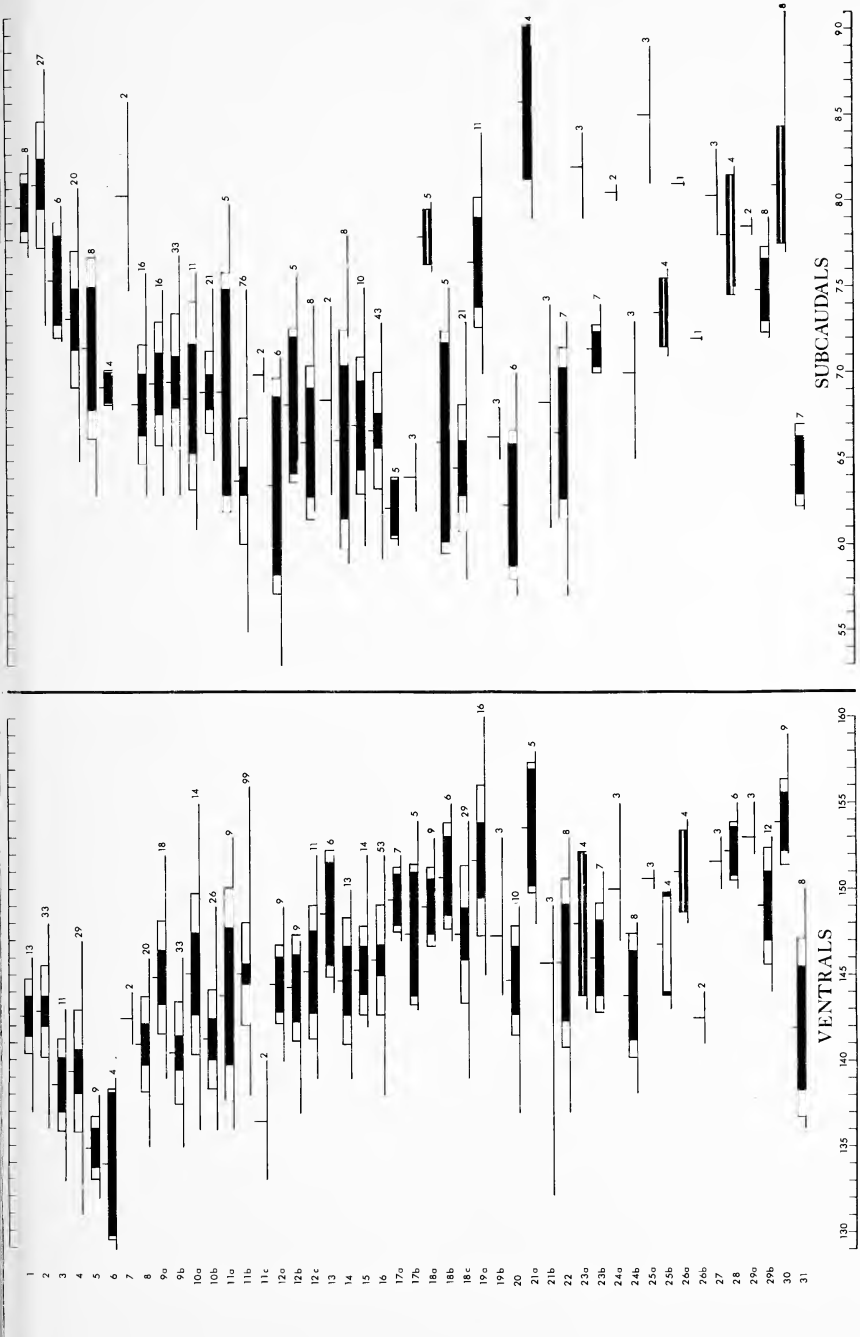

Fig. 4.—B) Univariate analysis of ventrals and subcaudals arranged in order of the samples Fig. 4A. Horizontal line represents the range of variation, vertical line the mean, black rectangle two standard errors on either side of the mean, open rectangle one standard deviation on either side of the mean.

Table 2.—*Variation in numbers of head scales in* Liophis reginae. *Numbers in parentheses = sample size.*

Preoculars	1-1 (477)	1-2 (5)	2-2 (3)						
Postoculars	1-1 (2)	1-2 (1)	2-2 (482)	2-3 (1)					
Supralabials	6-7 (1)	7-7 (1)	7-8 (4)	7-9 (1)	8-8 (468)	8-9 (6)	9-9 (5)		
Infralabials	8-8 (5)	8-9 (5)	8-10 (2)	8-11 (1)	9-9 (12)	9-10 (32)	10-10 (426)	10-11 (5)	11-11 (3)
Supralabials Enter orbit	$\frac{3+4+5}{4+5}$ (2)	$\frac{3+4}{4+5}$ (4)	4+5 (465)	4+5+6 (3)	$\frac{4+5+6}{5+6}$ (1)	$\frac{4+5}{5+6}$ (7)	$\frac{4+5}{4+5+6}$ (2)		
Temporals	1+1 (5)	$\frac{1+1}{1+2}$ (18)	1+2 (462)	2+2 (1)					

19) is intermediate, with ventral numbers increasing to the south and decreasing to the northeast (samples 3–6). The greatest difference between adjacent samples is between Suriname and eastern Amazonia. I have not examined, however, specimens from the area between Belém, Brazil (sample 9a), and French Guiana (sample 4). There may be a cline in ventral number between these two regions, or perhaps partial gene flow around the Guiana Shield. There do not appear to be well-defined steps in the ventral counts of the cis-Andean populations, except the Venezuelan-Trinidad versus the Guyana-Surinam samples, and the coastal Brazil sample (sample 31), and its adjacent, but allpatric samples (samples 24a, 26a, 27, 28, 29a) from inland southeast Brazil. The latter discordance is observed in several other species of snakes with similar distributions (*Typhlops brongersmianus, Chironius fuscus, Liophis miliaris, Liophis poecilogyrus*). Geological and other historical evidence suggests that the vegetation and climate of that particular coastal zone of Brazil was probably connected to the Amazonian Forest within the past few thousand years, and gene flow between populations of both areas was relatively recent or perhaps continuous to the present time (Dixon, 1979).

The number of subcaudals also shows both concordant and discordant variation patterns (Fig. 4). *Liophis reginae* samples from northern Venezuela, Trinidad, and eastern Venezuela (samples 1, 2, 7) have high numbers of subcaudals. Adjacent Guyana, Suriname, and Colombia snakes (samples 3, 4, 5, 6, 12b) have low numbers of subcaudals, as do those from the Atlantic coastal zone of Brazil and most of western cis-Andean South America. Paraguay and eastern Brazil (exclusive of Atlantic Coast) samples have high numbers of subcaudals. Samples of *L. reginae* from south of the Amazon Basin suggest that there is little gene flow as expressed in subcaudal numbers, between the caatinga/cerrado populations of Brazil and the southern Perú/eastern Bolivia populations along any given latitude between 10° to 20°S. Samples from near Isla Bananal, Brazil (19a) and northern Argentina (29b) tend to be intermediate between western South American samples (18b, 18c, 19b, 20, 21b, 22, 23b, 24b, 26b) and eastern South American samples (18a, 21a, 23a, 24a, 25a, 26a, 27, 28, 29a, 30). The difference observed may be an artifact of combined samples along the various latitudes or they may reflect true differences between allopatric samples. In either case, the result appears as a "rassenkreis" (Fig. 4) because adequate samples are not available from Pantanal region of western Brazil, eastern Bolivia, and northern Paraguay. The tail length/total length ratios follow the same pattern as the subcaudals, but the numbers of maxillary teeth are totally discordant.

Two hundred twenty seven *L. reginae* from the Peruvian Amazon show a relatively smooth, north to south, cline in most characters examined. The number of ventrals, subcaudals, and tail length/total length ratios increase (11b, 12c, 14, 15, 16, 17b, 18c, 22), whereas the number of maxillary teeth decreases. A comparison of large samples (Ecuador versus Perú) suggests that some characters of the populations between these two countries are significantly different. However, when subsets of the adjacent samples (northern Perú, southern Ecuador) are compared, there is a relatively smooth cline between the samples. This merely suggests that some of the significant differences between samples are the result of clustering of subsets of samples by country, and not by geographic zones. The entire Amazon sample shows little variation from east to west along the same latitude and vegetation zone (9a, 10a, 11a, 11b, 12a, 12b, 12c). However, considerable north to south variation is noted along different latitudes.

Allocation of names.—There are seven names associated with *L. reginae* (the names listed below are those recognized as subspecies, and synonyms):

reginae reginae (Linnaeus, 1758; Fig. 3B)
  violaceus (Lacepede, 1789)
  graphicus (Shaw, 1802)

Guyana, Suriname, and French Guiana

reginae semilineata (Wagler, 1824; Fig. 3D)
  oligolepis (Boulenger, 1905)

Amazonian Ecuador, Colombia, Perú, Bolivia, Venezuela, Brazil, also Atlantic Forest of Brazil

reginae macrostoma (Amaral, 1935)
  reginae maculicauda (Hoge, 1954)

Chaco Boreal and Cerrado vegetation of Brazil, Argentina, Paraguay, and Bolivia

reginae zweifeli (Roze, 1959; Fig. 3C)

Montane zones of Venezuela and Trinidad

Three names, *ornata* (Jan, 1863), *viridicyanea* (Jan and Sordelli, 1866), and *maculata* (Steindachner, 1867), assumed to be varieties of *L. reginae,* belong to other species. The holotype of *ornata* (MHNG 108:39) was examined and found to be an example of *L. miliaris.* The holotype of *viridicynaea* has not been located, but the color pattern, squamation and illustration furnished by Jan and Sordelli (1866) indicate that this name belongs to *L. poecilogyrus.* The syntypic material of *maculata* is apparently lost. Franz Tiedemann of the Austrian Natural History Museum (personal communication) stated that they have no Natterer material from "Ypenema," Brazil, the type locality, but have 32 specimens of *L. reginae* collected by Natterer from other Brazilian localities. A detailed examination of Steindachner's (1867) description of *maculata* suggests that he had more than one species present, and possibly two genera. He speaks of scale rows around the body and subcaudal number as 15 and 62–68 in young individuals and 17 and 80–90 in old specimens, respectively, and of highly variable color patterns. The squamation and color descriptions presented could represent Brazilian *Rhadinaea* as well as *Liophis.* Until Steindachner's series of specimens are located, his name must reside as *species inquirendae.*

Key to subspecies.—The following key is provided to aid in recognizing subspecies of *L. reginae.* The characters utilized are those that are average for those populations occupying specific geographic areas (Fig. 2).

1. Dorsum spotted with black and yellow; black lateral caudal stripe faint or absent 2
– Dorsum greenish, olive, grayish, never yellow and black spotted; black lateral caudal stripe always present and distinct 3
2. Subcaudals average 80 (69–88), (Venezuela, Trinidad, northern Guyana) . . *zweifeli*
– Subcaudals average 65 (55–78), (cis-Andean middle slopes of Perú and Bolivia) . . . . *semilineata*
3. Scale rows one and two pale colored 4
– Scale rows one and two colored like rest of dorsum 5
4. Dorsum with dense pale and dark paravertebral flecking, subcaudals average 74 (63–80), (French Guiana, Suriname, Guyana) . . . . *reginae*
– Dorsum without dense pale and dark paravertebral flecking, subcaudals average 67 (57–71), (Amazonian lowlands of central and southern Perú) . . . . *semilineata*
5. Subcaudal area with ventrolateral black spots, flecks, or smudges, subcaudals average 81 (75–91), (southern Goiás, São Paulo and south and southwest Paraná, Brazil and Argentina) . . . . *macrostoma*
– Subcaudal area immaculate, subcaudals average 70 (55–81), (Amazonian South America and Atlantic coastal Brazil) . . . . *semilineata*

Liophis williamsi (Roze)
Fig. 3A

Distribution.—*Liophis williamsi* is known only from the ground-floor leaf litter of cloud forest zones of the eastern Andes of Venezuela, from Rancho Grande, Aragua, to Cerro El Avila, Distrito Federal (Fig. 2).

Type series.—Roze's (1958) name is the only one that has been applied to this species. Marcuzzi (1950) mistakenly discussed this species under *Leimadophis bimaculatus opisthotaenia* (=*L. epinephelus*), a species that occurs in the western part of the Venezuelan Andes near Mérida.

I have examined the type series and four additional specimens. There is strong sexual dimorphism in the number of ventrals and subcaudals, but not in tail length/total length ratios, maxillary teeth, or color pattern.

Variation.—The ventrals of four males vary from 155–169 (mean = 160.3); subcaudals vary from 58–66 (mean = 60.8). Three females have ventrals that vary from 146–150 (mean = 147.4); subcaudals 53–62 (mean = 58.0). The maxillary teeth vary from 19–22 (mean = 20.5). The tail length/total length ratios (%) vary from 20.7–22.6 (mean = 21.7). There are no scale row reductions, all specimens having 17-17-17 dorsal scale rows. Supralabials, supralabials entering orbit, loreals, and postoculars are invariably 7, 3+4, 1, 2, respectively. The anal plate is divided. The infralabials vary as follows: 9-9 (4), 10-10 (2); preoculars 0-1 (1), 1-1 (4), 2-2 (2); temporals 1+2 (6), 1+1 (1). Maximum total length is 465 mm in males and females.

Pattern.—The dorsal color pattern consists of anterior blackish spots, bars and/or blotches surrounded by a dark brown ground color. At midbody the darker spots tend to form black paravertebral lines on scale rows seven or seven and eight. The zone between the fourth and seventh scale rows is pale brown or yellowish brown, the upper half of the fourth scale row is pale yellow, lower half of fourth and upper two-thirds of third black, lower one-third of third yellowish, and all of second and first scale rows brown. The dorsolateral dark stripes unite above the tail and form a single line to the tip of the tail. The dorsal surface of the head varies from brown to blackish brown, with or without obscure black spotting. A black line extends from below the nostril to the last supralabial and occasionally onto the nape, usually covering the upper one-fourth of the supralabials. The middle portion of the supralabials is white, whereas the lower one-third may be entirely black, or white with large black spots concentrated on the central portion of the lower one-third of each labial. The white area of the supralabial may extend past the last supralabial to the third or fourth scale row of the nape. The infralabials may be entirely black, or mostly black with white edging. The chin and throat may be white with a few black marks, or almost entirely black with a few white-edged scales. The venter and subcaudal surface may be completely white with a few black flecks, or venter densely spotted with black on a gray to pinkish ground color with the subcaudals gray, with or without a midventral black line extending from anal plate to tip of the tail.

Hemipenis.—The hemipenis has a smooth apical disc, and a sinistral sulcus that forks one-third to one-half its distance from the base. The structure is very spinose, without calyces. Roze (1958) indicated that the specimen he examined had a calyculate zone near the apex of the *sulcus spermaticus,* but neither Myers (1974:20) nor I have been able to locate such a zone on the specimens we have examined.

Comments.—A color pattern similar to that of the head and trunk of *L. williamsi* is also present in *L. epinephelus fraseri* from central Perú. The patterns are so similar that I originally thought *L. williamsi* was represented by two widely disjunct allopatric populations. However, after examining a large number of individuals of the *L. reginae* group, I am convinced that pattern types within this complex are repetitive within and between species, and pattern alone will not insure proper identification.

One additional species seems related to this complex, an altitudinal isolate from Cochabamba, Bolivia, that shows a scale row reduction mode similar to that found in some individuals of *L. reginae.* The general shape of the head and body, the tail/total length ratios, and variable color pattern suggest a relationship to both *L. reginae* and *L. epinephelus.* I designate this undescribed population as:

Liophis andinus new species
Fig. 5 and 6

Holotype.—Carnegie Museum of Natural History (CM) R2808, adult male, from Incachaca, 2500 m, Cochabamba, Bolivia, collected by J. Steinbach in October 1921.

Paratopotypes.—CM R2777, R2797–98, R2780–81, R2804–07; American Museum of Natural History 36012, 36014, 36016.

Distribution.—Known only from the type-locality (Fig. 2).

Diagnosis.—*Liophis andinus* is distinguished from all species of *Liophis* except *L. reginae* by having 15-15-15 dorsal scale rows, generally without reduction (one reduced to 14 posteriorly), rather than 19-17-17, 19-17-15, 17-17-17, or 17-17-15 dorsal scale rows; and from all species of *Liophis* by having three (very rarely two) supralabials entering the orbit rather than two.

Description of holotype.—Adult male, total length 485 mm; tail length 130 mm; tail/total length ratio 0.268; head length 15.8 mm, head width 8.0 mm; diameter of orbit 2.7 mm; nostril to eye distance 2.8 mm; ventrals 150, subcaudals 68; supralabials and infralabials 8-8; preoculars and postoculars 2-2; temporals 1+2; loreal 1-1; third, fourth, and fifth supralabial entering orbit on each side; maxillary teeth 24, last two enlarged and separated from remainder by a diastema equal in width to the basal length of three prediastemal teeth; *in situ* hemipenis 9 subcaudals in length, slightly bilobed, forked *sulcus spermaticus,* naked basal pocket, smooth distal, apical disc. Color pattern (in preservative) as follows: top of head brown or olive brown, side of head with broad black streak from edge of rostral, through eye to above and/or slightly beyond last supralabial; upper edge of preocular with small cream spot; infralabials, throat and first few ventrals immaculate cream;

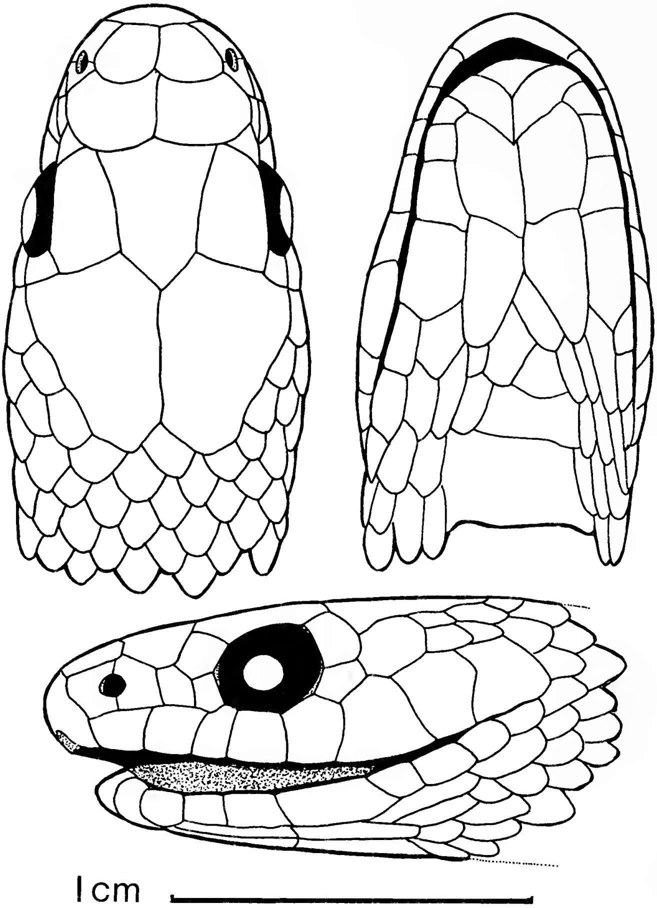

Fig. 5.—A dorsal, ventral, and lateral view of the head of the holotype of *Liophis andinus* (CM R2808).

supralabials cream except for dorsal edge which is black; midbody pattern consists of cream ventrals with dark scattered flecks; upper edge of first scale row and lower edge of second scale row with small black dot at their alternate apexes, a thin black edge on each of these two scale rows connects the small black dots, giving an appearance of a zigzag line; upper half of third and lower third of fourth scale rows with straight-edged black line; upper third of sixth and all of seventh scale rows black, lower edge straight, upper edge undulating; eighth (middorsal) scale row faintly speckled, otherwise cream; lateral interspaces

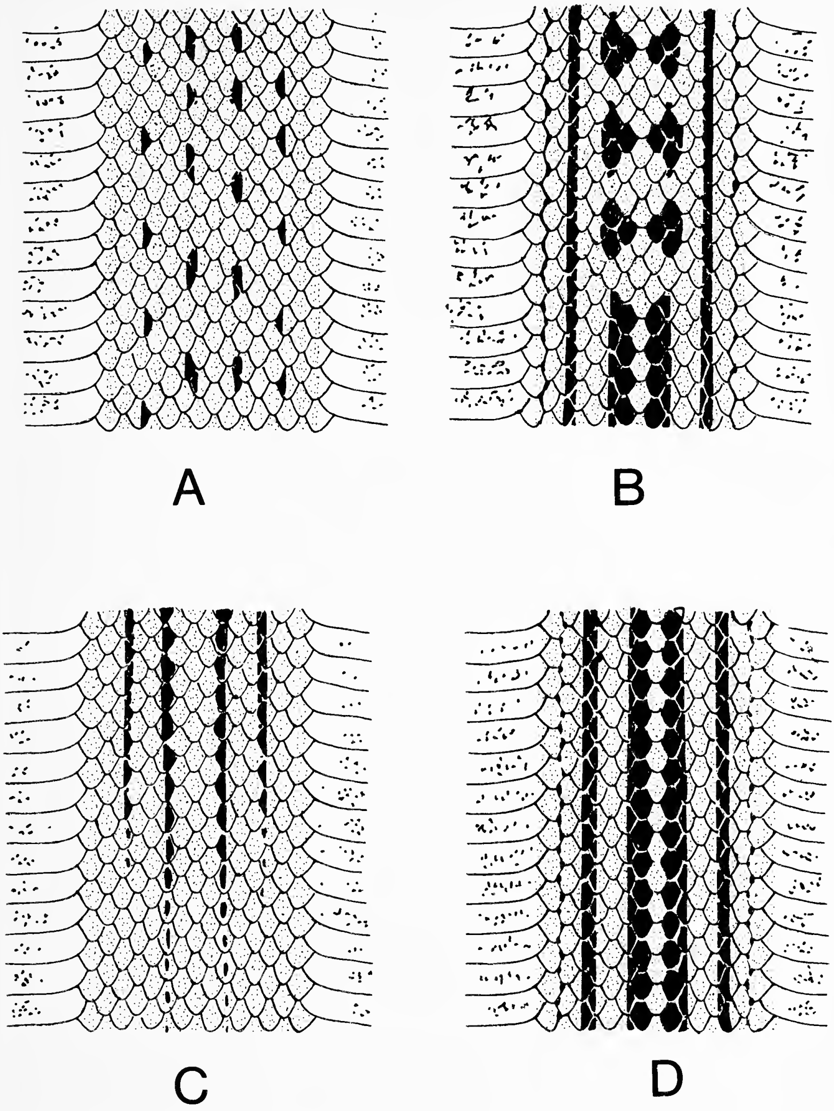

Fig. 6.—The midbody color patterns of the type series of *Liophis andinus* with the exception of CM R2797 which appears to be patternless. A) represents CM R2798; B) CM R2780; C) CM R2781, R2804, R2806–07, AMNH 36012, 36014, 36016; D) CM R2777, R2805, R2808.

between black lines probably cream, but specimen is darkened in formalin and light ground colors are obscure; black stripe of third and fourth scale rows continues onto the tail where it occupies the upper half of the first and lower tip of the proximal lateral caudal scales, and passes through the middle third of the first scale row distally; subcaudals immaculate cream.

Variation.—The following data are based upon the type series; means and sample size are in parentheses, measurements in millimeters; total length of five males with complete tails 406–570 (490.0), seven females 445–700 (606.6); tail/total length ratios of males 0.268–0.283 (0.272), females 0.238–0.261 (0.253); head length of both sexes 14.4–21.6 (17.8); head width 8.0–11.7 (10.0); nostril to eye distance 2.8–4.9 (4.3); diameter of orbit 2.7–4.9 (4.28); head width/head length ratios 0.51–0.59 (0.543); ventrals of males 148–151 (149.8), females 153–156 (154.6); subcaudals of males 67–72 (70.1), females 64–68 (65.8); maxillary teeth of males 23–26 (24.3) females, 24–27 (25.0). Scale features of the head vary as follows: preoculars 1-1 (8), 1-2 (1), 2-2 (4); postoculars 2-2 in all; loreal 1-1 in all; supralabials 8-8 (11), 7-8 (1), 8-9 (1); infralabials, 8-8 (8), 7-7 (1), 7-8 (1), 8-9 (1), 9-9 (2); temporals, 1+2 (11), 1+3 (2); supralabials entering orbit, 3+4+5 (11), 3+4+5/4+5+6 (1), 3+4/3+4+5 (1).

The color pattern is obscure in most specimens because of darkening by formalin. However, "in fluid" observation of the pattern reveals at least five midbody patterns (Fig. 6, unicolored pattern not figured), of which figures C and D represent about 83% of the individuals. The venter appears to be cream or yellow with some dark flecking in all individuals. The subcaudal area appears to be immaculate cream or yellow. The cream or yellow spot on the upper edge of the preocular is distinct in 10 individuals and obscure in three. In one specimen, an obscure cream spot also appears on the upper edge of the suprapostocular.

The *in situ* hemipenis varies in length from 8 to 9½ (8.5) subcaudals. It is slightly bilobed, the lobes usually indicated at the level of the seventh or eighth subcaudal. The *sulcus spermaticus* divides about the level of the third subcaudal. There is a naked basal pocket present in all specimens. There seem to be six proximal rows of relatively large spines while the remainder of the hemipenis is covered with densely set, smaller spinules. The outer edge of the distal end of the hemipenis bears a relatively large, smooth apical disc.

SPECIMENS EXAMINED

Liophis andinus.—BOLIVIA: Incachaca, AMNH 36012, 36014, 36016, CM R2777, R2797–98, R2780–81, R2804–08.

Liophis reginae macrostoma.—ARGENTINA: "northern," MHNG 1552.34; Iguazu Falls, FMNH 9252, 9379; Puerto Iguazú, IML 194. BRAZIL: no specific locality, MCZ 1991; Agudos, KU 124638; Anhangaí, MZUSP 1659; Annapolis, AMNH 62230, 62233; Aruaña, MZUSP 2182; Assis, USNM 165586; "Bahia" BMNH 149.80, MCZ 2952; Burití, MZUSP 5352; Corumbataí, MZUSP 4007; Crato, MZUSP 5244; Franca, MZUSP 828; Itaqua, USNM 100752; Pirapora, MZUSP 829; Posto Diauarum, MZUSP 3691–92, 5512, São Felipe, MZUSP 5715; São Luis de Cáceres, MZUSP 1370; "São Paulo", MCZ 17809–10, UMMZ 62817–18; Taubaté, USNM 76390; Usina Sinimbú, Mangabeira, MZUSP 2940–42, 3337; Utiarití, MZUSP 4743; Vespasiano, MZUSP 2776; Xavantina, BMNH 1972. 4.20. PARAGUAY: Asunción, BMNH 1930.11.27.202, FMNH 13160; Primavera, BMNH 1956.1.3.34, 1960.1.3.39, 1962.80; Rosario, BMNH 1962.82; 2.7 km N San Antonio, UMMZ 14321.

Liophis reginae reginae.—FRENCH GUIANA: Maripasoula, MCZ 77512. GUYANA: no specific locality, AMNH 3595, 17680; Acarahy Mountains, KU 69825; New River BMNH 1939.1.1.87–88, Wismar, UMMZ 77506 (2). SURINAME: no specific localtiy, MCZ 16387, RMNH 12510, USNM 5434, 6117; 3 km SE Blakawatra, RMNH 1877; Brokabaka, RMNH 1859; Brokopondo, MCZ 149538, 152599–601; SE of Carl Francois, RMNH 1841; Lely Mountains airstrip, RMNH 1650; 12 km NE Lely Mountains airstrip, RMNH 1682; Lelydrop, AMNH 104623; Loksihatti, RMNH 771; 13 km W Moengo, RMNH 387; Republiek, Para Kreek, RMNH 84; R-V Nature Reserve, Foenjue Island, Coppename River, MCZ 152601; Sam Kreek, AMNH 104621; Uitkyk, CM 44301; Zanderij, BMNH 1946.4.4.54.

Liophis reginae semilineata.—BOLIVIA: no specific locality, AMNH 2985, 4440; Abuná, UMMZ 56874; Buena Vista, UMMZ 60721–22, 64153 (2), 67910–16; AMNH 36006, FMNH 35690, 35702; "Beni, AMNH 101877; Cachuela, AMNH 22523; Cauriaco, AMNH 101875; Chamblaya, BMNH 1902.5.29.96; Chiquitas, FMNH 195908; Coretolla, AMNH 101837; Guayara Merin, USMN 123970; Huachi, AMNH 22473, 22479, 22503; La Perseveranda, AMNH 101833; Las Yungas, CM 19, 24, 27; Manao, UMMZ 56870–72, 56882; Riberalta, AMNH 22257; Río Iténez, AMNH 101873; Río Madre de Dios, UMMZ 56886, 59786; Río Mamore, AMNH 101835; Rurrinabaque, AMNH 22445, 22522, Sacramento, MZUSP 4151; 10 km E San Antonio, AMNH 101874; 10 km W San Pedro, AMNH 101834; 4 km N Santa Cruz, AMNH 101836; Santa Rosa, AMNH 101830–32, 101838–40; Trinidad, AMNH 101876. BRAZIL: no specific locality, MNHP 1912-483, 1912-484, 1912-485, 1912-485A, 1912-485B; Abuná, UMMZ 56877; "Amazonas", AMNH 14543; north bank of Amazon, three hours downstream from Leticia, Colombia, LACM 103621; Angra dos Reis, MZUSP 2419; "Bahia," BMNH 62.1.30.57. MCZ 3285, Bahia, AMNH 22281; Barcarena, KU 128102; Barra do Tapirapés, AMNH 93575–83, MZUSP 3799, 4326, 4336; Belém, KU 127273–74, 124593, 124599, 128103, 140180; 50 km from Belém, MCZ 53200; Boca do Acre, MZUSP 5754; Cachimbo, MZUSP 3335–36; Calama, MZUSP 5901; Campo Novo, MZUSP 5924; Canindé, MZUSP 4238–40, 4251, 4276, 4282; Canutama, MZUSP 5762; Foz do Jamarí, MZUSP 5905; Hyutanahã, USNM 28945; Igapo-Assú, BMNH 1946.1.4.66; Igarapé Belém, AMNH 115019–21; Lago Catu, MZUSP 1826; Manaus, AMNH 64897, CAS 49796; MZUSP 3053; Marajo Island, BMNH 1923.11.9.117–21; Mavés, AMNH 89784, 91643–44; Novo Aripuanã, MZUSP 5917; Óbidos, MCZ 1204 (2), 2574 (2), UMMZ 56310; Oriximiná MZUSP 5487; Pacotí, MZUSP 3632; "Pará," BMNH 45.8.25, MCZ 898, 1171, 2880, 2882, 3292, 5690; Plácido de Castro, MZUSP 2556; Porto Velho, MZUSP 3751–52, 4632; Porto Velho, MZUSP 3691–92; Puruzinho, MZUSP 5908; Río Branco, MZUSP 2555; "Río de Janeiro," MCZ 3944, 6792; Río Doce, MCZ 17957, MZUSP 830; Río Jurúa, MZUSP 833; San Carlos, MZUSP 5904; Santa Leopoldina, MZUSP 832; Santarém, MCZ 1162 (3), 3682, MZUSP 1250; Tapaúa, MZUSP 5769; Valença, MZUSP 5812–13. Colombia: "La Selva," MCZ 62256; Leticia, AMNH 78986, 95075, KU 124938, LACM 103622, MCZ 48978–80, 57249; Tarapaca, CAS 135343. Ecuador: no specific locality (or doubtful locality), AMNH 15210, 24147, BMNH 89.4.8.1. (2), LACM 2540; Abitagua, FMNH 25812–14, 28025, 28060; Alpayacu, FMNH 4069; Arajuno, USNM (JAP) 776; Baños, UMMZ 88964; near Baños, UMMZ 92021, 92023; between Baños and Abitagua, UMMZ 92024–27, 92030; Cabeceras del Río Arajuno, USNM (GOV) 8304–05, 8310; Cabeceras del Río Capahuari, USNM (GOV) 7225, 7413; Canelos, USNM (GOV) 7327; Chichirota, USNM(GOV) 7296, 7416; Concepción, USNM (GOV) 7325; Copataza, USNM (GOV) 7280–82; Dureno, KU 105413; El Topo, BMNH 1912.11.1.36–39; Lago Agrio, KU 126035; Limóncocha, UIMNH 54665, 61248–51, 61253–56, 63524, 82477–81, 92245, Llunchi, UMMZ 84761; Loreto, USNM (JAP) 3742, USNM (GOV) 7292, 7324, 7410, Macuma, UIMNH 62868, USNM (JAP) 8650–52; Mera, KU 98626, 121324–26, 133533; Montalvo, USNM (GOV) 7287–88, 7408; Mount Tunguragna, FMNH 36623; Palmera, AMNH 36042; Paragachi, USNM (GOV) 7469; 8387; Plan de Milagro, USNM (JAP) 7024; Pucayacu, USNM (GOV) 7297; Puyo, AMNH 36043–44; Riobamba and Canelos, AMNH 35926, headwaters of Río Bobonaza, USNM (JAP) 8613; Río Corrientes, USNM (GOV) 7294; Río Cotopino, USNM (GOV) 7298; Río Curaray, FMNH 23486; region of upper Río Curaray, USNM (JAP) 3756; USNM (GOV) 7293, 7412; Río Napo, UMMZ 88966; Río Negro, KU 121327–28; Río Oglan, USNM (GOV) 7419; Río Pastaza, UMMZ 88967–68; upper Río Pastaza, USNM (JAP) 7938; north bank of Río Pastaza, between Baños and Abitagua, UMMZ 92022, 92029; Río Pindo, near Río Tigre, USNM (GOV) 7409, 7414–15; Río Pucuno, USNM (GOV) 6129; Río Sano, UMMZ 92028; Río Siquino, USNM (GOV) 7326, 7417–18; Río Villano, USNM (GOV) 7411; Río Suno, UMMZ 92031; Río Talin, USNM (GOV) 7295; San Francisco, UMMZ 88965; San José Viejo de Sumaco, USNM (GOV) 7276; Santa Cecilia, KU 105408, 105414, 109839, 112274, 148352–54, 152517, 158535; "Santiago/Zamora", UMMZ 82885; Shell Mera, USNM (GOV) 7284–85; Tiputini, USNM (JAP) 8626. Peru: no specific locality, ANSP 3702, 11294–95, 11539, 14282, 14284, 41289, 14301, FMNH 40045, MCZ 16356–57; Achinamisa, AMNH 52937; Ayendama, AMNH 52524, 52729; Balta, LSUMZ 14599–600, 28002–03; ridge between two Biabos, AMNH 52896; Cashiboya, AMNH 52915, 52866–68; Centro Unión, TCWC 42116–17; 44681, 44579, 44081–85, 40546–52, 40554; Cerros del Sira, AMNH 104292; Chanchamayo, AMNH 52188, 52691, FMNH 39642, 40639, 152302; Chancharía, USNM 193786; Chiaco-Bagua, MCZ 120277; Chipurana, AMNH 52209, 52218; Contamana, AMNH 52242; Estera Rohyana, AMNH 106268; Estirón, MZUSP 4378–79, 4384; Fundo Lotta, USNM 196057; Hacienda Pampayacu, MCZ 42404–05, 42418; Huacamayo, AMNH 21160; Igarapé Champuia, MZUSP 3344; Indiana, TCWC 44678; Iquitos, AMNH 52053, 52112, 52136, 52161–62, 52206, 52228, 52314, 52331, 52374, 52408, 52423, 52428, 52485, 52497, 52538–39, 52577, 52591, 52593, 52613, 52616, 52634, 52641, 52643, 52659–60, 52663, 52743–44, 52762, 52772, 52876–77, 52957, 52971, 52999, 53002, 53051, 53055, 53150, 53261, 53263, 53334, 53398, 53403, 53500, 54299, 54387, 54847, 54943, 55950, 56041, 56082, 56085, 56107–08, 56128, TCWC 38221, 39098, 40553, 41751, 44086–87, 44679, 46279, 47147–49, USNM 197272–78; Jenaro Herrera, MHNG 1567.81; Juliaca, AMNH 2959 (in error); La Divisioria, Sierra Azul, AMNH 107814, FMNH 56163–69; La Mar, Silva, FMNH 39642; Marcapata, FMNH 59175, 62956; Madre de Dios, FMNH 40039–41, 40234–35; Mishana, TCWC 42113–14, USNM 197272 (2); Monte Alegre, AMNH 52783; Monte Carmelo, AMNH 55548, 55555, 55622, 55627, 55629, 55634, 55636, 55641, 55645, 55653, 55655–56, 55918; Morona Cocha, AMNH 53135; Moropon, TCWC 38129–20, 38222, 42115, 44672–77, 39101; Moyobamba, BMNH 74.8.4.20, 74.8.4.69; FMNH 5715; Nazareth, FMNH 5673; Orellana (Reforma), AMNH 52095, 52909, 55670; Oxapampa, FMNH 134479; Pachisa, AMNH 52565; Pacaya, AMNH 53597; near Palca, FMNH 134470; Pampa Hermosa, Río Cushabatay, AMNH 53377, 53403, 53425–26, 53502, 53509–12, 53514–17, 53522, 55450, 55474, 55713, 55720–21, 55739, 55747, 55763, 55755–66, 55770, 55792, 55794, 55798, 55837, 55851, 55854, 55856, 55858, 55860–61, 55895, 55961, 55982, 55986, 55999, 56005, 56008–09, 56022; Pampa Hermosa, Río Ucayali, AMNH 52023–26, 52030, 53550, 53576–77; Panya, AMNH 52281, 52347–48; Paraíso, TCWC 42112; Parinari, AMNH 55680; Parvenio, AMNH 52457; Petras, ANSP 11469, 11671; Pozuzo, FMNH 5579; Puerto Mairo, FMNH 3678; Pucallpa, AMNH 71157-58; Punga, AMNH 52039, 52041, 52081, 52387, 53482–83, 56045, Quince Mil, FMNH 168384; 40 km NE Quince Mil, LSUMZ 32553; Quinton, AMNH 21161; headwaters, Río Aspusana, AMNH 52096; Río Itaya, near Iquitos, AMNH 52109, 52111, 52221, 52676, 52802, 53653, 53710, 53176, 53758, 53775, 53811, 53818, 54038, 54073, 54086, 54096, 54136, 54267, 54292, 54303, 54376, 54394–96, 54399, 54401, 54407, 54417, 54419, 54458, 54666, 54669, 54713, 54723, 54726, 54745, 54750, 54778, 54977, 55026, 55054, 55079, 55106–07, 55124, 55158, 55166, 55173, 55194, 56113, 56116; upper Río Marañon, BMNH 1913.6.4.5–6; upper Río Nieva, AMNH 55901; Río Putumayo, FMNH 37436; Río Samiria and Parinari Canyon, AMNH 5271, 57299–302; upper Río Ucayali, AMNH 71135, 7111–14; Río Ucayali, UMMZ 51254 (2); Roaboya, AMNH 52235, 52477, 52482, 52799, 52888, 53095, 54433, 55690–91; Sacanche, USNM 196056; San Ramón, FMNH 152302; Sarayacu, BMNH 81.5.13.37; Sobral, AMNH 55350, 55345; Suhuayo (Contamana) AMNH 53007; Suhuaya (Rean Rean), AMNH 53578; Tingo María, USNM (WS) 3113, USNM 193767–85; Tocache Nuevo, USNM 196058; Utuquina, AMNH 52938; Valle de Iscozazin, Chontilla, LACM 76806; Yanamono, TCWC 39099–100, 42118, 44080, 44680; Yarinacocha, FMNH 45591, 56123–24, 56145–49.

Liophis reginae zweifeli.—GUYANA: Mabaruma Compound, USNM 164207–10; north slopes of Mount Roraima, BMNH 1971.1724. TRINIDAD: no specific locality, BMNH 1947.3.3.27, USNM 17757–58; Arima, AMNH 81462; Arima-Blanchiceusse Rd., AMNH 73136; Brickfield, FMNH 49958; Mayaro, MCZ 49069; Mount Aripo, BMNH 1940.3.11.85; Rio Grande Forest, Sangre Grande, AMNH 81464, 85953; San Rafael, FMNH 49957; Tamana Caves, Mount Tamana, MCZ 100654; near Valencia, MCZ 81517; Vega de Dropouche Rd., AMNH 85954. VENEZUELA: Aricagua, BMNH 1905.5.31.55; Arabopó, UMMZ 85279; Caracas, MHNG 367.56, MBUCV 505; 9 km S Caracas, USNM 196332; Caripito, AMNH 67877–78, 98260–61; Carúpano, ANSP 5510; Capibara, USNM (FN) 35446; Cerro Turumiquire, AMNH 29317, FMNH 17833–36; Cerro Yapacana, RMNH 2276, 2285; Cuchiuano, AMNH 29332; Cumaná, UMMZ 56038; El Estánque, Borburata, MBUCV 3082; El Junquito, MBUCV 3083, SCN 4318; El Limón, CM 7355; El Vigía, CM 8001; El Yaque, Near Turumiquire, CM 7969; Los Canales, Naiguatá, CM 22780; 4 km NW

Montalbán, USNM (FN) 19641; 2.7 km NE Peña Blanca, KU 167586; planta eléctrica de Curpupao, AMNH 59430; Puerto Cabello, UIMNH 93850; Rancho Grande, AMNH 98262, BMNH 1970.237, CAS 138485, FMNH 204477, KU 167585, MBUCV 95–96, 621, 659, 3076–81, MCZ 62496, 81518, SCN 15103, UIMNH 22663, 63600, UMMZ 124225–33, 128390; San Antonio de Maturín, MCZ 9979; 5 km S San Juan de las Galdonas, RMNH 2363; Sorte, Chivacoa, SCN 10551; Viverios Guayabal, altos de Pipe, MCZ 112411.

Liophis reginae subsp.—TOBAGO: Pigeon Peak Trace, USNM 228069.

Liophis reginae semilineata × *L. r. macrostoma.*—ARGENTINA: Río Pescado, Oran, IML 115; Salta, IML 600. BOLIVIA: Chamblaya, BMNH 1902.5.29.96. BRAZIL: Porto Velho, Río Tapirapés, MZUSP 3751, 3752, 3797, 4326, 4336, 4362.

Liophis reginae reginae × *L. r. zweifeli*—GUYANA: Berbice, BMNH 53.4.6; Demerara, BMNH 55.8.28, 55.8.28.48; Dunoon, UMMZ 53912, 53968—69; Kartabo, AMNH 18170, 67876; Lama Creek, AMNH 36105; Matali, AMNH 61541; Stabu, FMNH 30959, 30962.

Liophis williamsi.—VENEZUELA: Cerro El Avila, UIMNH 63607: Colonia Tovar, CM 7393, USNM 121206; El Junquito, MCZ 51329; Rancho Grande, MBUCV 3044, UMMZ 124221, 124224.

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GEOGRAPHIC AND SECONDARY SEXUAL VARIATION IN THE MORPHOLOGY OF *EPTESICUS FUSCUS*

CHRISTOPHER D. BURNETT[1,2]

ABSTRACT

This study describes geographic and secondary sexual variation in the morphology of the big brown bat, *Eptesicus fuscus*. The two aspects of morphology examined were wing size (three characters) and skull size (10 characters). Approximately 5000 specimens were measured and divided into 97 geographic groups distributed throughout the North American range of the species.

Females were significantly larger than males for 12 of the 13 characters studies, but the absolute differences were small (1.3–3.8%), and both the degree and direction of sexual dimorphism were geographically variable. The degree of dimorphism was positively correlated with litter size and moisture and negatively correlated with temperature, suggesting the importance of wingloading, moisture stress, and thermoregulation as factors contributing to sexual dimorphism.

Most of the morphological characters differed significantly from a random spatial distribution, and the geographic patterns of wing and skull variation were randomly distributed with respect to each other. Wing size exhibited a strong trend toward larger size at lower latitudes, whereas skull size showed a reverse, but more complex, pattern. Insular and peninsular subspecies were clearly differentiated, but there was considerable morphological overlap among continental subspecies. Modification of continental subspecies boundaries substantially improved discrimination rates. The pattern of morphological differentiation among insular subspecies cannot be explained by a reduction of gene flow from a Central American dispersal origin.

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INTRODUCTION

Eptesicus fuscus is one of the most widely distributed mammals in North America, ranging across southern Canada, the continental United States, most of Mexico and Central America, and the Greater Antilles (Hall, 1981). It consequently inhabits climatic regions as disparate as temperate deserts and tropical rain forests. The extraordinary ecological amplitude of *E. fuscus* combined with its sedentary movement patterns (Beer, 1955; Hitchcock 1965; Davis et al., 1968; Barbour and Davis, 1969; Mills et al., 1975) make this species an excellent candidate for the study of adaptive variation. In addition, the occurrence of several insular populations allows an assessment of the differentiating effect of geographic barriers to gene flow. Previous studies of geographic variation in *E. fuscus* have reported varying degrees of differentiation within geographically limited areas (Allen, 1933; Engels, 1936; Cockrum, 1952; Jones, 1964; Howard, 1967; Long and Severson, 1969), but no quantitative assessment of variation throughout the North American range of the species has been made.

The literature also indicates that females of *E. fuscus* are generally larger than males (Engels, 1936; Phillips, 1966; Patterson and Davis, 1968), and data on sexual dimorphism in this species have been used to support both sides of the recent debate over the causes of sexual size dimorphism in vespertilionid bats (Myers, 1978; Williams and Findley, 1979).

In this paper, I describe the geographic patterns of morphological variation throughout the North American range of *E. fuscus*. I begin by considering whether sexual dimorphism warrants separate treatment of males and females and whether patterns of variation in the two sexes are concordant. Next, the patterns of variation in wing and skull character complexes are described and compared. Finally, I quantify the degree of differentiation among subspecies and revise currently recognized subspecies boundaries to maximize discrimination among the continental subspecies. The geographic and climatic correlates of morphological variation in *E. fuscus* are examined in a separate paper (Burnett, 1983).

MATERIALS AND METHODS

Data Collection.—I recorded three wing and 10 skull dimensions (Fig. 1) from 4791 adult skin and skull specimens housed in 61 collections in the United States, Canada, and Mexico (Appendix I). Morphological characters included: 1) measurements that could be repeated with accuracy, 2) measurements frequently used by mammalian systematists to allow comparison with other studies, 3) wing and skull characters to allow comparison of two functional complexes, and 4) the subset of 19 original characters which best discriminated among six subspecies in a preliminary discriminant function analysis on 23 widely scattered populations. Measurements were taken with Helios, knife-blade, dial calipers and recorded to the nearest 0.1 mm. Museum number, collection

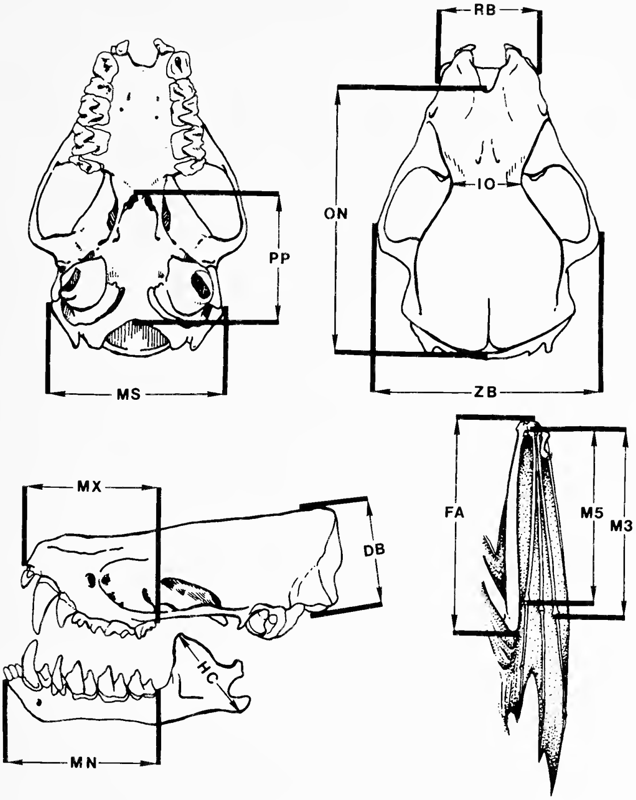

Fig. 1.—Illustration of wing and skull characters of *Eptesicus fuscus* used in this study: FA, forearm length; M3, third metacarpal length; M5, fifth metacarpal length; MN, mandibular toothrow length; HC, height of coronoid process; ON, occipitonasal length; MX, maxillary toothrow length; PP, postpalatal length; ZB, zygomatic breadth; MS, mastoid breadth; IO, interorbital breadth; RB, rostral breadth; DB, depth of braincase. Skull diagrams after Hall (1981). Wing and skull illustrations not to scale.

date, collection locality (to county), sex, and reproductive status of females were recorded from the specimen labels.

Because my primary purpose was to describe continent-wide trends, I arranged specimens into geographic groups (GG's) by pooling adjacent collection localities until statistically meaningful sample sizes were obtained. The distribution and reference numbers of the resulting 97 geographic groups are shown in Fig. 2. Mean sample sizes (±SE) for these groups were 20.7 (±1.1) for males and 23.0 (±1.2) for females. Fourteen male and 11 female GG's were composed of fewer than 10 individuals, but these groups were retained because of the large geographic gaps that would have otherwise resulted. The use of small sample sizes for a few localities is further justified by the very low within population coefficients of variation that bats show for most linear measurements (Long, 1968).

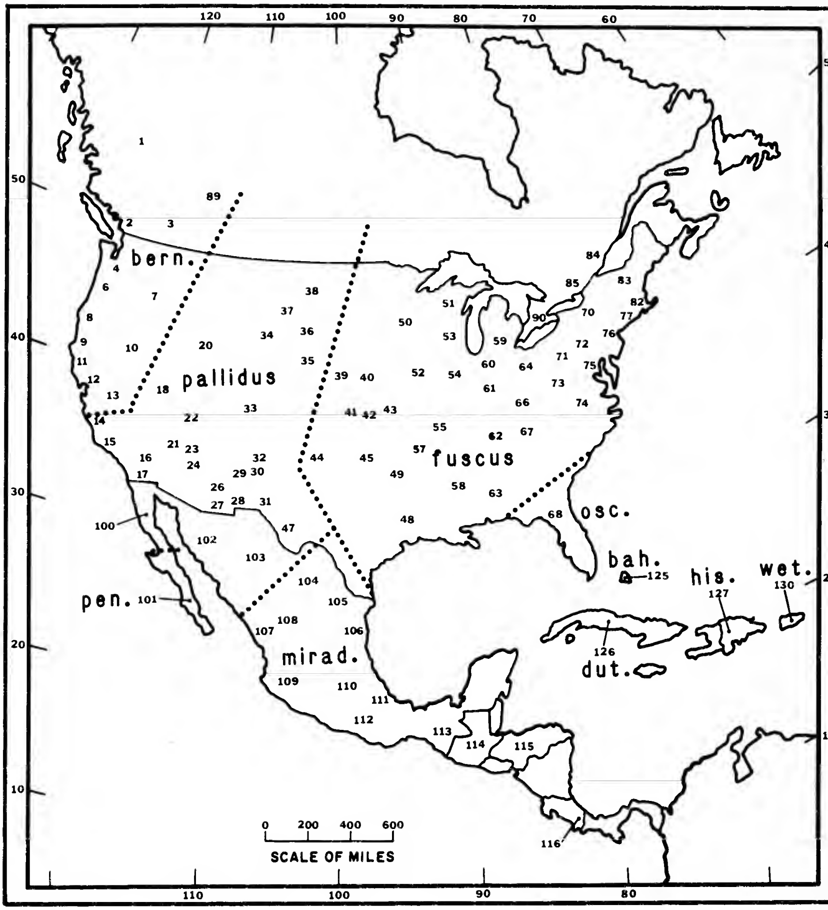

Fig. 2.—Map of *Eptesicus fuscus* geographic groups (GG's) used in this study. All GG's were represented by male and female samples except GG 111 (males only) and GG's 18, 31, and 115 (females only). Total GG's: male = 94, female = 96, both sexes represented = 93. Dotted lines indicate subspecies boundaries revised from Hall (1981) on the basis of discriminant function analyses (see Table 3).

Data Analysis.—Descriptive statistics on the 13 univariate characters were computed separately for males and females for each of the 97 geographic groups. The resulting GG means provided the basis for subsequent analyses. Principal components analyses (PCA) of the combined male and female means were used to further summarize overall morphological variation. I kept wing and skull variables separate, assuming that they represent different functional complexes and that pooling them would obscure their differences. To determine if the directions of greatest variance were uniform among groups (Neff and Marcus, 1980), principal component analyses were also performed on each of 12 widely scattered GG's. Student's *t*-tests were used to assess the overall degree of secondary sexual dimorphism using the univariate group means, the principal component scores, and the ratios FA/ON and M3/M5 (Fenton, 1972). Student's *t*-tests were also conducted for sexual dimorphism in each of 13 widely scattered GG's, and covariance analysis was used to test for sexual dimorphism in wing size after adjusting males and females to a common body size.

The first step in the analysis of geographic variation was to test each variable for departure from spatial randomness. By constructing a matrix of phenetic distances between all pairs of localities and a comparable matrix of geographic distances, Mantel's *Z* statistic was computed on the null hypothesis of random association between the two matrices (Sokal, 1979). I constructed phenetic distance matrices in which the elements were computed as $X_{ij} = |X_i - X_j|$, where X_i and X_j are the values of variable X (morphometric means) at localities i and j respectively. Similarly, I constructed a geographic distance matrix using map distances (km) between pairs of points. Because some paths of connection between GG's cross water barriers which I assumed to be ordinarily impassable to bats, nine GG's were eliminated (GG's 101, 113, 114, 115, 116, 125, 126, 127, 130) along with groups for which data on only one sex were available (GG's 18, 31, 111, 115) before conducting Mantel's tests.

To graphically display patterns of variation, I used the "contouring" feature of the computer program, SYMAP (Dougenik and Sheehan, 1975), to produce isarithmic maps. Male and female maps were based on 94 and 96 control points (GG's) respectively, and the range of data values for each variable was divided into five or six equal intervals. Impermeable "barriers" were placed around the four island samples and between Baja California and mainland Mexico to prevent interpolation across bodies of water that I assumed to be barriers to the movement of *E. fuscus.*

To assess the adequacy of currently recognized subspecies boundaries, I performed discriminant function analyses for each sex on a subset of the GG's using subspecies boundaries (Hall, 1981) to assign the *a priori* groups. I then made bivariate plots of the first principal components of wing size versus skull size for all GG's and drew envelopes around the samples of each subspecies. If there was morphological overlap between geographically distant portions of two subspecies, I made no changes. But if there was geographic as well as morphological overlap, I reassigned the subspecies of GG's to minimize overlap in morphological and geographic space. I then repeated the discriminant function analyses and compared the percent of cases correctly classified obtained using the modified boundaries with those obtained initially.

All analyses were carried out on an IBM 370/168 computer at the Boston University Academic Computing Center. Descriptive univariate statistics, *t*-tests, covariance analyses, principal components analyses, and discriminant function/canonical variates analyses, were performed with SPSS programs (Nie et al., 1975). Mantel's tests were performed using the GEOVAR series of programs developed by David Mallis (Sokal, 1979). I modified these programs, written for use on a Univac computer, to be compatible with the Boston University IBM system. Two-dimensional plots of the principal component scores were produced with SAS programs (SAS Institute, 1979). Three-dimensional plots of subspecies centroids on the first three canonical variate axes were generated by a program I wrote using DISSPLA subroutines (Integrated Software Systems Corporation, 1975). Hard copies of these plots were produced on an FR-80 laser device.

RESULTS

Descriptive Statistics and Sexual Dimorphism

Descriptive statistics based on sample means from the 93 geographic groups for which data were available for males and females are in Table 1. Descriptive statistics for each GG and other data not included here

Table 1.—*Descriptive statistics and one-tailed* t-*tests of secondary sexual dimorphism in* Eptesicus fuscus, *based on sample means from 93 geographic groups* ($df = 184$). *Significance levels:* *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

	Mean (Minimum-maximum) in mm		CV		♀/♂	
Character	Male	Female	Male	Female	Ratio	*t*-value
FA	46.1 (41.9–51.3)	47.2 (42.5–51.3)	3.2	3.0	1.024	5.20***
M3	42.3 (38.1–47.6)	43.4 (39.2–46.9)	3.4	2.9	1.026	5.22***
M5	40.0 (35.8–44.5)	41.0 (36.6–44.2)	3.3	3.1	1.025	5.37***
MN	8.3 (7.4–9.1)	8.5 (7.5–9.0)	3.0	2.9	1.024	3.50***
HC	5.8 (5.1–6.5)	6.0 (5.3–6.5)	3.9	3.7	1.034	6.21***
ON	16.0 (14.3–17.5)	16.3 (14.6–17.4)	2.9	2.8	1.019	5.04***
MX	7.9 (7.1–8.6)	8.0 (7.1–8.6)	2.9	2.7	1.013	4.16***
PP	7.1 (6.4–7.6)	7.2 (6.5–7.6)	2.5	2.5	1.014	4.78***
ZB	12.5 (11.1–13.5)	12.8 (11.3–13.7)	3.1	3.0	1.024	4.85***
MS	9.8 (8.3–10.3)	10.0 (8.6–10.5)	3.1	3.0	1.020	4.34***
IO	4.2 (3.8–4.4)	4.2 (3.8–4.5)	2.7	2.9	1.000	1.23
RB	5.9 (5.0–6.2)	6.0 (5.1–6.4)	3.3	3.5	1.017	3.06**
DB	5.2 (5.0–6.0)	5.4 (5.0–6.0)	7.9	9.0	1.038	2.17**
FA/ON	2.88 (2.78–3.07)	2.89 (2.79–3.09)	2.2	2.1	1.003	−1.17
M3/M5	1.06 (1.04–1.10)	1.06 (1.04–1.09)	0.8	0.9	0.999	−0.81
PC1W	−0.39 (−3.18–2.96)	0.32 (−2.62–2.73)				2.66**
PC1S	−0.22 (−4.52–1.22)	0.18 (−4.26–1.94)				5.34***

are in Burnett (1982). The first two principal components of skull variation (PC1S and PC2S) had eigenvalues greater than one (Table 2) and accounted for more variation than any one of the original variables; they were retained for subsequent analysis. PC1S accounts for 78% of

Table 2.—*Results of principal component analyses of interlocality variation in* Eptesicus fuscus. *Wing and skull characters were analyzed separately, and only components with eigenvalues* >1 *were retained.*

	Character loadings				
	Wing	PC1W	Skull	PC1S	PC2S
	FA	0.336	MN	0.959	0.090
	M3	0.338	HC	0.892	0.296
	M5	0.337	ON	0.972	0.113
			MX	0.930	0.116
			PP	0.908	−0.253
			ZB	0.971	0.001
			MS	0.906	−0.317
			IO	0.676	−0.612
			RB	0.947	−0.077
			DB	0.591	0.736
Variance explained		97.8%		78.2%	12.1%
Eigenvalue		2.94		7.82	1.21

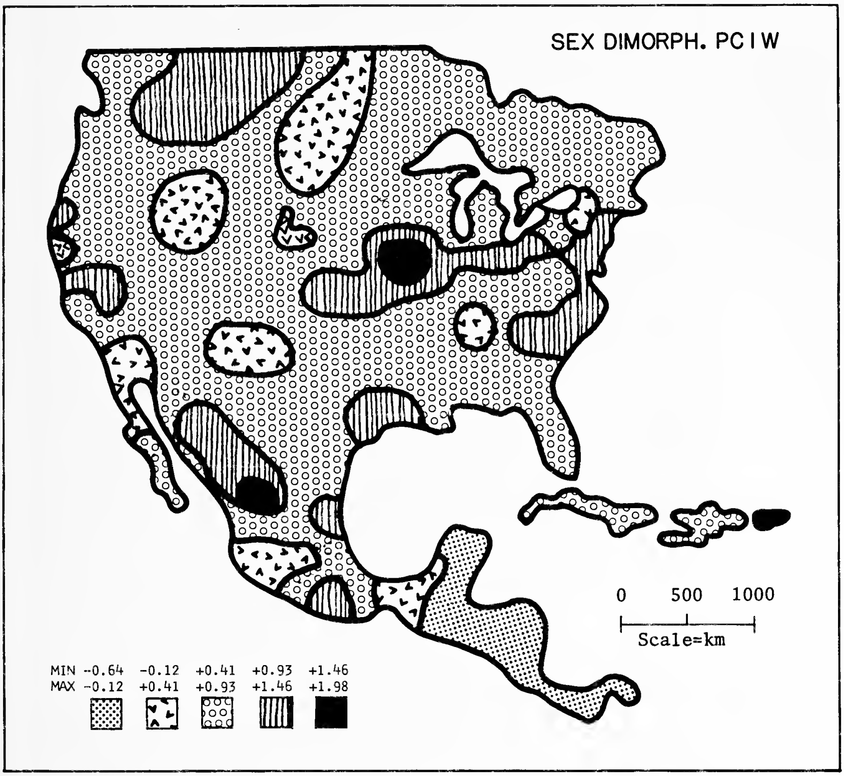

Fig. 3.—Isarithmic (contour) map of the degree of sexual dimorphism in the first principal component of wing variation in *Eptesicus fuscus*. Darker shading indicates greater dimorphism favoring females.

the variation in the 10 skull variables and thus provides a good measure of overall skull size (Humphries et al., 1981). Only the first principal component of wing variation (PC1W) was extracted by the eigenvalue >1 criterion, but it accounts for 98% of the variation in the three wing characters (Table 2). PC1W thus provides an excellent summary of variation in wing size. Comparison of the character loadings obtained from separate PCA's on 12 widely scattered geographic groups indicated that the directions of greatest variance are similar throughout the species.

Females are significantly larger than males for all univariate characters except interorbital breadth (IO), which was the same for both sexes (Table 1). The first principal component scores for wing and skull characters are also significantly greater in females. The sexual differ-

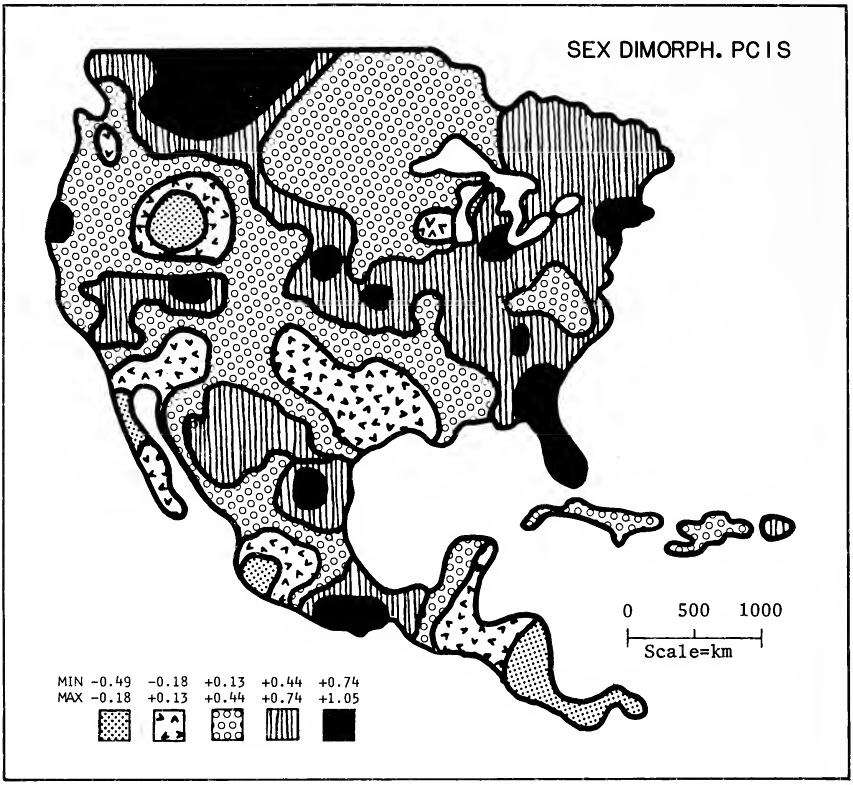

Fig. 4.—Isarithmic map of the degree of sexual dimorphism in the first principal component of skull variation in *Eptesicus fuscus*.

ences are small, however, ranging from 1.3 to 3.8% (Table 1). Using forearm (FA) and occipitonasal (ON) lengths as measures of wing and body size, respectively, the ratio FA/ON shows that relative wing length is not significantly greater in females than in males. Likewise, the ratio M3/M5 shows that relative wing width is statistically equal in males and females.

Analysis of the group means, however, may not be representative for the entire range of the species. The results of *t*-tests conducted on 13 GG's selected from diverse localities and subspecies showed considerable variation in the characters that are dimorphic. A few cases of greater male size were also found, indicating that the direction of dimorphism also varies.

Using the differences between male and female first principal com-

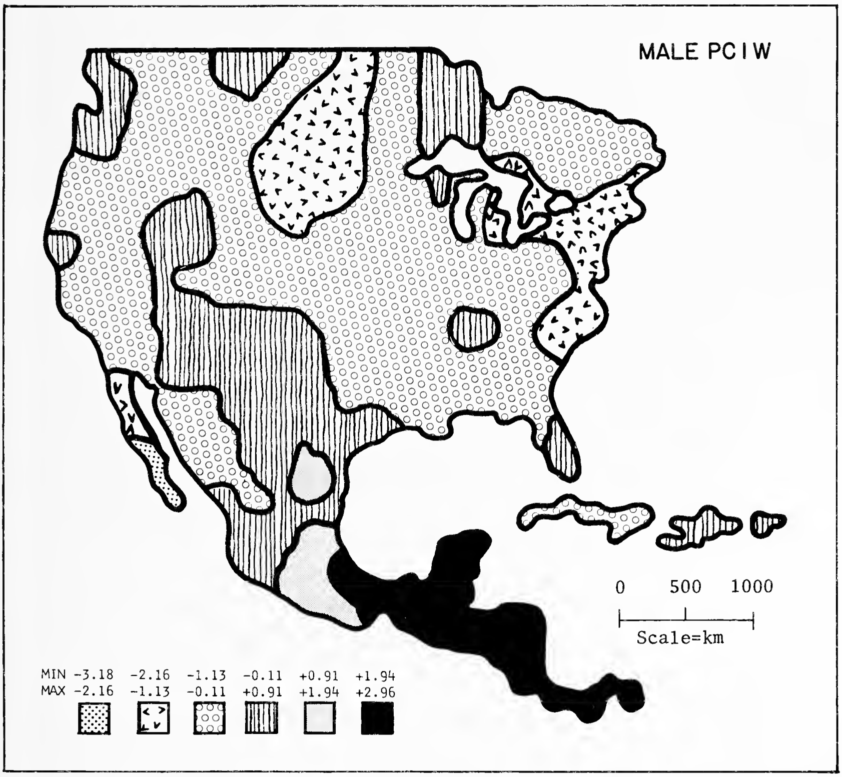

Fig. 5.—Isarithmic map of the first principal component of wing variation (PC1W) in male *Eptesicus fuscus.*

ponent scores as indices of dimorphism, the geographic patterns of variation in the degree of wing and skull size dimorphism were mapped (Figs. 3–4). The pattern of wing dimorphism does not differ significantly from a random distribution. Nevertheless, inspection of the maps reveals two interesting trends: a trend of increasing dimorphism favoring females toward the east, and a reverse trend of dimorphism favoring larger males at low latitudes. Based on the significant differences between males and females and the geographically variable nature of this dimorphism, I chose to treat the sexes separately in subsequent analyses.

Geographic Patterns of Variation

The results of the Mantel's tests showed the patterns of variation of all the wing variables and all but two male (PP, MS) and four female

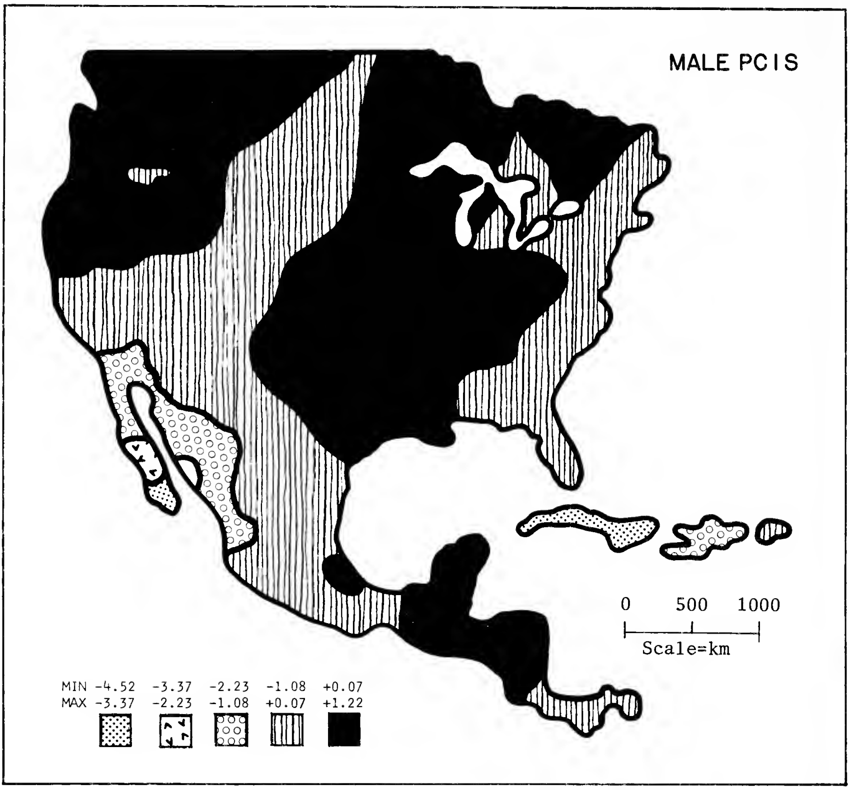

Fig. 6.—Isarithmic map of the first principal component of skull variation (PC1S) in male *Eptesicus fuscus.*

(MN, PP, ZB, MS) skull variables to be significantly different from a random distribution. To assess the influence of the spatially random skull variables on later analyses, I removed the three most random variables (PP, ZB, and MS), conducted a PCA on the seven remaining skull variables, and mapped the resulting first principal component scores. No major differences were found between the maps based on the reduced and full sets of skull variables. Because only two variables were random for both sexes (PP, MS) and because neither of these dominated the principal component scores, the spatially random variables were retained.

The geographic patterns of the first principal components of male wing and skull variation are illustrated in Figs. 5–6. Female patterns differ in detail, but the general trends are the same. A point distribution

Table 3.—*Comparison of discriminant function classification rates for nine subspecies of* Eptesicus fuscus *obtained using subspecies boundaries from Hall (1981) (Before) with those obtained using modified boundaries (After).*

Subspecies	Percent of cases correctly classified					
	Males			Females		
	Before	After	Change	Before	After	Change
bahamensis	100	100	0	97	97	0
bernardinus	49	69	+20	76	73	−3
dutertreus	—	—	—	81	81	0
fuscus	82	80	−2	57	65	+8
hispaniolae	—	—	—	100	100	0
miradorensis	88	89	+1	85	90	+5
pallidus	29	53	+24	29	33	+4
peninsulae	96	96	0	100	100	0
wetmorei	—	—	—	47	47	0
Overall	67	76	+9	66	70	+4

coefficient of 2.7 was obtained for these maps, indicating that the distribution of control points (geographic group localities) provides a highly reliable data base for interpolation (Dougenik and Sheehan, 1975). Nevertheless, the purpose of these maps is to reveal general trends.

Inspection of the map of wing variation (Fig. 5) reveals a strong trend toward increased size at lower latitudes. The major deviations from this general trend are small-winged bats in Baja California (GG 101), the Bahamas (GG 125), and Cuba (GG 126) and large-winged bats in the northwest, Alberta (GG 89), and northern Wisconsin/Michigan (GG 51). Large-winged bats also occur in the southwestern United States.

In contrast to the relatively simple and concordant patterns shown by the wing characters, the skull characters exhibited a more complex picture. As represented by the first principal component of skull variation (PC1S), overall skull size is largest in the northwest and along a midcontinental band extending from Canada to Central America (Fig. 6). Baja California, the Bahamas, and Cuba again have unusually small bats. All skull and wing characters for both sexes exhibit a trend of increasing size eastward across the Greater Antilles.

Subspecies Discrimination

I obtained adequate data to allow discriminant function analyses (DFA) on six subspecies for males and nine subspecies for females (Table 3). The following subsets of geographic groups were selected to represent the subspecies with more than one group: *bernardinus,* 2, 3, 6, 7, 10, 11, 13, and 15; *pallidus,* 1, 89, 38, 35, 44, 16, 17, 100, and 104; *fuscus,* 50, 40, 45, 105, 63, 75, 82, and 85; and *miradorensis,* 107,

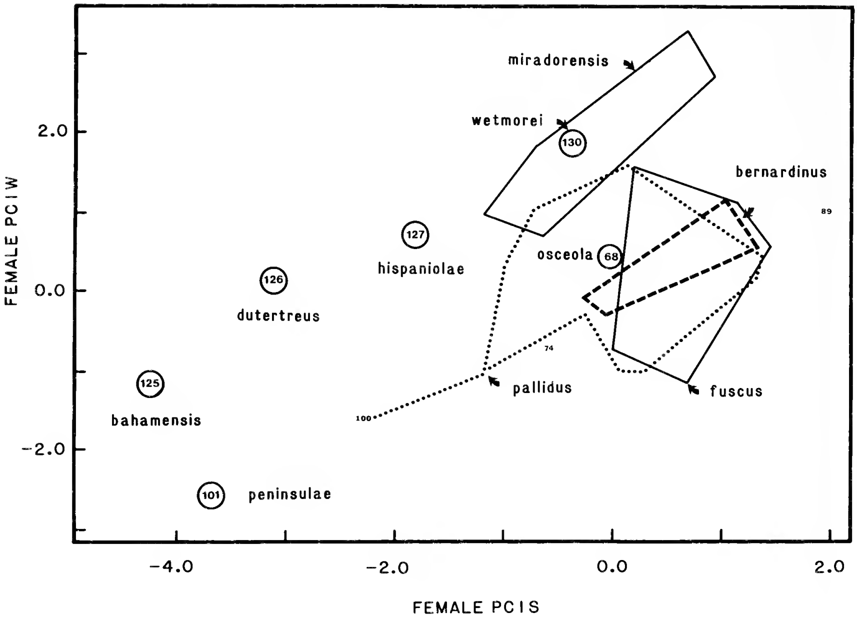

Fig. 7.—Plot of the first principal component of wing variation (PC1W) versus the first principal component of skull variation (PC1S) for 96 geographic groups of female *Eptesicus fuscus.* Circled GG numbers indicate insular and peninsular subspecies (see Fig. 2). Polygons enclose the GG's for each continental subspecies as defined by Hall (1981). GG's 74 and 89 are outliers from *E. f. fuscus.*

108, 106, 109, 110, 112, 113, and 114. To maximize sample sizes, the frequently missing skull character, zygomatic breadth (ZB), was omitted from the analysis. Preliminary DFA's did not include ZB as a significant discriminating variable for either males or females.

Using subspecies boundaries depicted in Hall (1981) as the basis for the *a priori* groups, the overall rates of correct classification were 67% for males and 66% for females (Table 3). The classification rates of only 29% for *E. f. pallidus,* however, suggested that the boundaries of this subspecies could be improved.

A bivariate plot of the first principal components of wing and skull variation for the 96 female groups coded by subspecies showed good separation among the insular and peninsular subspecies but extensive morphological overlap among the continental subspecies (Fig. 7). Using this plot, I made the following changes in subspecies designation: GG's 1 and 89, *pallidus* to *bernardinus*; GG's 14 and 15, *bernardinus* to *pallidus*; GG's 39 and 44, *pallidus* to *fuscus*; GG 104, *pallidus* to

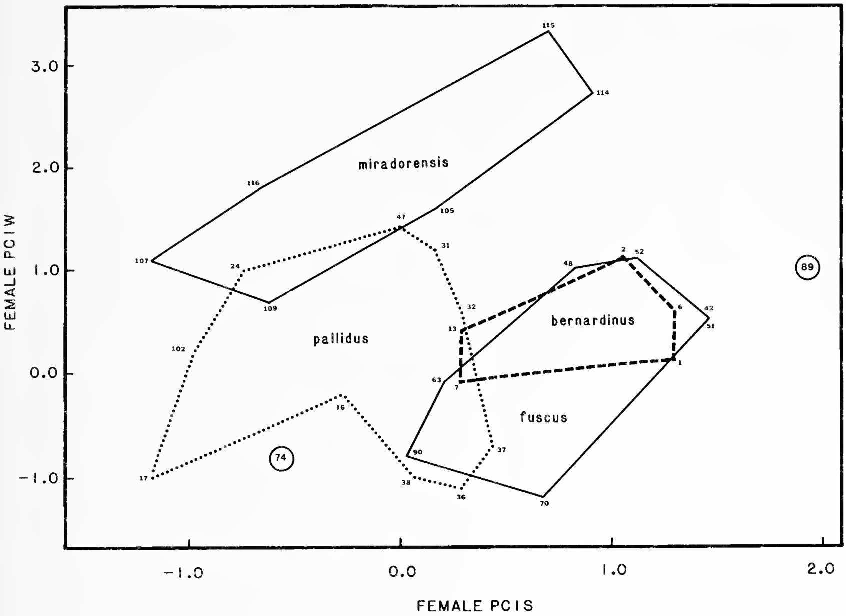

Fig. 8.—Plot of the first principal component of wing variation (PC1W) versus the first principal component of skull variation (PC1S) for females of the four continental subspecies of *Eptesicus fuscus*. Polygons enclose the GG's for each subspecies as modified by this study (see Fig. 9). Only the morphologically peripheral GG's for each subspecies are indicated. GG's 74 and 89 were outliers.

miradorensis; GG 105, *fuscus* to *miradorensis*. Fig. 2 shows the revised subspecies boundaries. The corresponding plot of principal component scores for the continental subspecies shows greatly reduced overlap between *pallidus* and *fuscus* and *bernardinus* (Fig. 8). In addition, discrimination between *fuscus* and *miradorensis* is improved. Classification rates were improved in males, increasing by 20% (from 49 to 69%) in *bernardinus* and 24% (from 29 to 53%) in *pallidus* (Table 3). Male *miradorensis* as well as female *fuscus, miradorensis,* and *pallidus* all improved slightly. The only losses of discrimination were a 3% drop in female *bernardinus* and a 2% drop in male *fuscus*. The complete classification results produced by the final discriminant analyses are given for males and females in Tables 4 and 5. For males, four significant discriminant functions were extracted and 11 of the 12 eligible variables were entered in order of decreasing discriminating ability as follows: MS, DB, FA, IO, RB, HC, MX, ON, MN, PP, and M5 (M3 was not used). Six significant functions were obtained for females and

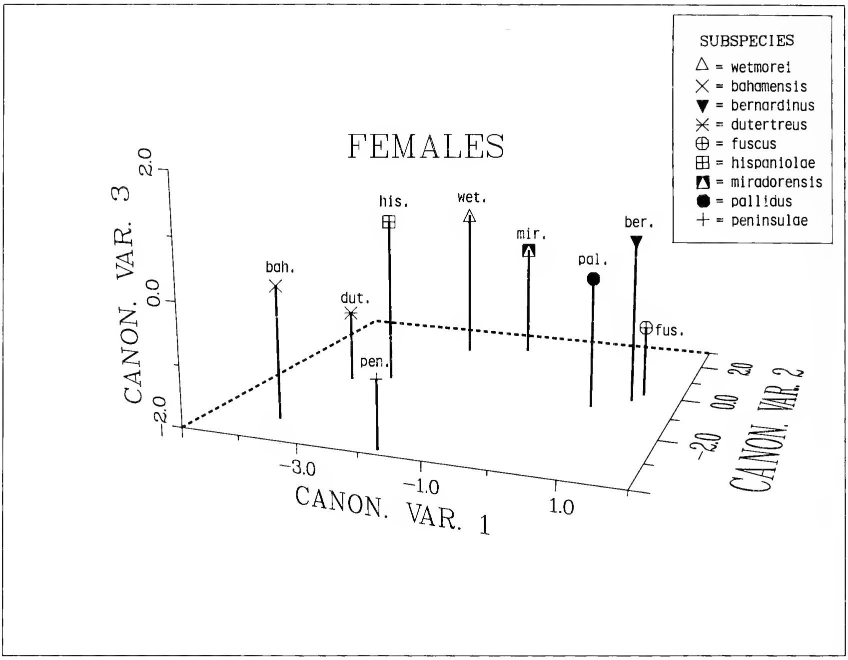

Fig. 9.—Plot of the female group centroids of nine subspecies of *Eptesicus fuscus* on the first three canonical variate axes.

Table 4.—*Classification results of discriminant function analysis on six subspecies of male* Eptesicus fuscus.

		Predicted group membership					
Group	Cases	*baham-ensis*	*bernar-dinus*	*fuscus*	*mira-dorensis*	*pal-lidus*	*penin-sulae*
bahamensis	18	18 100%	0 0%	0 0%	0 0%	0 0%	0 0%
bernardinus	121	0 0%	83 69%	21 17%	5 4%	12 10%	0 0%
fuscus	179	0 0%	23 13%	143 80%	5 3%	8 5%	0 0%
miradorensis	105	0 0%	4 4%	4 4%	93 89%	4 4%	0 0%
pallidus	79	0 0%	14 17%	18 23%	2 3%	42 53%	3 4%
peninsulae	23	1 4%	0 0%	0 0%	0 0%	0 0%	22 96%

Percent of "grouped" cases correctly classified: 76.38%

all 12 variables were entered into the analysis in the following order: MS, DB, RB, FA, IO, HC, MX, ON, PP, MN, M3, and M5.

The degree of differentiation among subspecies is summarized by plotting the group centroids of each subspecies on the first three canonical variate axes (Fig. 9). The most distinct populations are the very small subspecies from Baja California (*peninsulae*) and the Bahamas (*bahamensis*). The Antillean subspecies (*dutertreus, hispaniolae,* and *wetmorei*) are also well differentiated, and it is interesting to note that their relative positions in morphological space reflect their geographic locations. The tight clustering of the four continental subspecies (*fuscus, pallidus, bernardinus,* and *miradorensis*) reflects their high degree of morphological overlap relative to the insular and peninsular subspecies.

DISCUSSION

Sexual Dimorphism

Attempts to explain sexual dimorphism have usually invoked the concepts of sexual selection (Darwin, 1859; Trivers, 1972) or niche partitioning (Selander, 1966; Wilson, 1975). It has been argued recently, however, that for mammals the most common selective pressures favoring large size in females are related to several aspects of reproductive physiology (Ralls, 1976). As one of the mammalian taxa in which females are often larger than males, vespertilionid bats provide a suitable group for investigating Ralls' "big mother" hypothesis. Indeed, two alternative theories have been proposed to explain the advantages of larger female size in the Vespertilionidae since Ralls' review paper.

Myers (1978) proposed that sexual size dimorphism in vespertilionid bats is related to the extra mass females carry during pregnancy and lactation. Specifically, he proposed reduction of the proportionate load of the fetus(es), reduction of the relative cost of producing milk, and an increase in the quantity of ingested insects females can carry as the advantages of large size in female bats. Myers made two predictions based on this wing-loading hypothesis: 1) a greater degree of sexual dimorphism should be found in females carrying or feeding a greater mass of fetal tissue or young, and 2) if males and females had the same body size, female wings would still be larger than male wings.

I tested the first prediction by comparing the degree of dimorphism in groups of *E. fuscus* with litter sizes of one versus groups with litter sizes of two. The embryo data I obtained from specimen labels agree with previous accounts describing the litter size of *E. fuscus* as two in eastern and one in western North America (Cockrum, 1955; Kunz, 1974). I used GG's 4–38 to represent the west and GG's 48–83 to represent the east, omitting GG's with questionable or variable litter sizes. Following Myers (1978), I used the difference between average

Table 5.—*Classification results of discriminant function analysis on nine subspecies of female* Eptesicus fuscus.

		Predicted group membership								
Actual group	No. of cases	*wetmorei*	*bahamensis*	*bernardinus*	*dutertreus*	*fuscus*	*hispaniolae*	*miradorensis*	*pallidus*	*peninsulae*
wetmorei	17	8 47%	0 0%	0 0%	0 0%	0 0%	0 0%	9 53%	0 0%	0 0%
bahamensis	31	0 0%	30 97%	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	1 3%
bernardinus	169	0 0%	0 0%	123 73%	0 0%	24 14%	0 0%	2 1%	20 12%	0 0%
dutertreus	16	0 0%	0 0%	0 0%	13 81%	0 0%	2 13%	1 6%	0 0%	0 0%
fuscus	141	0 0%	0 0%	29 21%	0 0%	91 65%	0 0%	9 6%	12 8%	0 0%
hispaniolae	11	0 0%	0 0%	0 0%	0 0%	0 0%	11 100%	0 0%	0 0%	0 0%
miradorensis	144	5 4%	0 0%	5 4%	0 0%	3 2%	0 0%	130 90%	1 1%	0 0%
pallidus	105	0 0%	1 1%	38 36%	0 0%	19 18%	0 0%	7 7%	35 33%	5 5%
peninsulae	16	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	16 100%

Percent of "grouped" cases correctly classified: 70.31%

Table 6.—*Results of covariance analyses for secondary sexual dimorphism of forearm length (adjusted by occipitonasal length) in selected geographic groups of* Eptesicus fuscus. *Significance levels:* *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; *N.S.*, $P > 0.05$.

Subspecies (GG)	Adjusted FA (N) in mm		Equality of slopes	Equality of adjusted means
	Male	Female		
bernardinus (4)	47.0 (29)	48.5 (22)	N.S.	***
bernardinus (7)	46.0 (23)	46.5 (42)	N.S.	N.S.
bernardinus (8)	46.2 (16)	47.8 (18)	N.S.	*
bernardinus (11)	46.8 (16)	47.1 (23)	**	N.S.
bernardinus (13)	46.4 (28)	47.3 (28)	N.S.	N.S.
pallidus (16)	45.2 (27)	46.4 (18)	N.S.	*
pallidus (17)	44.7 (19)	45.1 (25)	N.S.	N.S.
pallidus (29)	47.5 (47)	47.5 (27)	N.S.	N.S.
pallidus (30)	47.6 (30)	47.1 (25)	N.S.	N.S.
pallidus (32)	46.9 (25)	47.6 (26)	*	N.S.
pallidus (37)	45.0 (24)	45.5 (36)	N.S.	N.S.
pallidus (102)	45.5 (26)	46.8 (26)	*	**
pallidus (103)	46.6 (23)	47.2 (23)	N.S.	N.S.
fuscus (41)	45.8 (22)	47.2 (32)	N.S.	**
fuscus (59)	44.8 (33)	45.5 (24)	N.S.	N.S.
fuscus (61)	45.6 (34)	46.4 (34)	*	*
fuscus (75)	44.6 (36)	45.3 (37)	N.S.	N.S.
fuscus (82)	44.6 (23)	45.0 (36)	N.S.	N.S.
peninsulae (101)	41.9 (23)	42.3 (19)	N.S.	N.S.
miradorensis (108)	48.1 (20)	48.6 (22)	N.S.	N.S.
bahamensis (125)	44.7 (25)	44.8 (30)	N.S.	N.S.
dutertreus (126)	45.5 (10)	47.0 (14)	N.S.	*
Overall means	46.5 (93)	46.8 (39)	N.S.	*
Overall PC1W, PC1S	−0.3 (93)	−0.1 (93)	N.S.	***

female and male forearm lengths to measure "degree of dimorphism." Using a one-tailed Mann-Whitney *U*-test (Siegel, 1956), the degree of dimorphism in *E. fuscus* proved to be significantly greater in the east ($\bar{X} = 1.25$, $N = 29$) than in the west ($\bar{X} = 1.01$, $N = 30$, $U = 329.0$, $P = 0.05$) in agreement with Myers' first prediction.

To test Myers' second prediction, I used covariance analysis (Kleinbaum and Kupper, 1978) to "remove" the effect of body size and to test for the significance of the remaining difference between the "adjusted" mean male and female forearm lengths. Occipitonasal length (ON), the character with the highest loading on the first principal component of skull variation (Table 2), was used as the body size covariate. The results of these analyses (Table 6) showed the adjusted means for females to be significantly larger in seven of the 22 GG's tested. In two of these cases, however, the assumption of equality of slopes was violated. Adjusted "wing size" was also significantly greater in females using univariate (FA adjusted by ON) and multivariate (PC1W ad-

Table 7.—*Spearman rank-order correlations between degree of sexual dimorphism in wing and skull size in* Eptesicus fuscus *and climatic variables. Significance levels:* *, $P < 0.05$; **, $P < 0.01$; *all others,* $P > 0.05$.

Climatic variable	N	Wing (♀PC1W-♂PC1W)	Skull (♀PC1S-♂PC1S)
Mean annual temperature	93	0.10	−0.13
Mean January temperature	93	0.03	−0.20*
Mean July temperature	93	0.07	0.02
Mean daily maximum temperature, January	87	−0.07	−0.26**
Mean daily maximum temperature, July	87	−0.01	−0.07
Mean daily minimum temperature, January	87	0.07	−0.16
Mean daily minimum temperature, July	87	0.20*	0.04
Length of freeze-free period	93	0.03	−0.18*
Actual evapotranspiration	93	0.23**	0.09
Mean annual precipitation	93	0.19*	0.06
Mean relative humidity, January	89	0.24**	0.11
Mean relative humidity, July	89	0.20*	0.00

justed by PC1S) GG mean data. Thus, limited support was found for Myers' second prediction.

Williams and Findley (1979) found weaker support for these predictions in their data than did Myers. Williams and Findley found adjusted forearm length to be greater in males for the New Mexico sample they studied. This "reverse" dimorphism was also observed in my New Mexico sample, GG 30 (probably the same specimens used by Williams and Findley), but this GG is not representative of the species as a whole.

Williams and Findley (1979) proposed that the primary factor selecting for larger body size in female vespertilionids is the greater energetic efficiency of larger body size in maintaining homeothermy during gestation. I interpret their hypothesis to predict a greater degree of sexual dimorphism favoring larger females where cold stress during the gestation period is greater. Because it is difficult to determine the operative environmental temperatures (Bakken, 1976) to which bats are actually exposed even where detailed roost temperature data are available (Burnett and August, 1981), a rigorous test of Williams and Findley's hypothesis is not possible. Nevertheless, I correlated the degree of wing and skull dimorphism with 12 climatic variables because of the general importance of bioclimatic trends (Table 7).

Skull dimorphism was significantly, negatively correlated with three of the temperature variables, indicating relatively larger females where temperatures are colder. Significant positive correlations between wing dimorphism and the four moisture variables were found and may be due to sexual differences in roosting sites. In arid regions, any wing-loading advantage which females obtain from larger wings may be offset by excessive evaporation. Males should be less subject to moisture stress because their roosting sites are probably cooler (Barbour and Davis, 1969).

The occurrence of geographic variation in the social organization of several species of bats (Bradbury, 1977) suggests another set of factors with potential for affecting sexual dimorphism. For example, in low latitude, nonhibernating populations, it may be possible for male *E. fuscus* to obtain sole mating access to females. Perhaps sexual selection is the cause of dimorphism favoring males at low latitudes.

My results do not resolve the question of which selective forces, if any, are most important in causing sexual dimorphism, but they do encourage further investigation of both the wing-loading and thermoregulation hypotheses. More importantly, the demonstration that the degree and even the direction of dimorphism in *E. fuscus* are geographically variable constitutes a strong warning that generalizations derived from geographically limited data are unwarranted.

Geographic Variation and Subspecies Discrimination

To compare the variation of wing and skull character complexes, I used Mantel's Z statistic to test the degree of association between the first principal components of wing and skull variation for each sex. The phenetic distance matrices of PC1W and PC1S did not depart significantly from a random association with each other for either sex (males: $t = 1.385$, $P > 0.10$; females: $t = 0.760$, $P > 0.15$), emphasizing that there is no relationship between the geographic patterns of wing and skull variation in *E. fuscus.* These results suggest that different causal factors are responsible for regional trends in these two functional complexes. The variable chosen to represent "size" in *E. fuscus* will thus have an important influence on the outcome of ecological and evolutionary interpretations regarding body size (Burnett, 1983).

The problem of describing intraspecific variation in *E. fuscus* is complicated by the high degree of morphological overlap between *pallidus* and adjacent subspecies. While the overall rates of correct classification using the revised subspecies boundaries are 76 and 70% for males and females, the corresponding rates for *pallidus* are 53 and 33% (Table 3). Considering differentiation between *pallidus* and *fuscus* first, the greatest morphological overlap occurs between the *pallidus* groups 34–38, and the geographically distant *fuscus* groups, 63, 73, 76, and 77 (Figs. 2 and 8). Conversely, the *fuscus* groups geographically closest to *pallidus* (39–42, 44, and 48) are morphologically distinct from neighboring *pallidus.* The boundary between *pallidus* and *fuscus* is, thus, a morphologically abrupt one. A more gradual transition appears to exist between *pallidus* and *bernardinus,* where there is a tendency for the geographically closer groups of the two species to be morphologically similar. The transition between *pallidus* and *miradorensis* is part of a long cline along the eastern edge of the range of *pallidus* which includes geographic groups 34, 32, 31, 47, 104, and 105 (Figs. 2 and 8). Just to the west, however, a sharp transition occurs between groups 103 and 104. Another sharp break occurs between the *pallidus* groups 16 and 17, followed by a long cline of decreasing size along Baja California to *peninsulae* (Fig. 7). *E. fuscus peninsulae* is restricted to Baja California Sur and is easily distinguished from *pallidus* of northern Baja California by its extremely small size. In sum, the geographically central position of *pallidus* is reflected in its morphologically central position. The high rates of misclassification obtained for it, however, can be attributed to morphological convergence with geographically distant populations as well as to clinal transitions to adjacent subspecies in several areas.

After *pallidus,* the continental subspecies with the lowest classification rates is *bernardinus,* with 69% of the males and 73% of the females being classified correctly (Table 3). This subspecies was most often confused with *fuscus,* despite the great geographic distance between the nearest populations. Few specimens were available from the Great Basin and Columbia Plateau regions where *bernardinus* meets *pallidus,* but the fact that the geographically closest pair of these subspecies (GG's 7 and 13) are morphologically similar (Fig. 8) suggests a gradual transition between these subspecies.

Overlap between the eastern subspecies, *fuscus,* and *pallidus* was described above. Conclusions about the nature of the boundary between *fuscus* and *miradorensis* are prevented by the lack of specimens from southern Texas, but the morphologically most similar groups are geographically closest, suggesting a gradual transition. Because few intact specimens were available from the area mapped by Hall (1981) as the Florida subspecies, *osceola,* I pooled specimens from this area with those from the coastal plains of Georgia and South Carolina. Despite pooling, this geographic group (GG 68) was morphologicaly distinct from *fuscus* (Fig. 7). Unfortunately, sample sizes were still too small to include the *osceola* samples in the discriminant analyses.

In *miradorensis,* males and females were correctly classified in at least 90% of the cases analyzed (Table 3). Variation within this subspecies forms a cline of increasing wing and skull size from Mexico to Honduras. The samples from Costa Rica/Panama indicate a slight reversal of the trend, and the few specimens available from Colombia suggest that wing size decreases slightly but that skull size continues to increase into South America.

Of the four insular subspecies from the Caribbean for which I had sufficient data, all were well differentiated from each other. The subspecies from New Providence and adjacent islands, *bahamensis,* was correctly classified in 100% of the male and 97% of the female cases (Table 3). One female specimen was placed in the Baja California subspecies, *peninsulae* (Table 5), which resembles *bahamensis* in its very small size. Specimens from Bahamian islands other than New Providence were assigned to the Cuban subspecies, *dutertreus,* by Koopman et al. (1957), but I pooled the specimens from all the Bahama Islands in the discriminant analyses.

My sample of *dutertreus* was confused with the neighboring *hispaniolae* in 13% of the cases and with mainland *miradorensis* in 6% of the cases (Table 5). Silva Taboada (1979) found no significant differences in forearm or occipitopremaxillary lengths within samples of *dutertreus* from western, central, and eastern Cuba. He did, however, find highly significant differences between the pooled samples from Cuba and the small subspecies, *petersoni,* from nearby Isla de Pinos.

The subspecies from Hispaniola, *hispaniolae,* was correctly classified 100% of the time, but the Puerto Rican subspecies, *wetmorei,* was misclassified as mainland *miradorensis* in 53% of the cases (Table 5). In their review of the zoogeography of Antillean bats, Baker and Genoways (1978) argued that *E. fuscus* colonized the Antilles from the west, either from the Yucatan peninsula or the Central American mainland. If this dispersal hypothesis is correct, the observed pattern of morphological variation strongly suggests that reduced gene flow has not been the dominant cause of insular differentiation. This is because morphological distance from the mainland subspecies decreases with increasing geographic distance eastward across the archipelago (Figs. 7 and 9, Table 5). If reduced gene flow was the dominant differentiating force, morphological and geographic distances should be directly, rather than inversely, related. Considerable difference of opinion exists, however, regarding the complex historical biogeography and geology of the Caribbean islands (Pregill, 1981; MacFadden, 1981). Interpretation of variation among the insular subspecies should, therefore, not rule out other biogeographic scenarios. For example, the large size of *Eptesicus guadeloupensis* (Genoways and Baker, 1975), coupled with its possible origin from the northern coast of South America (Baker and Genoways, 1978), suggests a route of dispersal that is consistent with a gene flow model of differentiation among Caribbean *Eptesicus.* The possible importance of selective factors in differentiation among insular subspecies of *E. fuscus* is discussed in a companion paper (Burnett, 1983).

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APPENDIX I

SUMMARY OF SPECIMENS EXAMINED

The number of specimens examined are enclosed in parentheses following the collection numbers and their acronyms (Choate and Genoways, 1975).

1. UAMZ (21)	2. UBC (37)	3. BCPM (28)	15. NMC (66)
17. ROM (107)	22. ENCB (36)	25. UAMC (30)	32. MNA (50)
33. NAU (22)	37. UA (54)	38. ASUZC (88)	41. CAS (100)
58. SDSNH (41)	64. MVZ (372)	68. UCLA (56)	75. UCM (35)
78. UCONN (80)	79. DMNH (40)	81. USNM (361)	82. ABS (1)
84. AS (57)	85. TTRS (10)	86. FSM (27)	91. FMNH (72)
96. UIMNH (235)	98. JMM (81)	99. ISU (33)	107. UNI (8)
108. MHP (60)	115. KU (565)	120. UKEN (41)	122. LSUMZ (21)
144. MSU (42)	148. UMMZ (126)	155. MMNH (34)	157. FACM (40)
162. MOU (50)	170. VMKSC (38)	171. UNSM (41)	177. DCM (15)
178. UNHP (6)	184. MSB (228)	186. AMNH (194)	188. CU (24)
191. NYSM (12)	195. NCSU (6)	200. CMNH (65)	209. OSU (90)
211. OU (13)	219. CM (144)	221. ANSP (47)	238. MWU (26)
245. TCWC (147)	248. TTU (62)	252. MALB (45)	259. UU (37)
274. UPS (183)	276. WWC (12)	279. WVMSC (18)	281. MPM (6)
283. UWZM (21)	285. UWSP (26)	This study (158)	Total = 4,791

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RESOURCE EXPLOITATION IN AMAZONIA: ETHNOECOLOGICAL EXAMPLES FROM FOUR POPULATIONS

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Abstract

Delineation of Amazonian ecological typologies has become more sophisticated as research in the region progresses. Scientific understanding of Amazon ecosystems, however, is still regarded as far from sufficient. Existing ecological typologies of the Amazonian biome are discussed and evaluated and examples of ethnoecological knowledge systems from four Amazon populations are presented. It is suggested that folk knowledge systems represent an important source of information for scientists concerned with typology elaboration and for planners interested in the formation of development strategies. It is concluded that there exists an urgent need for further ethnoecological investigations of indigenous populations in Amazonia.

Introduction

The development of the Amazon region of South America, particularly within the Brazilian portion of Amazonia, has progressed at a

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rapid rate since 1970. Interest in, and enthusiasm for, the development of the region has been prompted more by extra-regional economic imperatives than by specific information regarding the region's resource base. Development policies and programs for the Amazon region have been designed and implemented despite a general consensus among scientists that our understanding of Amazon ecosystems (both macro and micro) is far from sufficient. This paper will briefly outline existing ecological typologies employed by researchers in their investigations of the Amazon Basin, suggest some limitations associated with these typologies, and present specific examples (drawn from four ethnoecological investigations) of indigenous (Amerindian and *caboclo*) concepts of ecological zones and ecosystemic relationships within zones.

Ethnoecology has been defined as the study of indigenous perceptions of natural divisions in the biological world and of plant-animal-human relationships within these divisions (Posey, 1981). These cognitively defined ecological categories do not exist in isolation; thus, ethnoecology must also deal with the perceptions of interrelatedness between, as well as within, "natural" divisions. The study of natural phenomena by means of ethnoecological analysis has proven to be a rich source of ecological data that is directly relevant to modern development strategies and planning (Brokensha et al., 1980; Posey, 1983). The principal purpose of this paper is to demonstrate that indigenous and folk perceptions of the environment constitute a grossly underutilized source of information about Amazonia, and that modern science and traditional knowledge must be linked if we are to ensure rational (and sustainable) development and productivity in the Amazon Basin.

THE SETTING

The Amazon Basin (Amazon region, Amazonia) encompasses an area roughly 7,000,000 km^2 in size within which is found the largest tract of tropical rainforest in the world. It has been estimated that 20 percent of the Amazon's 557 million ha of rainforest has already been destroyed (UNESCO, 1978:22). In the Brazilian Amazon alone, approximately 100,000 ha are being cleared annually (Barbira-Scazzocchio, 1980:iii). The extent and rapidity of such deforestation has initiated a cycle of soil compaction and erosion, the destruction of nutrient cycles, and flooding (Sioli, 1973:323; Gentry and Lopez-Parodi, 1980; Moran, 1981:4). The resulting water pollution, with its associated changes in pH, suspended and dissolved loads, and turbidity, reduces riverine productivity and threatens aquatic life (Schubart, 1977; Lovejoy and Schubart, 1981:21). Species endangerment and extinctions resulting in large part from habitat destruction very likely will become a regular feature of the ecological reality of Amazonia. Indeed, Gottlieb

(1981:23) has estimated that 90 percent of the natural inventory of organisms will become extinct before even basic genetic and taxonomic descriptions can be made.

Human populations in Amazonia have suffered significantly from efforts to develop and "conquer" the region. Entire Amerindian groups have been eliminated (Indigena, 1974; Davis, 1977); in just the last 75 years, at least 87 Amerindian groups have become extinct in the Brazilian portion of Amazonia alone (Ribeiro, 1970:238). *Caboclos,* the rural peasantry of Amazonia, have experienced tremendous change resulting from the direct and indirect effects of development including the disruption and breakdown of village life, destruction of subsistence systems, and pernicious poverty (Parker, 1981). Where development has penetrated directly into traditional *caboclo* areas, the local residents have frequently been labelled squatters, expelled (often forcibly) from the lands they have worked decades if not generations, and forced into dependency relationships in *favelas* and cities (Velho, 1972; CNBB-CEP, 1976; Pinto, 1977; Wood and Schmink, 1979).

With the extinction of each indigenous population and the destruction of each *caboclo* community, humanity loses a priceless accumulation of practical knowledge about life in, and adaptation to, tropical ecosystems. The significant human and ecological price paid for Amazonian development has yielded few rewards; most development projects remain viable primarily because they continue to receive government subsidies (Goodland, 1975:40; Mahar, 1979). The Brazilian government has encouraged, and often supported through a variety of incentives, immense development projects (for example, the Jari silviculture effort in northeastern Amazonia), but almost without exception they have failed to generate anticipated profits. For example, roughly 85 percent of the recently established cattle ranches in the Paragominas region of the Brazilian state of Pará are already unproductive due to pasture degradation (Hecht, 1981:96).

One underlying cause for the difficulties that have beset "modern" development in Amazonia has been a tendency among observers to generalize about the ecology of the region. Amazonia has too often been viewed as a region of vast homogeneous landscapes. Ironically, these perceptions of Amazonian homogeneity have yielded diametrically opposed schools of thought regarding the development of the region. On the one hand, Amazonia is seen as an enormous "counterfeit paradise" in which development threatens the fragile balance of the Amazon rainforest ecosystem (for example, Meggers, 1971; Goodland and Irwin, 1975). The opposing school views Amazonia as a vast region of untold resource wealth, its sheer size and homogeneity (in terms of the rainforest ecosystem) the best argument against those who fear that significant, and/or irreversible, damage will result from development activities (for example, Rebelo, 1973; Pandolfo, 1978; Schmithusen, 1978). While the propensity to view the Amazon as a homogeneous landscape is understandable given the assumed isomorphism between the region and the humid rainforest, it nevertheless overlooks the fact that it is an incredibly diverse region with numerous ecological and micro-ecological zones.

Western science has become increasingly sophisticated in its understanding of the complexity of Amazonian ecology, but indigenous and folk knowledge systems are still generally ignored as sources of valuable ecological information. Recent publications by Brokensha et al. (1980) and Klee (1980) provide evidence, from a worldwide perspective, of the importance and applicability of indigenous knowledge systems in modern development planning and program assessment. Indigenous ecological knowledge can offer important lessons for sustained productivity in Amazonia. Unfortunately, sustainability has not been a feature of development programs in contemporary Amazonia.

AMAZONIAN ECOLOGICAL TYPOLOGIES

Broad scale scientific interest in the Amazon region only began during the last century; consequently, ecological typologies are of rather recent vintage. Early classificatory descriptions of Amazonia were, to say the least, very general. Wissler (1917) simply classified all of the Amazon Basin surrounded by the Brazilian and Guiana shield complexes under the general label "manioc area" (cited in Moran, 1981:7). Steward's seven volume *Handbook of South American Indians* (1946–59), a standard reference, grouped the myriad Amerindian groups together under the category "tropical forest cultures" and described much of the Amazon region and its inhabitants as "marginal," with little or no evidence of "advanced" agriculture or civilization.

The degree of generalization employed in ecological descriptions of Amazonia remained, for the most part, unchanged until the middle of the present century. Beginning around 1950, and continuing until quite recently, researchers have predicated their discussions of Amazonian ecology upon the distinction between *terra firme* and *várzea* environments (De Carmargo, 1949; Wagley, 1953; Denevan, 1966; Lathrap, 1970; Meggers, 1971; Sternberg, 1975). The *terra firme,* lowlands of Amazonia not subject to inundation, constitute about 98 percent of the Amazon Basin. The *várzea* (floodplain) is estimated to cover no more than 2 percent of Amazonia. The importance of the *terra firme–várzea* dichotomy is directly related to the commonly held belief that the soils of the *terra firme* are extremely impoverished and thus incapable of sustaining intensive agriculture without massive capital inputs. The *várzea,* on the other hand, is perceived as an important ecological zone and potential development area due to its annual rejuvenation that results from flooding and subsequent deposition of nutrient-rich sediments. Though the distinction between these two landscapes is a logical one, it nevertheless is of only marginal utility in the elaboration of ecological typologies because it treats vast areas as undifferentiated landscapes.

Denevan (1976), unsatisfied with the *terra firme–várzea* division, was one of the first researchers to attempt, systematically, a detailed typology of the Amazonian biome. He proposed a classification system in which six categories were articulated: (1) humid forest; (2) seasonal forest; (3) montane forest; (4) dry savanna; (5) wet savanna; and (6) floodplain. Despite this improvement in typological detail, it should be noted that the humid (tropical) rainforest was still treated as a homogeneous entity. Pires (1974) has identified two types of *terra firme* humid forest—*mata pesada* (mature upland forest) and *mata de cipó* (liana forest). Prance (1979) has recognized three categories of humid *terra firme* forest in his classification system of Amazon vegetation: (1) high forest with large biomass; (2) liana forest; and (3) low forest with reduced biomass.

The treatment accorded the *várzea* landscape is illustrative of the fledgling nature of ecological typologies developed for the Amazon region. Early descriptions divided the floodplain into two categories—"*várzea*" was employed for areas that only experienced seasonal inundation, whereas "*igapó*" was used to denote permanently inundated areas (De Carmargo, 1949; Lima, 1956). This scheme prevailed until Sioli (1967, 1975*a*) suggested a more detailed description of floodplain structure in which the principal elements were: (1) main river; (2) natural levees (*restingas*); (3) channel islands; (4) *paranás* (side channels); (5) floodable grasslands; (6) *várzea* lakes; (7) sand bars (point, convex, barranco); and (8) *igapó* (back swamps). Although Sioli specifically developed this structural scheme for the lower Amazon floodplain, it has often been employed by others as a standard description for all floodplain areas in Amazonia. Parker (1981) has demonstrated the need for further articulation of floodplain typology due to significant variations in fluvial dynamics found within and among floodplain zones in Amazonia. *Caboclos,* the principal inhabitants of floodplain environments in contemporary Amazonia, recognize four different types of *várzea* based upon the source (cause) of flooding: (1) *várzea de chuva* (rain); (2) *várzea de rio* (river); (3) *várzea de maré* (tidal); (4) *várzea de mar* (sea) (Sombroek, 1966).

Geochemical investigations of fluvial environments within Amazonia have identified three distinct types of rivers—white-water, black-water, and clear-water (see Gibbs, 1967, and Sioli, 1968, for further discussion). This differentiation of river types has contributed to considerable terminological confusion in ecological typologies of the *vár-*

zea, particularly with regard to the use of *igapó.* While some observers (Irmler, 1977; Sioli, 1975*b*; Smith, 1981) have limited the use of "*igapó*" to black-water areas (regardless of the duration of flooding), others have applied it to both clear- and black-water areas (Pires, 1974; Sioli, 1975*a*). Sioli (1975*a*:212) has also used *igapó* to refer to the permanently flooded *terra firme* side of *várzea* lakes. The issue is yet further complicated by the fact that *igapó* is still employed by some observers to denote permanently flooded areas (Sternberg, 1975:18).

Prance (1979), in an effort to reduce the confusion, has suggested a biogeographical classification of inundated areas that includes: (1) seasonal *várzea*—forest flooded by regular annual cycles of white-water rivers; (2) seasonal *igapó*—forest flooded by regular annual cycles of black- and clear-water rivers; (3) mangrove—forest flooded twice daily by salt-water tides; (4) tidal *várzea*—forest flooded twice daily by freshwater backed up by tides; (5) floodplain forest—forest irregularly flooded by rainfall; (6) permanent white-water swamp forest; and (7) permanent *igapó,* or black-water forest. Parker (1983) has noted that this classification scheme may foster additional confusion because it only deals with inundated areas that are covered by forest—an important feature of the middle and lower Amazon floodplain, as well as portions of the estuarine floodplain, is that they contain extensive areas covered by grasses (Lima, 1956; Fittkau et al., 1975; Sioli, 1975*a,* 1975*b*; Sternberg, 1975; Smith, 1981).

It is evident from the foregoing discussion that progress is being made in our understanding of, and appreciation for, the ecological heterogeneity of Amazonia. Knowledge of ecosystem structures and dynamics continues to be enhanced as research results are made available (Denevan, 1982; Hecht, 1982). However, it is our belief that the extent of ecological/biological heterogeneity in the Amazon region cannot be fully appreciated without consideration and scientific investigation of folk knowledge systems of Amazonian peoples. Recent investigations by such researchers as Reichel-Dolmatoff (1976, 1978), Smole (1976), Carneiro (1978), Posey (1979, 1981), Vickers (1979), Beckerman (1980), Moran (1981:41–57), Chernela (1982), and Denevan et al., (1982), support this belief by the demonstration of the sophistication, diversity, and richness of folk knowledge about Amazonian flora, fauna, and ecological relationships. The goal of this paper is to provide further evidence in support of the argument that folk knowledge systems are of crucial importance to the development of the Amazon Basin, and that they must be studied and incorporated into scientific and development enterprises in the region.

Following are brief examples of folk ecological knowledge systems derived from investigations of four Amazon communities. Two indigenous societies, the Kayapó of Brazil and the Yekuana of Venezuela, both situated on the *terra firme,* and two *caboclo* communities, Coari in western Amazonia and Limoeiro do Ajuru of eastern Amazonia, both located within floodplain areas (*vârzea*), will be discussed (Fig. 1). Thus, the two major adaptive systems found in Amazonia—Amerindian and *caboclo*—and the two principal geographic landscapes of the region—the *terra firme* and the *vârzea*—are represented.

THE KAYAPÓ: LONG-TERM RESOURCE MANAGEMENT AND SEMI-DOMESTICATION

The Kayapó Indians occupy a two million ha reserve in the Brazilian states of Pará and Mato Grosso do Norte (Fig. 1). The approximately 2500 Kayapó live in nine widely dispersed villages. The discussion presented here is based upon fieldwork conducted in Gorotire, the largest of these villages (Posey, 1979).

Within the territory of the Kayapó, three major environmental divisions are found—*kapôt* (grassland), *krãi* (mountains), and *bà* (forest). Major ecological zones are recognized within each division (Table 1), and within zones a number of discrete ecological categories are further distinguished. Ideally, villages are situated near as many different ecological zones as possible to maximize resource diversity. Near the village of Gorotire, for example, the Kayapó recognize eight major ecological zones and two types of transitional zones (Fig. 2).

Specific plants and animals are associated with each ecological zone. The Kayapó possess an intimate knowledge of animal behavior and know which animals are associated with particular plants. In turn, plant types are linked with soil types. Thus, each ecological zone is an integrated system of plant—animal—soil relationships. Table 2 summarizes selected systemic relationships for one of the major ecological zones of the Gorotire area—the *bà-ràràrà* (natural forest with intermittent openings).

The Kayapó, despite having relatively stationary villages, are nonetheless semi-nomadic, spending 4–5 months away from the village each year. They have evolved an intriguing system of "forest fields" to ensure the availability of foodstuffs during extended periods away from the village. A variety of wild plants, most of which grow naturally in the *bà-ràràrà,* are collected as the Kayapó travel through the forest, and a number of these are replanted near established campsites (usually within defecation areas). At least 54 species of wild plants, the majority of which are tuberous, are used by the Kayapó in this replanting scheme. Posey (1982) has proposed that this replanting in the proximity of campsites is a form of plant semi-domestication. The Kayapó are thus able to obtain adequate food with minimal effort while away from the village by harvesting these "forest fields."

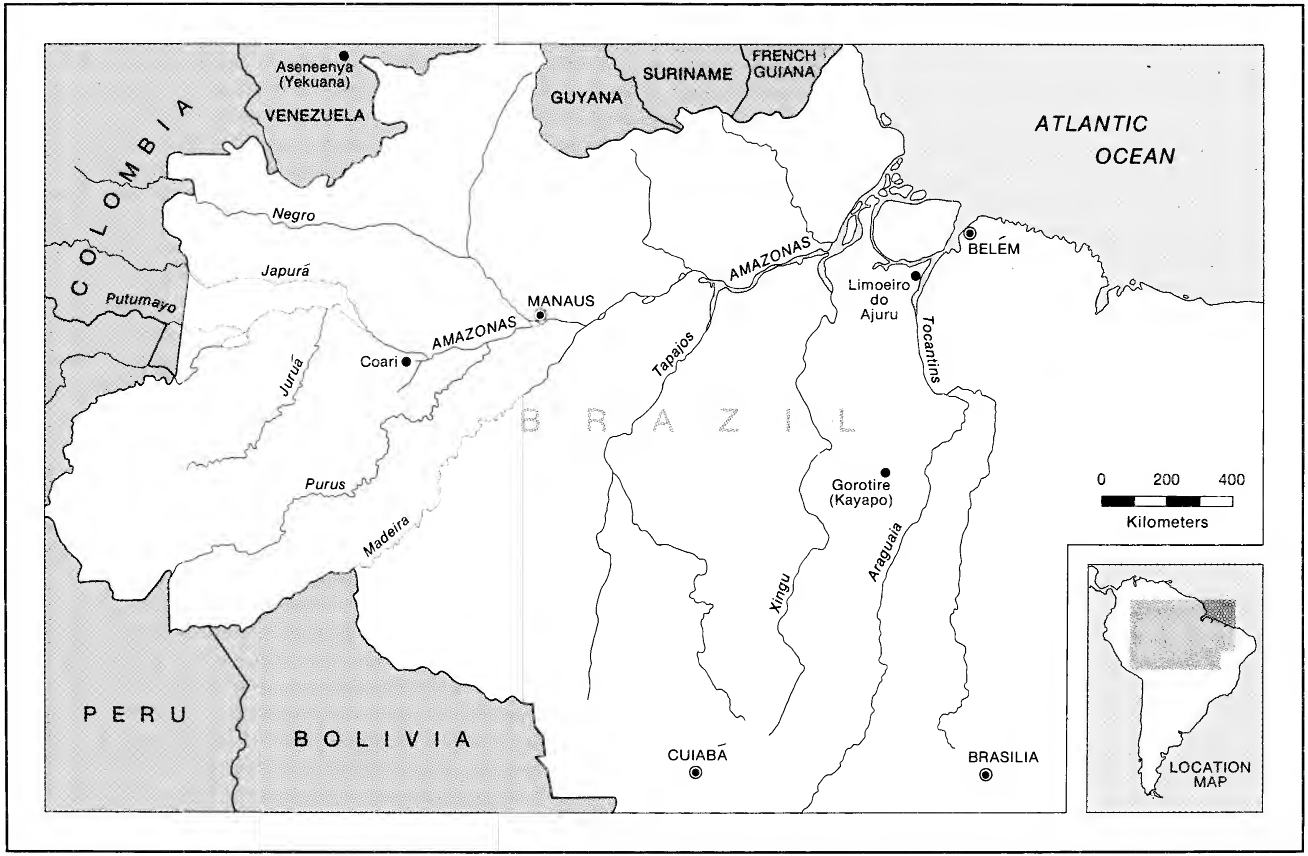

Fig. 1.—Locator map showing the four study areas.

Table 1.—*Major ecological zones recognized by the Kayapó.*

<table>
<tr><th colspan="2">Kayapó designation</th><th></th></tr>
<tr><th>Major zone</th><th>Subzone</th><th>Characteristics</th></tr>
<tr><td>Kapôt</td><td></td><td>grassland, savanna</td></tr>
<tr><td></td><td>Kapôt-kêm</td><td>short grass lands</td></tr>
<tr><td></td><td>Kapôt-kamẽpti</td><td>savanna with tree stands</td></tr>
<tr><td></td><td>Kapôt-kam-bôiprek</td><td>high grass lands</td></tr>
<tr><td></td><td>Pyka-ti |ô| krãi</td><td>savanna with intermittent trees</td></tr>
<tr><td>Krãi</td><td></td><td>mountains</td></tr>
<tr><td>Bà</td><td></td><td>forest</td></tr>
<tr><td></td><td>bà-kamrek</td><td>gallery forest</td></tr>
<tr><td></td><td>bà-êpti</td><td>dense jungle</td></tr>
<tr><td></td><td>bà-kati</td><td>high forest</td></tr>
<tr><td></td><td>bà-ràràrà</td><td>forest with intermittent openings</td></tr>
</table>

The Kayapó folk taxonomic system reveals a preference for "transitional" ecological zones that grade between two or more semantic (named) zones. The village of Gorotire is situated amidst one of these transitional zones which enables the inhabitants to exploit the maximum species diversity that such zones support (Fig. 2). The propensity for a "graded continuum" rather than mutually exclusive ecological categories is also reflected in the Kayapó perception of forest and garden. Abandoned Kayapó gardens are thought to replicate the natural open forest (*bà-ràràrà*) common to the general area. Kayapó slash/burn gardens are never really abandoned as is often assumed of most indigenous agriculturists. Though production from domesticates plunges after two or three years, a variety of plants and fruits continue to be collected—yams and taro for 5–6 years, bananas (*Musa* spp.) for up to 15 years, *urucú* (*Bixa orellana*) for 20 years or more, and *cupa* (*Cissus gongylodes*) for at least 30 years. Old gardens also provide a variety of foods that attract wildlife—for example, *porco do mato* (*Tayassu pecari*), coati (*Nasua nasua*), deer, paca (*Cuniculus paca*), agouti (*Dasyprocta* spp.), and a wide variety of bird species. The Kayapó, aware of the attractiveness of old gardens for wildlife, have purposefully dispersed their gardens so as to effectively manage game populations over a large area. Perhaps of equal importance, plants in the natural reforestation sequence are extremely important sources of medicinals.

The Kayapó also manipulate animals other than mammals. For example, nine species of stingless bees (Meliponidae) have been identified which may be considered semi-domesticates (Table 3). Table 4 lists principal species of Apidae utilized by the Kayapó along with their uses and distinctive traits—these are only a small portion of the total number of bee types recognized by the Kayapó.

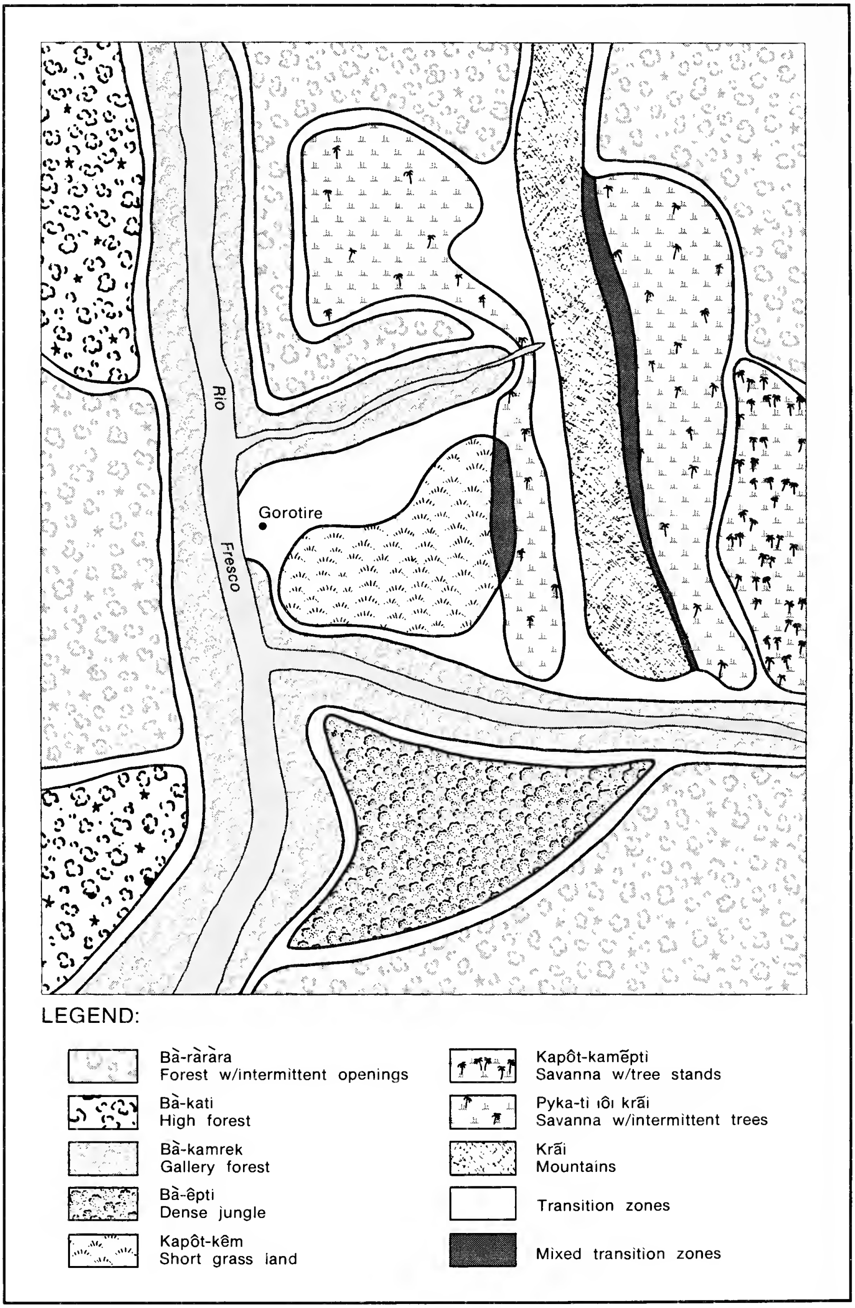

Fig. 2.—Ecological zones surrounding the village of Gorotire as perceived by the Kayapó.

Table 2.—*Selected soil-plant-animal relationships in the bà-ràrà.*

Soil type(s) where plant grows	Plant	Animal(s)[1] associated with plant	Use of plant	
			Animal	Man
black, red	*Humeria balsamifera*	A, B, C, D, E	eat fruit	eat fruit
black, red	*Psidium guinaensis*	F	eat fruit and leaves	eat fruit
yellow	Zinziberaceae	F	eat leaves	use root for tea, smoke leaves
yellow	*Paschieria* sp.			use for paint
red, yellow	*Cataset* sp.			medicinal
red, yellow	Bignonicaceae	C, F	eat leaves	medicinal
black, red, yellow	*Cisampelus* sp.	C, D	eat fruit	fish bait
black	Piperaceae	A, B, C, D	eat fruit	fish bait
yellow	*Amasonia* sp.			prophylaxis
black	*Oenocarpus distichus*	A, B, C, D	eat fruit	eat fruit
black, red, yellow	*Macrostaychia* sp.	H	?	use wood
black, yellow	*Monotagima* sp.	F	eat leaves and roots	grind leaves, eat roots
black, red	*Myrsia* sp.	A, C, D, F	eat fruit and leaves	eat fruit
black, yellow	*Cecropia leucocoma*	H, F	eat fruit and leaves	
red	Paulipodiaceae			medicinal
red	*Clarisia ilicifolia*	F	eat leaves	medicinal
red, yellow	*Centrosema carajaense*			fish poison
red, yellow	*Cassia hoffmanseggii*	C, D, F	eat fruit and leaves	medicinal

[1] A = white lipped peccary.
B = white paca.
C = agouti.
D = tortoise.
E = red paca.
F = red agouti.
G = deer.
H = tapir.

Table 3.—*Semi-domesticated (manipulated) species of Apidae utilized by the Kayapó.*

Kayapó designation	Scientific designation
Ngài-pêrê-ỳ[1]	*Apis millifera*
Ngài-ñy-tyk-ti[1, 2]	*Melipona seminigra cf. pernigra*
Ngài-kumrenx[1, 2]	*Melipona rufiventris flavolineata*
Ngài-re[1]	*Melipona compressipes cf. fasciculata* or *afinis*
mykrwàt[1]	*Frieseomelitta* sp.
udjỳ[1, 2]	*Trigona amlthea*
kukraire[1, 2]	*Trigona dallatorreana*
mehnôrã-kamrek[3]	*Trigona cilipes pellucida*
mehnôrã-tyk[3]	*Scaura longula*

[1] Species whose nests are systematically raided in subsequent seasons.
[2] Species whose nests are taken to the village.
[3] Species that are encouraged to build nests in dry posts in the houses.

Natural resource concentrations ("resource islands") are also known and periodically exploited by the Kayapó. There is an intentional association between resource islands, "forest fields," and campsites, as is revealed in Fig. 3. Visits to "forest fields" and resource islands, other than those prompted by hunting trips, are most often determined by ceremonial cycles.

This brief but representative survey of Kayapó ethnoecological knowledge suggests there is a great deal that both the scientific and developmental communities can learn from the Amerindian about ecological zonation and ecosystemic relationships within and between zones. Furthermore, resource concentrations can be identified, including those intentionally manipulated to increase productivity of semidomesticated plants and wild animal species. The perception of agriculture as part of a natural continuum with the tropical forest is perhaps the most valuable lesson from the Kayapó because of its implications for long-term resource management and utilization of gardens and forest resources.

THE YEKUANA: GARDEN SITE SELECTION AND CONFIGURATION

The Yekuana Indian community of Aseneenya is located in southern Venezuela (Fig. 1) within the broad expanse of *terra firme* that blankets the Guiana Shield (a pre-Cambrian crystalline rock complex covering much of northern Amazonia). While the location of the community is not within the catchment area of the Amazon River, the area is included in general discussions of Amazonian ecosystems, particularly the rain-

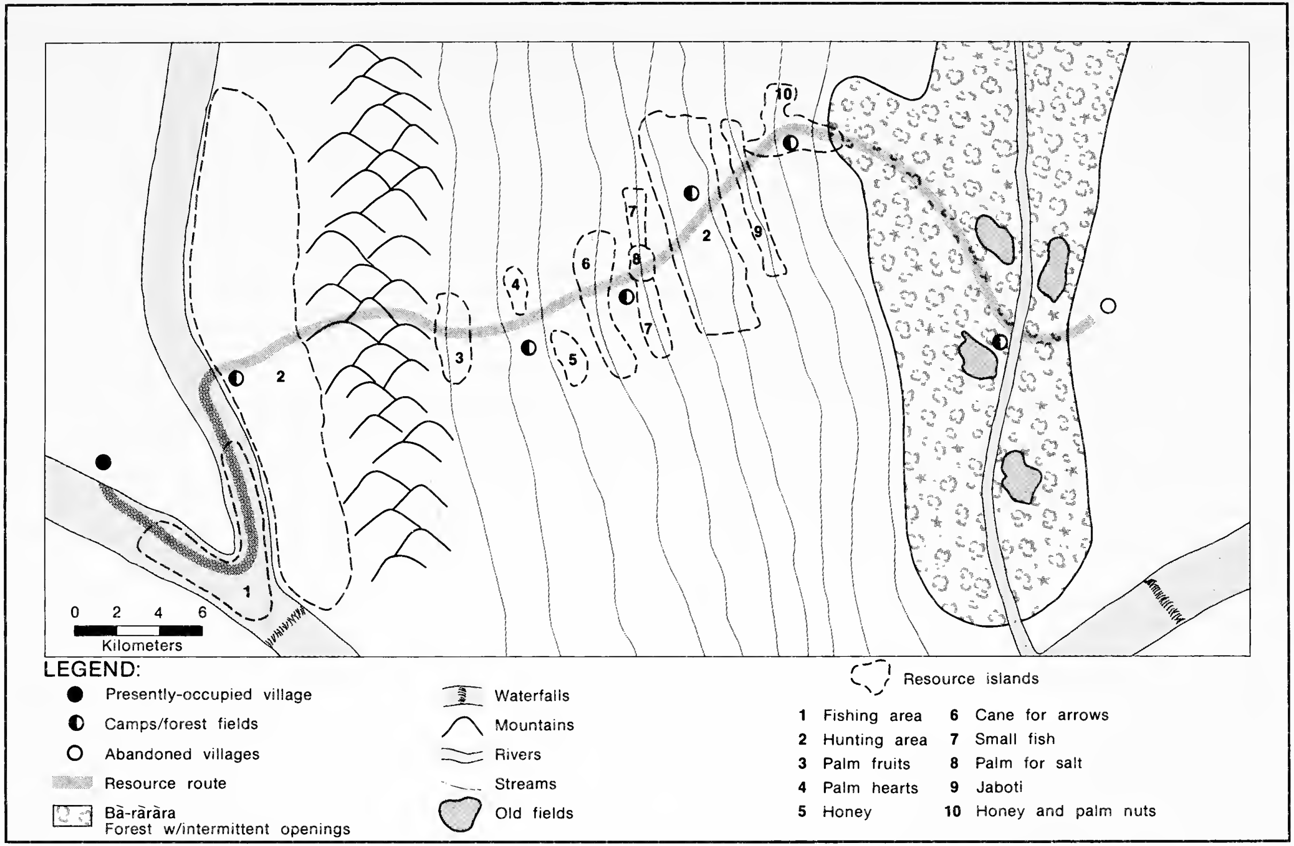

Fig. 3.—Resource islands and campsites associated with "forest fields."

Table 4.—*Principal species of Apidae utilized by the Kayapó.*

		Wax use[1]			Honey availability		Other uses[2]				Aggres-sive-ness[3]	
Kayapó designation	Scientific designation	U	C	M	Season	Amount	LE	PE	POE	RU		Distinctive traits
ngài-pêrê-ỳ	*Apia melligera*	+	+		all year	very much			+		A	honey taken during New Moon
ngài-ñy-tỳk-ti	*Melipona semiligra*	+	+	+	dry	average					B	bee parts used for hunting magic
ngài-kumrenx	*Melipona rufiventris*	+	+	+	all year	average						
ngài-re	*Melipona compressipes*	+	+	+	all year	much						markings like tapir
ngài-kàk-ñy	*Partamona* sp.											wax used in magic
mykrwàt	*Frieseomelitta* sp.	+	+	+	all year	average	+	+	+			
udjỳ	*Trigona amlthea*				dry	average				+		bee parts used for hunting magic
kukraire	*Trigona dallatorreana*				all year	much			+		C	break off limb with nest and run to expel bees
mehnôrà-kamrek	*Trigona cilipes*			+	all year	little				+		eyes like jaguar
mehnôrà-tỳk	*Scaura longula*			+	all year	little				+		used for jaguar hunting magic
kangàrà-krà-kamrek	*Oxytrigona tataira*	+	+	+	all year	average	+	+	+		A	cut tree to take honey
kangàrà-krà-tyk	*Oxytrigona* sp.	+	+	+	all year	average	+	+	+		B	bee causes blisters on skin
kangàrà-udja-ti	*Oxytrigona* sp.	+	+	+	all year	average	+	+	+		A	used in hunting magic
kangàrà-ti	*Oxytrigona* sp.	+	+	+	all year	average	+	+	+		A	
mỳre	*Trigona pallena*	+	+	+	all year	average					C	sometimes fell tree
ngôi-têñk	*Trigona* sp.		+		all year	average						live in termite nests
djô	*Trigona fuscipennis*	+	+	+	all year	little						live in termite hills
imrê-ti-re	*Trigona clinnchamayoensis*				all year	little	+	+	+			live in ant nests

Table 4.—*Continued.*

Kayapó designation	Scientific designation	Wax use[1]			Honey availability		Other uses[2]				Aggres-siveness[3]	Distinctive traits
		U	C	M	Season	Amount	LE	PE	POE	RU		
kukoire-kà	*Partamona* sp.				all year	average					C	nests in termite nests
ϑ'i	*Tetragona* sp.				dry	little						very acidic honey; fell tree
tôn-mỳ	*Tetragona* sp.	+	+	+	dry	average				+		fell tree
ri	*Tetragona* sp.	+	+	+	all year	much				+		bees thought to be "stupid" and weak
mehr-xi-we'i	*Tetragona goettie*	+	+	+	all year	average						found only in Xingu
mènire-udgà	*Tetragona quandrangula*	+	+	+	all year	average						opening of nest like a vagina
mehnôdjành	*Frieseomelitta varia*				dry	little				+		smoke from wax used for curing
mehñykamrek	*Tetragona apinnipea*	+	+	+	dry	little	+	+	+		C	burn wax; smoke causes dizziness
mehñy-tyk	*Tetragona banneri*	+	+	+	dry	little					C	
pyka-kam	*Tetragona fulvivintria*	+	+	+	dry	little				+	C	bee deposits drops of resin on skin

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[1] U = utilitarian.
C = ceremonial.
M = medicinal.

[2] LE = larvae eaten.
PE = pupae eaten.
PEO = pollen eaten.
RU = resin used.

[3] Nests of aggressive bees are raided using smoke and fire to expel bees first.
A = very aggressive.
B = moderately aggressive.
C = slightly aggressive.

forest ecosystem. Often considered an area of relatively poor soils and scarce resources, this *terra firme* zone is successfully exploited by the Yekuana who base their subsistence upon shifting cultivation, hunting, fishing, and gathering.

The Yekuana practice a system of shifting cultivation that includes site selection, forest clearing, burning, cropping, and fallowing (see Fuchs, 1964, and Frechione, 1981:52–92, for more detailed discussions of each of these stages). Like other Yekuana subsistence pursuits, the successful implementation of their cultivation system requires in-depth knowledge concerning microenvironments, natural resources, and ecological relationships. In order to illustrate the nature of this type of knowledge, the criteria employed by the Yekuana in garden site selection, and the subsequent locations and combinations of crops grown within gardens, will be described.

The primary factor influencing the agricultural system of the Yekuana is the sharply defined distribution of annual precipitation. In the Aseneenya area, 90 percent of the annual rainfall occurs between April and October. Garden sites must be selected, cleared, and burned before the onset of the rains or they cannot be cropped that year. A complex classification of edaphic and vegetative characteristics is employed by the Yekuana in selecting garden sites. Knowledge of microenvironments with suitable edaphic and vegetative characteristics is obtained by the Yekuana on frequent hunting and gathering expeditions into the surrounding tropical forest. Discounted as garden sites are the following areas: (1) savanna areas—savanna grasslands do not provide sufficient vegetation for burning, and the soil is difficult to penetrate with digging sticks; (2) *moriche* palm forest—areas with *moriche* palm (*Mauritia flexuosa*) stands are considered "too wet" due to poor drainage; (3) other wet, poorly drained areas in the forest; (4) forest areas located on slopes of more than 45°; and (5) sacred areas used as cemeteries. There are no other sanctions, spiritual or sacred, regarding garden locations; however, if a person is killed during garden-making activities, the garden site cannot be used.

In areas not discounted by the above factors, soil type remains the primary determinant. The Yekuana word for soil, and earth in general, is *nono.* The Yekuana distinguish soil types based upon color and texture. Six soil colors are recognized: (1) *judumato nono*—black soil; (2) *seweichato nono*—red soil; (3) *seweichechato nono*—brown soil; (4) *tajededato nono*—white soil; (5) *seenato nono*—ochre soil; (6) *takajeyato nono*—yellow soil. Four soil textures are noted by the Yekuana. They are: (1) *sadadajato nono*—sandy soil; (2) *ädiñajato nono*—clayey soil; (3) *tajucuidaijiato nono*—rocky soil; (4) *sichuwetöjano nono*—wormy soil.

Another indicator used by the Yekuana in locating favorable garden sites is the composition of the standing vegetation. Indicators of good soil are:

1) *Siñatajano*—an area where a good deal of vines and lianas are present.
2) *Suduchijano*—a forest area where a considerable amount of bamboo is encountered.
3) *Nawöyujano*—an area where the wild plantain is found.
4) *Yadiwömajano*—an area where the *Yadiwöma* tree grows. This is a large tree which is used for making doors, tables, and benches. It grows in both good and poor soils. Hence, it is only a partial indicator of soil quality and it is necessary to consider other variables in areas where *Yadiwöma* grows.
5) *Kariyejano*—an area where the *Kariye* tree grows. It generally indicates soil suitable for musaceous crops.

The existence of a small, running stream is considered favorable when choosing a garden site, especially if it serves to keep the area well-drained. A stream also provides the "coolness" considered necessary for some crops.

For agricultural purposes, a number of general microzones based upon a combination of soil color, texture, and microclimatic factors are identified by the Yekuana. Each cultivated plant is considered to grow best when propagated in a particular soil type (Table 5). Overall, a black, slightly sandy soil is preferred for gardens. This soil type corresponds to the perceived requirements of manioc, which are always given paramount attention by the Yekuana (Frechione, 1981:92–98). A single garden site, however, frequently encompasses a number of soil types, each of which is planted with those cultigens best suited to the soil and microzonal characteristics. This results in a patch intercropped planting pattern in which different crops occupy patches, or zones, within the gardens (Fig. 4). Mixed intercropping, the practice of interplanting two or more crops simultaneously within some patches/zones, also occurs if the crops share similar preferred microzonal characteristics (Table 6)—and if other considerations do not discount the intercropping of the plants. However, when mixed intercropping does exist, it is often for specific crop combinations and usually occurs only for a short period of time during the garden's productive lifespan. For example, if manioc is to be cultivated in a garden, it is always planted first in the appropriate section (or sections). Corn, which has similar preferred microenvironmental characteristics as manioc, is then interplanted among the manioc mounds. Squash and tania, which also share similar preferred locational characteristics, are often sparsely interplanted within the manioc section. Corn is harvested after about three months and is not replanted. Squash is harvested in four months, and

Table 5.—*Major cultigens of the Yekuana and preferred soil/microclimate characteristics for their cultivation.*

	Soil color				Soil texture			Micro-climate
Cultigen[1]	Black	Red	Brown	Yellow	Sandy	Clayey	Wormy	Humid[2]
manioc	1		2	3	x			
plantain	1	3	2			x	x	x
corn[3]	1				x			
pineapple	1	2				x		x
sugar cane	1				x	x	x	x
papaya				anywhere				
tania	1				x			
yam	1				x			
sweet pototo	1				x			
squash	1				x			
topiro				anywhere				
watermellon	1				x			x
chile pepper[4]								
bottle gourd				anywhere				
tobacco[4]								
jute	1					x		x
cotton	1				x			

Numbers indicate order of preference for soil color.

[1] See Table 7 for scientific identifications.

[2] That is, an area bordering a running stream.

[3] Corn should also be planted beside logs left after burning. These logs provide nutrients as they decay and protect the corn seedlings.

[4] These cultigens should be planted in areas with a lot of ash from burning, or at the site of a partially or completely burned stump.

tania about eight months after planting. Consequently, within approximately nine months, the manioc section becomes in effect a monocultural patch within the garden, and remains so for the remaining productive period of the garden (usually from two to four years). Other cultigen patches exhibit a similar pattern of temporal utilization, with a dominant, long-term crop and a number of sparsely interplanted secondary short-term crops.

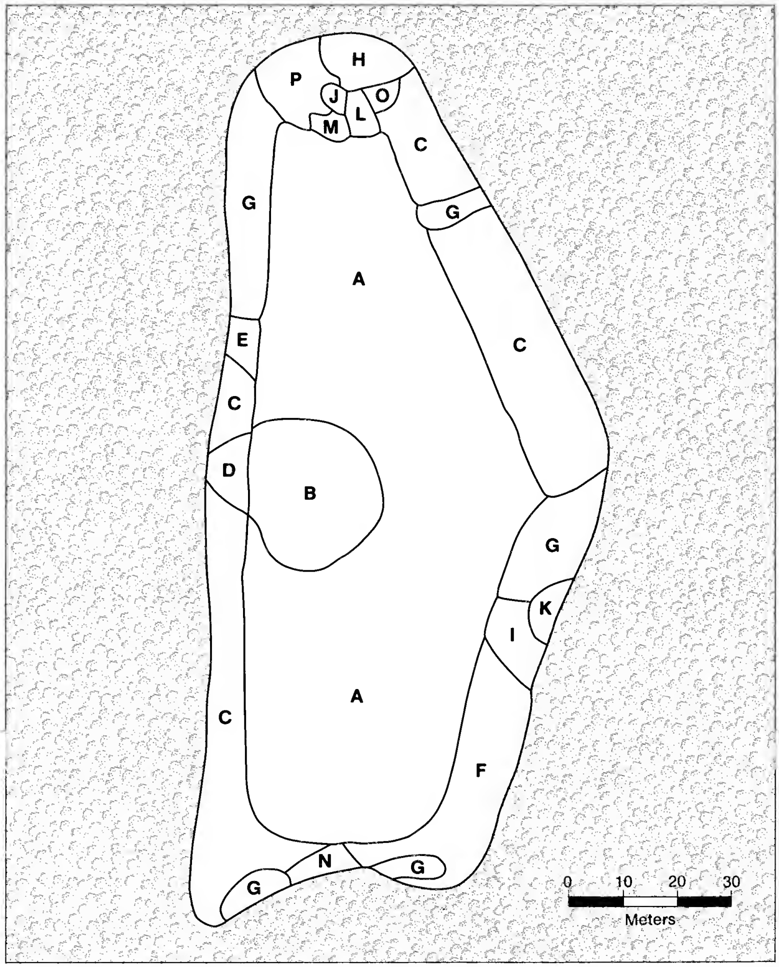
The Yekuana cultivate at least 76 different named varieties of food plants, representing some 15 different genera (Table 7). This great variety is an attempt to maintain the genetic diversity of staple food crops to insure adaptability to environmental variability (Hames, 1980: 20). Furthermore, varietal performance in each soil type and drainage condition is known by the Yekuana. The microenvironmental characteristics of gardens, therefore, determine which of the varieties will be planted. Consequently, the composition of gardens varies greatly in crop complexes (Table 6), and the gardens are not simply tangles of many different types of randomly interplanted crops.

Yekuana gardens generally range in size from 0.3 to 4.0 ha. Although monozones are found within gardens (Fig. 4: Sections A and C), entire monocropped gardens do not usually occur (Frechione, 1983). Yekuana gardens have been shown to attain manioc yields in excess of 30 tons per ha (Frechione, 1981:101). This high productivity is undoubtedly due to successful microzonal planting and the maintenance of high varietal diversity in cultigens. Thus monozoning, when geared to microenvironmental variations in soils and climates, can be productive in a mixed garden system. Monocropping on a larger scale, however, is considered to be environmentally degrading with resulting high risks of crop failures. Nonetheless, the Yekuana example offers evidence that, when properly managed, monozoning can be adapted to ecological heterogeneity in the Amazon Basin. This brief explication of Yekuana criteria for site selection, and the microenvironmental conditions best suited for cultigen propagation, provides one example of the in-depth knowledge of an indigenous population concerning the exploitation of their natural environment. It also suggests the degree of complexity of exploitative strategies that are necessary for the utilization of Amazonian ecosystems in a sustained-yield manner.

THE CABOCLOS OF COARI: RESOURCE UNITS AND VERTICAL LEVELS

The community of Coari is located within a *várzea* (floodplain) zone at the juncture of Lake Coari and the Amazon (Solimões) River (Fig. 1). *Terra firme* zones, however, are found interspersed throughout the *várzea* in this particular area. Life for the *caboclos* of Coari centers around the seasonal changes of water levels in the lakes, rivers, and streams near the community. Water levels are highest during June when maximum flooding usually occurs, and are lowest in October. The rainy season extends from January to April and the dry season from June to November—December and May are transition months. The average annual difference between high and low water levels in the Coari area is 10 meters. It should be noted, however, that unusually high floodwaters occur on average every 7 to 10 years. Although these high, damaging floods are infrequent and erratic, floral and faunal distributions, as well as human activities, are limited by their occurrence.

The *caboclos* of Coari gain their subsistence from a mix of shifting cultivation, fishing, hunting, and the collection of forest products. Most agricultural activities are carried out in *terra firme* areas scattered throughout the local *várzea. Caboclos* often plant part of their crop on the *várzea* to take advantage of the nutrient-rich alluvium of the flood-



LEGEND:

A	Manioc with corn; yams	**I**	Bottle gourd; tobacco
B	Manioc with corn; yams; squash	**J**	Papaya; corn
C	Plantain with corn	**K**	Chile pepper
D	Plantain with corn; squash	**L**	Tobacco
E	Plantain with corn; bottle gourd	**M**	Tania
F	Plantain with corn; tobacco	**N**	Papaya
G	Sugar cane	**O**	Tupiro
H	Fa'ada	**P**	Weeds

Fig. 4.—Planting patterns in a typical Yekuana garden.

plain. However, because erratic flooding can result in the loss of crops planted in the *várzea, caboclos* will not risk putting their entire agricultural effort into floodplain areas. Thus, the perception of a natural hazard, that is, flooding, has resulted in a conscious decision by *caboclos* to plant most of their crops on the less productive *terra firme* lands.

Hunting, fishing, and collecting take place in the forests, rivers, lakes, and streams near Coari. The area near the community encompasses numerous microecozones that the *caboclos* recognize and selectively exploit. Indeed, *caboclos* possess an intimate knowledge of local ecological variables and recognize at least 40 different types of "resource units" (*lugares de fartura*) where important resources are concentrated—either naturally or due to human manipulation. Fig. 5 shows the Coari area with some of the locations of these 40 resource units. Table 8 provides a glossary of the numbered units appearing in Fig. 5, and Table 9 describes some of the general characteristics of these resource units.

Within many of these resource units, *caboclos* also differentiate resource variability based upon verticality. Terrestrial/arboreal and aquatic "vertical levels" are recognized by local residents (Fig. 6). Different resources are found at different vertical levels, and resource distribution between levels also changes with season. Such knowledge enables the *caboclo* to locate desired resources and to know what techniques will be required to exploit them. For example, fish and turtles found in aquatic level A-1 (see Fig. 6) can be exploited with *arco e flecha* (bow and arrow), the *arpão* (harpoon), the *rapiché* (net with handle), or the *zagaia* (three-pronged spear), while those found in level A-5 are exploited with the *camuri* (buoy with hook and line), the *jatecá* (turtle harpoon), or the *linha comprida* (hook and line). Also indicated for terrestrial/arboreal vertical levels in Fig. 6 are "intermediate zones." These zones are interstitial movement corridors for birds and mammals and are the principal levels for sighting and hunting game.

Game is pursued in relation to the vertical level(s) occupied. Birds like the *jurutis, inambus* (*Tinamus braziliensis*), and *bacurau,* as well as anteaters (*tamanduas*) are found in level T-3 of the *castanhal* (Table 9) because their preferred foods (insects such as *formiga* and *suava*) are most abundant at that level. Certain birds—*graunas* (*Gnoremopsar chopi*) and *murures*—are found in levels T-3 and T-4 because of the prevalence of *taracuas* (another type of insect) in these levels. Other birds—*japós, japiins* (*Cacicus icteronotous*), *araras* (*Amazon festiva* and *Ara macao* among others), *periquitos* (various species) and *papagaios*—nest during the rainy season at level T-4 in the *castanhal.*

A complete description of *caboclo* knowledge concerning even one resource unit is beyond the scope of this paper (for more detail see Posey et al., 1983). However, in order to indicate the extent of eth-

Table 6.—*Patches/zones, crops, and areas in six Yekuana gardens.*

Patch/zone	Dominant	Intercropped plants	% of area	Area in square meters
		Site 1 (.88 ha, see Fig. 4)		
A	manioc	corn; yams	55.4	4874
B	manioc	corn; squash; yams	3.8	334
C	plantain	corn	20.7	1819
D	plantain	corn; squash	0.6	51
E	plantain	corn; bottle gourd	0.6	51
F	plantain	corn; tobacco	5.1	445
G	sugar cane		7.4	655
H	fa'ada		1.4	124
I		bottle gourd; tobacco	1.0	91
J		papaya; corn	0.6	51
K	chile pepper		0.6	51
L	tobacco		0.5	48
M	tania		0.4	31
N	papaya		0.2	16
O	tupiro		0.1	9
P	weeds		1.5	128
	Totals		100.0	8778
		Site 2 (.50 ha)		
A	manioc	corn	50.0	2500
B	pineapple	corn	21.0	1050
C	plantain	corn	20.0	1000
D	tania	corn	5.0	250
E	sugar cane		4.0	200
	Totals		100.0	5000
		Site 3 (.90 ha)		
A	manioc	tania; cashew	66.0	5940
B	plantain		18.5	1665
C	plantain	sweet potato	0.34	30.6
D	pineapple		13.6	1224
E	chile pepper		0.9	81
F	structure		0.66	59.5
	Totals	100.0	9000	
		Site 4 (3.35 ha)		
A	manioc	corn; squash; tania; yams; papaya; chile pepper	85.0	28,475
B	plantain	corn	11.0	3685
C	pineapple		3.0	1005
D	sugar cane		1.0	335
	Totals		100.0	33,500
		Site 5 (1.3 ha)		
A	pineapple		42.0	1105
B	pineapple	sweet potato	3.3	429
C	pineapple	bottle gourd	1.2	156

Table 6.—*Continued.*

Patch/zone	Dominant	Intercropped plants	% of area	Area in square meters
D	plantain		23.0	2990
E	plantain	sweet potato	8.2	1066
F	manioc		8.5	1105
G	manioc	sweet potato	0.92	119.6
H	sweet potato		7.5	975
I	sugar cane		2.0	260
J	tania		1.7	221
K	tania	sweet potato	0.6	78
L	adawata akido		0.04	5.2
M	cashew		0.04	5.2
N	weeds		1.0	130
	Totals		100.0	13,000
		Site 6 (.5 ha)		
A	plantain	tania; papaya	87.0	4350
B	plantain	squash	6.0	300
C	sugar cane		2.0	100
D	weeds	sugar cane; papaya	5.0	250
	Totals		100.0	5000

noecological knowledge possessed by the *caboclos* of Coari, a description of some of the interrelationships between resource units 6 (*chavascal*) and 17 (*castanhal*) will be presented.

A close relationship exists between the *chavascal* and *castanhal* and it is one of critical importance to the Coari *caboclos*. During the dry season, numerous animals come to the *chavascal* from the *castanhal* in search of water that can be found in the small pools and streams left by receding floodwaters. Small birds and mammals are also found in the *chavascal,* lured by the dry season vegetation that flourishes along the damp beaches (*praias*) that rim the *chavascal.* Likewise, wading birds are found in abundance, attracted by the multitude of small fish trapped in the shallow waters. Birds such as *massaricos* (*Hoploxysterus cayanus*) and *gaivotas,* and turtles (for example, *cabeçudo*) lay their eggs in the white sand beaches near the *chavascal.* Their eggs attract lizards, such as the *jacuraru* (*Tupinambis nigropunctatus*), as well as man. Carnivores such as the jaguars (*onças*) and eagles (*gavião*) move into the *chavascal* during the dry season attracted by the many small mammals and birds. It is worth noting that *caboclos* recognize that birds such as the *cujubim* (*Pipile cujubi*) and small mammals like the *paca* (*Cuniculus paca*) act as seed disseminators—these

Table 7.—*Yekuana cultigens.**

Scientific name	English	Spanish	Yekuana**	Number of varieties	Type of reproduction	Approximate period numbers of: for maturation in months	Approximate period numbers of: harvests from 1 site	Use
Manihot esculenta Crantz	manioc	yuca	kiyedi	30	vegetative	10.4	2–4	F
Musa paradisiaca	plantain	plátano	fadudu	8	vegetative	10.4	3–4	F
Musa sapientum	banana	cambur	fadudu	4	vegetative	10.4	3–4	F
Ananas sativus	pineapple	piña	anadeki	8	vegetative	12.5	2–3	F
Saccharum officinarium	sugar cane	caña	asichadu	2	vegetative	6.6	3–4	F
Xanthosoma sagittifolium	tania	ocumo	nati	2	vegetative	8.7	3–4	F
Dioscorea trifida	yam	mapuey	wihetsha	2	vegetative-seed	8.9	2–3	F
Dioscorea alata	yam	ñame	wayana	3	vegetative-seed	9.4	3–5	F
Ipomoea batatas	sweet potato	batata	saku	3	vegetative-seed	9	3–4	F
Zea mays	corn	maiz	aiña	2	seed	2.6	1	F
Cucurbita maxima	squash	aullama	tunamo	1	seed	4	1	F
Carica papaya	papaya	lechosa	mahaiya	2	seed	9	2–3	F
Capsicum	chile pepper	ají	whomi	3	seed-vegetative	4.7	4	F
Solanum topiro		tópiro	soka	2	seed	5.5	1	F
Citrullus vulgaris	watermellon	patilla	fatilla	1	seed	2.8	1	F
Lagenaria			fa'ada	1	seed	3	1	F
Inga		guamo	wajuhi	1	seed	20.9	***	F
			adawata akidi	1	seed	****	***	F
Lagenaria siceraria	bottle gourd	totuma		6	seed	3	1	M
Annas	jute	crowia	tukudi	1	vegetative	12.9	1	M
Gossypium barbadense	cotton	algodón	curaawa	1	seed	9.4		M
Nicotiana tabacum	tobacco	tabaco	wadecu	2	seed-vegetative	3.4	1	Ma
			kawai					Me
Banisteriopsis			kaahi*****	1				Ma

* Numerous medicinal and magical plants which are cultivated in Yekuana gardens are not included in this table because data on them were not rigorously collected. Hames (1980:6) notes that of 71 species of cultivated plants on which he collected data for the Yekuana of the Padamo River area, 32 species have magical uses.

** The Yekuana name for the cultigens listed is the generic term. Each variety also has an individual name.

*** The productive life of these tree species is not known.

**** The period of time required for this plant to begin production is not known.

***** This plant is cultivated exclusively by shaman, and is used to produce an hallucinogenic drug.

Use: F—food, M—manufacture, Ma—magical, Me—medicinal.

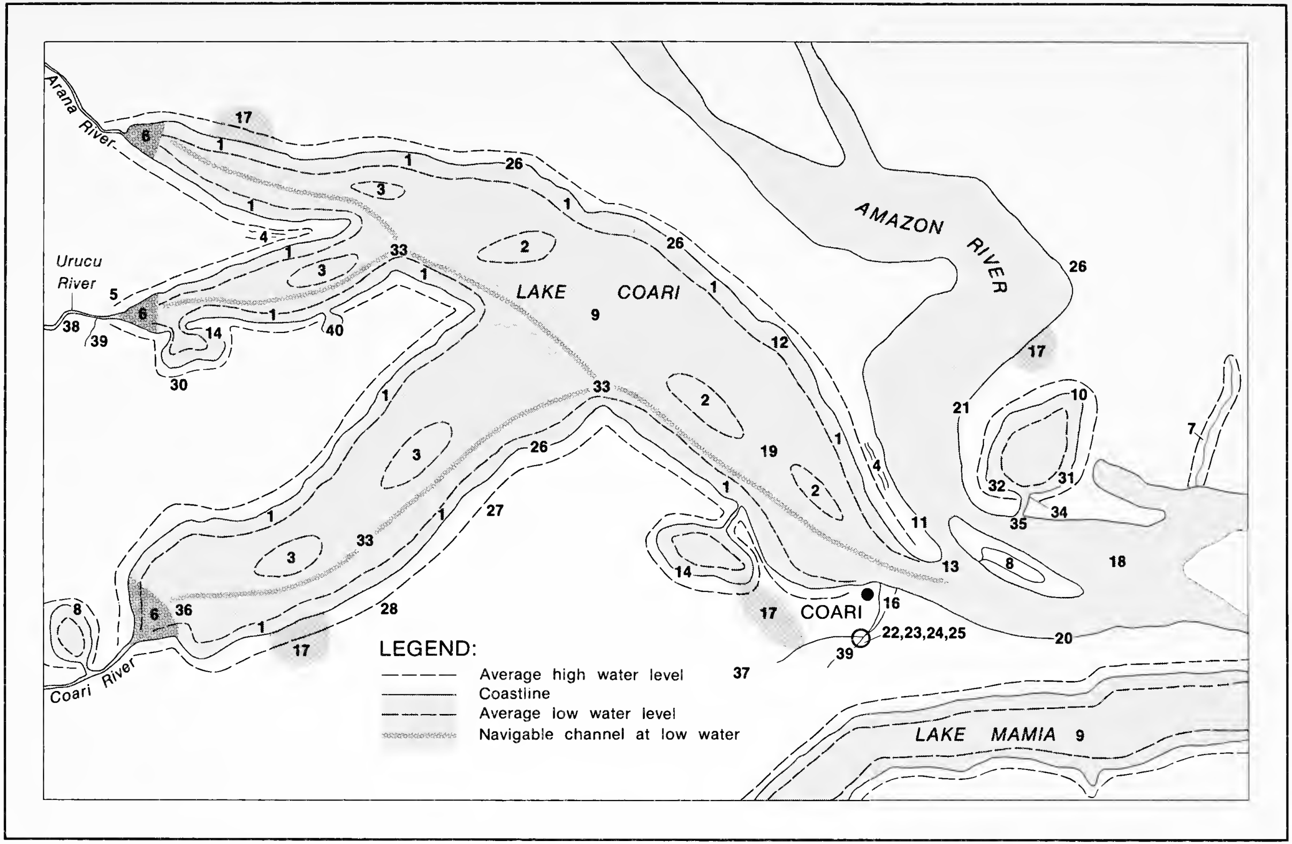


Fig. 5.—Location of major resource units in the Lake Coari area, and low-high water areas.

Table 8.—*Glossary of resource units appearing on Fig. 5, as defined by a caboclo of the Lake Coari region (numbers correspond to those presented on figure).*

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1. praia branca—dry season, white sandy beaches of Lake Coari where birds and turtles lay their eggs.
2. praia suja—dry season, wet or muddy beaches where a great number of birds feed.
3. praia verde—dry season beaches, covered in short vegetation, where birds feed on weeds and insects.
4. restinga—natural river levees, usually covered in forest, and not inundated during the dry season.
5. charco—swamp area found within the várzea ecological zone.
6. chavascal—transition area between rivers draining into Lake Coari and the lake itself, characterized by low vegetation which is mostly inundated during the rainy season and which during the dry season forms a labyrinth of dead-end river-like branches, ressacas, poços, and pocinhos surrounded by large areas of muddy land.
7. igapó—forest area which is flooded during the height of the rainy season.
8. laguinho—small lake connected to the river by a narrow stream during the rainy season, and only accessible by land during the dry season.
9. lago grande—large lake, such as Lake Coari or Lake Mamiá.
10. lago—lake connected to the river by a passage navigable by canoe or small boat.
11. costa—margin (bank) of the Amazon River.
12. enseada—gulf-like section of a large lake, usually characterized by calm waters.
13. encontro das águas—point where the Lake Coari water system flows into the Amazon River.
14. poço grande—deep section in a sharp turn of a smaller river, characteristic of the sinuosity of these rivers.
15. ressaca—lake-like formation connected to a small river.
16. igarapé—a black water stream flowing from deep in the forest to a river.
17. castanhal—the terra firme forest where the catanheiras (*Bertholetia exceltia*) are located.
18. águas fundas brancas—deep white waters of the Amazon, where the piraibas (*Brachyplatystoma* spp) are caught.
19. águas fundas pretas—deep water areas of Lake Coari, associated with scarcity of resource except when in close proximity to the banks of the lake.
20. barreiras—high vertical banks of the Amazon River, characterized by swift currents and an abundance of clay varieties.
21. embaubal—section of the várzea where embaúba trees (*Cecropia* spp) are predominant.
22. buritizal—a concentration of buriti palms (*Mauritia flexuosa*).
23. jauarizal—a concentration of jauari trees (*Astrocarium jauari*) usually at critical zones during periods of medium water level.
24. açaizal—a concentration of açai trees (*Euterpe edulis*) in the terra firme.
25. bacabal—a concentration of bacaba trees (*Oenocarpus distichus*) along igarapés.
26. aratizal—a concentration of arati (?) bushes at the critical zone during periods of medium water level.
27. capoeira alta—an abandoned garden site more than ten years old.
28. capoeira baixa—an abandoned garden site approximately five years old.
29. baixio—shallow section of the Amazon River opposite the channel side, characterized by the predominance of oeirana trees (*Salix martiana*).
30. tabocal—a concentration of green-and-yellow bamboo (*Guadua* spp) in the high várzea.

Table 8.—*Continued.*

31. canaranal—a floating meadow dominated by canarana (*Panicum spectabile*), commonly used as cattle fodder.
32. muriruzal—a floating meadow dominated by muriru (numerous species, see Smith 1981:14), providing food for both fish and turtles.
33. canal seco—navigable channel in the lake during low water.
34. boca de cima (lago)—point where a lake narrows into a stream before entering a river.
35. boca de baixo (rio)—point where the water from a lake flows into a river.
36. matupazal—a floating meadow dominated by matupá (?).
37. roçado novo—a recently planted slash-and-burn garden site.
38. roçado velho—a slash-and-burn garden site which is still being systematically utilized.
39. igarapezinho—a clear water rivulet which provides drinking water, also called a fonte.
40. pocinho—a small lake which does not dry up during periods of low water, usually located near ressacas and chavascals, and where fish are easy to catch by hand.

animals feed on the seeds of *chavascal* vegetation and through their droppings or patterns of storage spread the seeds to other areas.

During the rainy season, the *chavascal* is flooded and its resources become available to large fish. *Caboclos* exploit these fish using deep-water circular throwing nets, bows and arrows, and poles with line and hook. They also collect *arati* (*Anona densicoma*) fruit in their canoes. The primary focus of *caboclo* activity during the rainy season is, however, the *castanhal*. Here, the *caboclos* collect *castanhais* (Brazil nuts) for subsistence and for market. They also hunt the mammals and birds that have been forced, by the high waters in the *chavascal*, to the *castanhal*.

In addition to seasonal variations of floral and faunal resources in the *chavascal* and *castanhal*, there are daily movements, particularly of birds, into and out of these units. *Massaricos* (*Hoploxysterus cayanus*), *marrecos*, and *mergulhões* (*Ibycter formosus*) move between these two resource units at regular intervals during the day. In the early morning, *mergulhões* and *garças* (*Herodias egretta*) fish in the lakes and ponds near the *chavascal*, then move to the open areas to sun and dry themselves in the noon heat, and finally return to their roosts in the *castanhal* in the evening.

Though but a quick sketch of the knowledge that Coari *caboclos* possess regarding resources and ecological variations, it nonetheless indicates that *caboclo* ethnoecological knowledge represents an important resource to those concerned with developing the Amazon region.

Table 9.—*Some general characteristics of the resource units encountered in the Lake Coari region (numbers correspond to those presented on Fig. 5).*

No.	Resource unit	Water level when resource unit occurs	Water color	Vertical level(s)[1] where faunal components occur	Faunal components[2]
1	praia branca	low	black	T-2	B, I, Rt
2	praia suja	low	mixed	T-2	B, I
3	praia verde	low	black	T-2	A, B, I
4	restinga	low		T-1, 2, 3, 4	A, B, I, Rt
5	charco	low/medium	mixed	T-2; A-1	A, B, F, I, Rt
6	chavascal	low/medium	mixed	T-1, 2, 3; A-1	A, B, F, I, Rt
7	igapó	high	black/white/mixed	T-1, 2, 3; A-1, 2	A, B, F, I, Rt
8	laguinho	low	black/white/mixed	A-1, 2	B, F, I, Rt
9	lago grande	medium/high	black	A-1, 2, 3, 4	B, F, Rt
10	lago	low/medium	black/white/mixed	A-1, 2, 3	B, F, I, Rt
11	costa	low/medium/high	white	A-1, 2, 3, 4, 5	A, B, F, I
12	enseada	low/medium/high	black/white	T-1, 2, 3, 4, 5; A-1, 2, 3, 4, 5	A, B, F, I
13	encontro das águas	low/medium/high	black/white	A-1, 2, 3, 4, 5	A, B
14	poço grande	low/medium	mixed	A-1, 2, 3, 4	A, B, F, I, Rt
15	ressaca	low/medium	mixed	T-2, 3	A, B, F, I, Rt
16	igarapé	low/medium	black	T-1, 2; A-1	A, B, F, I, Rt
17	castanhal	low/medium/high		T-1, 2, 3, 4, 5	A, B, I
18	águas fundas brancas	low/medium	white	A-1, 2, 3, 4, 5	F
19	águas fundas pretas	low/medium/high	black	A-1, 2, 3, 4, 5	F
20	barreiras	low/medium/high	white	T-1, 2, 3, 4, 5; A-1, 2, 3, 4, 5	B, F, I

Table 9.—*Continued.*

No.	Resource unit	Water level when resource unit occurs	Water color	Vertical level(s)[1] where faunal components occur	Faunal components[2]
21	embaubal	low/medium/high	white	T-1, 2, 3; A-1, 2	A, B, F, I, Rt
22	buritizal	low/medium/high	black	T-1, 2, 3, 4, 5	A, B, I, Rt
23	jauarizal	low/medium/high	black/white	T-1, 2, 3; A-1, 2	A, B, F, I, Rt
24	açaizal			T-1, 2, 3, 4, 5	A, B, I, Rt
25	bacabal			T-1, 2, 3, 4, 5	A, B, I, Rt
26	aratizal	low/medium	black	T-1, 2; A-1, 2	A, B, F, I
27	capoeira alta			T-1, 2, 3, 4	A, B, I
28	capoeira balxa			T-1, 2, 3	A, B, I, Rt
29	baixio	low/medium	white	T-1, 2, 3; A-1, 2	A, B, F, I
30	tabocal			T-1, 2, 3, 4	A, B, I
31	canaranal	low/medium/high	black/white	T-1, 2; A-1	A, B, F, I
32	muriruzal	low/medium/high	black/white	A-1	B, F, I
33	canal seco	low	mixed	A-1, 5	A, B, F, Rt
34	boca de cima (lago)	low/medium	black	T-1, 2, 3, 4; A-1, 5	A, B, F, I
35	boca de baixo (rio)	low/medium	white	T-1, 2, 3; A-1, 5	A, B
36	matupazal	low/medium	black/white	T-2; A-1	A, B, F
37	roçado novo			T-1, 2	A, B, I, Rt
38	roçado velho			T-1, 2, 3, 4	A, B, I
39	igarapezinho	low/medium/high	black	T-1′; A-1	A, B, F, I
40	pocinho	low	white	A-1, 5	

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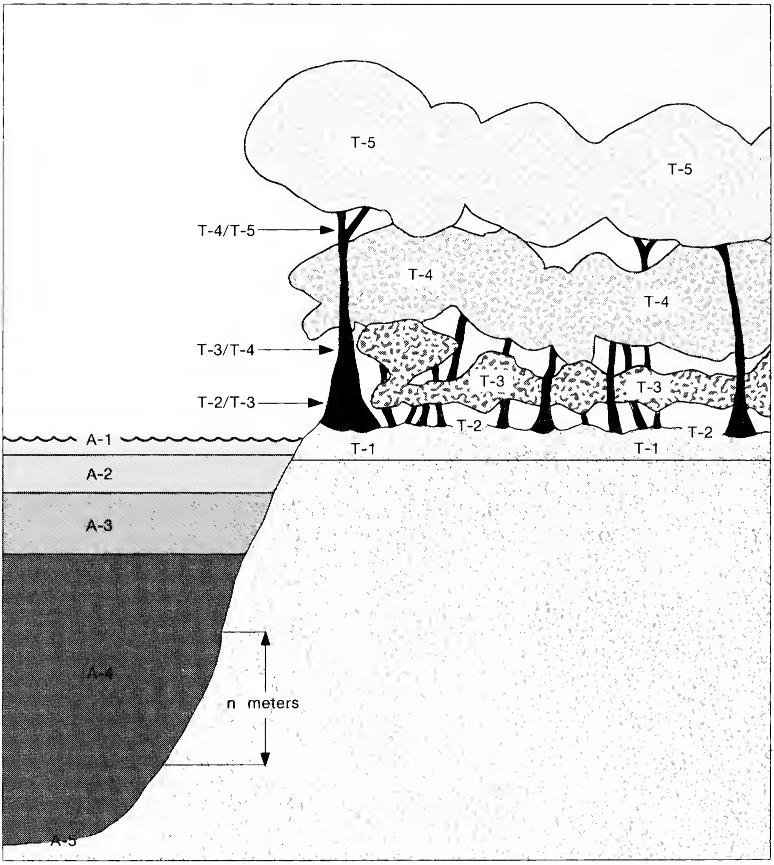
[1] See Fig. 6.

[2] Letters represent the following: A = animals (these are generally mammals); B = birds; F = fish; I = insects; Rt = reptiles/turtles.



LEGEND:

Aquatic Levels	Meters Below Surface	Terrestrial/Arboreal Levels	Meters Above Ground
A-1	0 to 1	T-1	(below ground)
A-2	1 to 4	T-2	-0.2 to 0
A-3	4 to 10	T-3	1 to 10
A-4	10 to n	T-4	7 to 15
A-5	river/lake bottom	T-5	15 to 30

THE CABOCLO COMMUNITY OF LIMOEIRO DO AJURU: RESOURCE ZONES AND EXPLOITATION TECHNOLOGIES

Limoeiro do Ajuru is located amidst a broad reach of *várzea* (floodplain) lands in the estuary region of Amazonia (Fig. 1). Unlike the *caboclo* community of Coari, where seasonal change in water levels is the key parameter of the local ecosystem, the most important feature in the Limoeiro do Ajuru area is the fluctuation in *daily* river levels (which averages about 3.4 m throughout the year). Indeed, the annual oscillation in maximum monthly river stages recorded over a 3-year period was 1 m or less (Fig. 7). Hence, and surprising to many observers, there is no high-water season of any consequence in the Limoeiro do Ajuru area—a characteristic that distinguishes the *várzea* of this area from other *várzea* zones found in Amazonia. Despite the fact that Limoeiro do Ajuru is situated more than 240 km from the mouth of the Amazon River, the change in daily river levels (and the flatness of the annual river stage profile) is due to the encounter between tidal forces and the enormous volume of water discharged by the Amazon River—average annual discharge is estimated to be 175,000 m^3s^{-1} (Oltman, 1967). The daily rise from 3 to 4 m in local watercourses results in the flooding of the dense rainforest (tidal *várzea* forest) that covers the surrounding landscape (there are no *várzea* lakes or floodable grasslands in the local area).

The regular inundation of the land limits the opportunity for, and the importance of, agriculture in the Limoeiro do Ajuru area. In contrast to the Coari area where *terra firme* is abundantly interspersed throughout the *várzea*, there are precious few pieces of land that are above daily flood levels and the majority of these parcels are subject to occasional inundation during peak flood periods. This poses a major problem for local residents insofar as the principal cultigen of the area, manioc (*Manihot esculenta*), is a root crop highly vulnerable to waterlogging. As a consequence of these conditions, and though most households have small *roças* (gardens), the exploitation of aquatic resources represents the most important component of the subsistence economy, and of local resource perceptions. As such, and given the scope of this paper, the discussion will focus upon this feature of the subsistence economy.

The fluvial dynamics of the estuarine *várzea*, and the location of the

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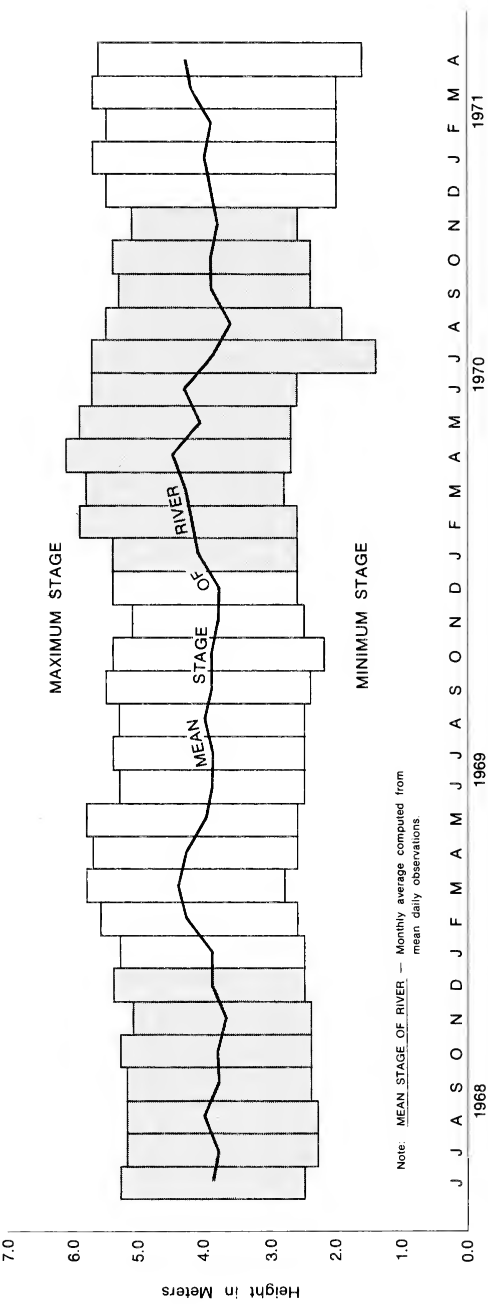
Fig. 6.—Schematic of aquatic and terrestrial/arboreal vertical levels from an Amazon River *várzea* ecological zone near Coari.



Note: MEAN STAGE OF RIVER — Monthly average computed from mean daily observations.

Fig. 7.—River stages at Caméta, Pará (55 km upriver from study area), June 1968–May 1971.

village itself, provide the *caboclo* of the Limoeiro do Ajuru area with several microenvironments to exploit. Eight major aquatic resource zones are identified by residents: the Tocantins River mouthbay, Tocantins River shore areas, Limoeiro River, *igarapé* (stream) mouths, large *igarapés,* small *igarapés,* flooded forests, and temporary summer pools (Fig. 8). Within zones, resource perceptions are further articulated on the basis of ecological variations. These ecological/resource zone subcategories are defined in terms of water depth, water temperature, distance from the river bank, type of river bank vegetation, time of day, meanders, point bars, mudflats, extended shallows, and the level and velocity of streamflow. The latter two are of importance because local watercourses have their streamflow direction reversed four times daily as well as experiencing two distinct high-water (*preamar*) and two low-water (*baixamar*) periods each day. In addition to the above factors, the time of year is also an important component of aquatic resource perception as many species of fish and aquatic animals are available only during specific periods of the year.

The *caboclos* of Limoeiro do Ajuru associate particular fish species with specific aquatic zones. For example, *cará, jijú* (*Hoplerythrinus unitaeniatus*), *trâira* (*Hoplias malavaricus*), *pira coroca, tambaquí* (*Colossoma macropomum*), *acarí,* and *piranha* (*Serrasalmus* spp.), are linked with flooded forest zones as well as with the small *igarapés* of the *centro* (interior forest locales). Indeed, fish feed on the fruits that fall into the flooded forest and fishing strategies of local residents are often tied to the fruiting periods of particular species—*tambaquí* (see above), a favorite of the local *caboclo* populace, is known to feed on the fruits of *maraja* (*Pyrenoglyphis maraja*) and *seringa* (*Hevea brasiliensis*) among others. *Dourado* (*Brachyplatystoma flavicans*), *mapará* (*Hypophthalmus* spp.), and *pacu* are typically found in the open waters of the Tocantins River mouthbay. Species commonly identified with *igarapês* are *itui, parapitinga* (*Colossoma bidens* ?), and *arucu branco* (*Leporinus trifasciatus*). *Tucunaré* (*Cichla* spp.) are common in Tocantins River shore areas and along the edge of rivers. As would be expected, the greatest number of fish species are associated with the main rivers of the local area (such as the Limoeiro River), and include *branquinha* (*Gasterotomus latior*), *curimata* (*Prochilodus nigricans*), *pirapucú,* and *pescada* (*Palgioscon squamosissimus*). Freshwater shrimp, *camarão* (*Macrobrachium amazonicum*), are found in abundance along the bottom of the large *igarapés* and rivers of the area.

Other faunal species are linked with specific aquatic resource zones. Caiman, for example *Caiman crocodilus* and *Paleosuchus trigonatus,* are most often found in large and small *igarapés* as well as the flooded forest. *Tracaja* (*Podocnemis unifilis*) is found in the flooded forest and *pitiu* (*P. sextuberculata*) in both the flooded forest and shallow areas

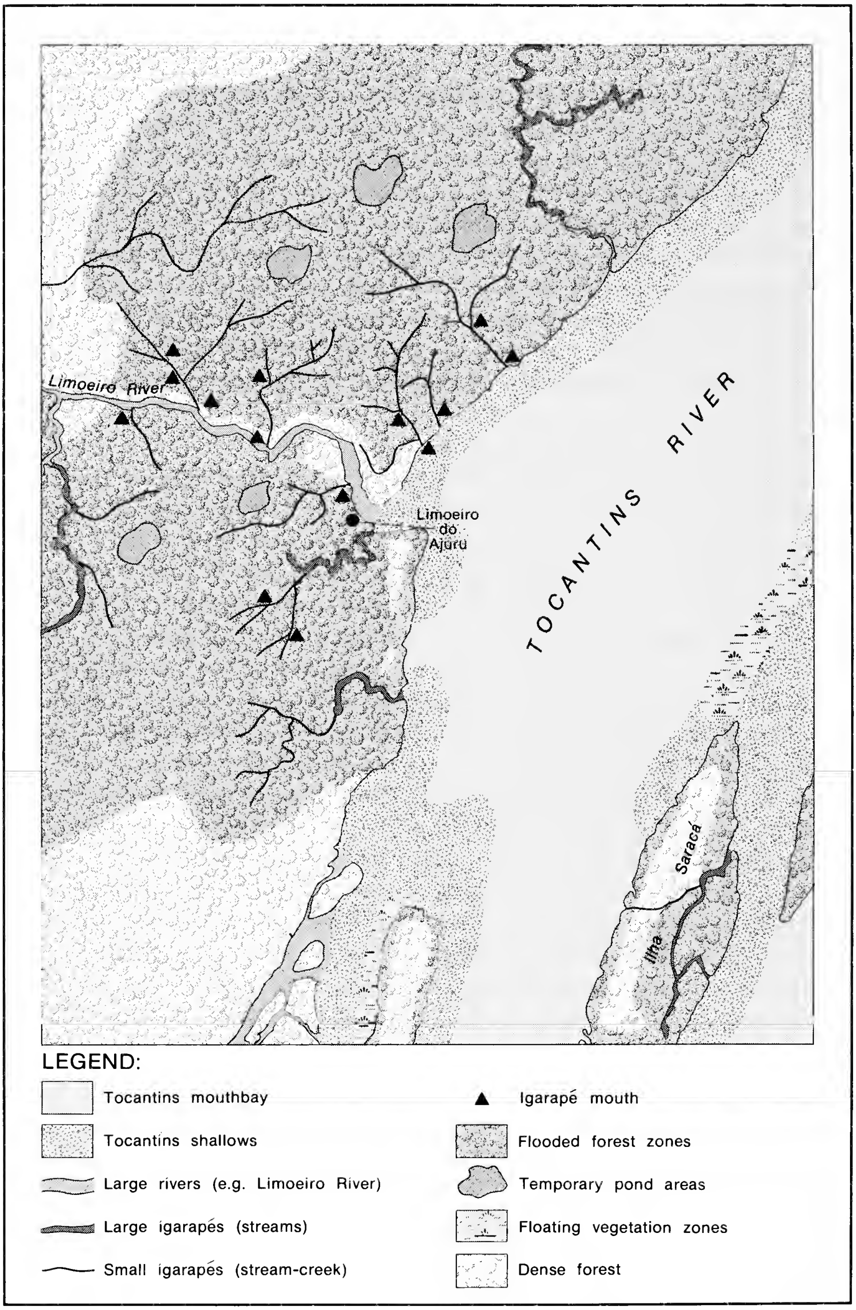


Fig. 8.—Aquatic resource zones in the proximity of Limoeiro do Ajuru.

Table 10.—*Aquatic resource zones and methods of exploitation at Limoeiro do Ajuru, Brazil.*

	Methods of exploitation										
Aquatic resource zones	1	2	3	4	5	6	7	8	9	10	11
Tocantins Mouthbay										X	
Tocantins Shore Area		X								X	
Limoeiro River		X	X	X				X	X	X	
Igarapé Mouths	X										
Large Igarapé			X	X				X	X	X	
Small Igarapé				X	X	X	X		X	X	
Flooded Forest					X	X			X		
Temporary Summer Ponds											X

1. *Pari* (fish weir).
2. *Cacuri* (permanent barrier trap).
3. *Matapi* (cylindrical shrimp trap).
4. *Espinhel* (trotline).
5. *Espeque/Zagaia* (pronged fish spear).
6. *Arco e Flecha* (bow and arrow).
7. *Timbo* (fish poisons).
8. *Tarefa* (circular throwing net).
9. *Canico* (fishing pole/line and hook).
10. *Malhadeira* (gill net).
11. *Gapoia* (temporary summer ponds).

of the Tocantins River mouthbay. *Jaboti* (*Testudo tabulata*) is identified with temporary summer ponds and small *terra firme* patches within the flooded *várzea* forest. Manatee (*Trichecus ininguis*), though rare, are found in the general area and are most often associated with large *igarapés.* Two freshwater dolphins, *Inia geoffrensis* and *Sotalia fluviatalis,* are common but not eaten by local residents because dolphins are believed to possess magical powers (Wagley, 1953:237–241).

Specific techniques and instruments are identified with reference to the exploitation of the various resource zones. These include the *pari* (fish weir), *cacuri* (permanent barrier trap), *matapi* (cylindrical shrimp trap), *caniço* (fishing pole), *espeque/zagaia* (pronged fish spear), *arco e flecha* (bow and arrow), *timbo* (fish poisons), *tarefa* (circular throwing net), *espinhel* (trotline), *gapoia* (drainage of summer ponds), and in recent years, the *malhadeira* (gill net). Table 10 shows the techniques/instruments that are associated with particular aquatic resource zones (see Parker, 1981:153–159, 274–285, for further discussion).

Two of the fishing instruments, the *pari* and the *cacuri,* deserve special mention because they represent specific instruments adapted for use in the *várzea* of the Limoeiro do Ajuru area where water levels fluctuate significantly each day. To construct a *pari,* a barrier made from lengths of split bamboo woven together with strips of vine is placed across the mouth of a small *igarapé* (stream). The barrier wall has a gate in the center that is left open as water levels begin to rise and fish move from the larger watercourses into smaller ones. Just before the water begins to recede, and the small streams empty, the gate is closed and the returning fish are thus trapped against the barrier. The fish swim into a central chamber area where they are easily removed by fishermen. The *pari* is elegant in its simplicity, temporary, and can be erected and taken down by a single individual.

The *cacuri* is designed with the same strategy in mind but has two important differences—it is permanent, and it is used in the larger watercourses such as the Limoeiro River (150–200 m wide) and along the Tocantins River shore area where the *pari* would be useless. The *cacuri* is a barrier trap consisting of a wall of tall stakes sunk into the river bottom and secured by vines for stability. The wall runs parallel to the river bank (or shore area) from about 5 to 20 m out into the water, depending on water depth. As the water level begins to drop, fish move away from bank areas in search of the security of deeper water. They encounter the barrier wall and are forced to swim along it until they are guided into a circular trap located at the center of the *cacuri* (both ends of the *cacuri* are set closer to the shore than the middle thus encouraging the fish toward the center). The circular trap is then secured and the fish retrieved.

Confronted with an environment that severely limits opportunities for agriculture, the *caboclos* of Limoeiro do Ajuru have evolved an elaborate matrix for the exploitation of aquatic resources. Within this matrix, aquatic resource zones and subzones, fish and aquatic animal species, time of year, and instrument/techniques are linked together to ensure an adequate source of protein year-round. This knowledge of aquatic resources, only briefly suggested here, is but one example of the knowledge possessed by the residents of this area of local environmental variation and nuance. Limoeiro do Ajuru *caboclos* hunt a wide range of game animals in the dry forest areas, employ myriad wild plant species for food and medicinal purposes, and have an elaborate classification system of woods, their specific properties and appropriate uses (Parker, 1981:296), and recognize and describe the characteristics of numerous insects found in the flooded forest—the list goes on. Such comprehensive ecological knowledge represents a significant source of data about the variation and richness of Amazon habitats.

SUMMARY

This paper has, albeit in brief fashion, surveyed four Amazon populations—two Amerindian societies and two *caboclo* communities—with regard to perceptions of specific ecological variations as well as resource utilization within their local areas. Long-term resource management strategies and the semi-domestication of plants and animals (Kayapó), the selection and configuration of garden sites based upon edaphic-vegetative-climatic associations (Yekuana), the elaboration of complex resource unit typologies and vertical zonation within resource zones (Coari), and *várzea* resource zones and related exploitation technologies (Limoeiro do Ajuru), are illustrative of the extraordinary knowledge that peoples indigenous to the Amazon region possess. A significant range of habitat, ecosystems, and resources are suggested by these four examples alone—the fact that the foregoing is but a meager representation of the ethnoecological data and information collected from these four populations, and that there remain so many groups and communities yet to be studied in a multitude of ecological settings, should convince the reader of the enormous potential that folk knowledge systems in Amazonia pose for scientific understanding of the region and the elaboration of rational, sustainable development strategies.

Development of the Amazon region has proceeded, *and will continue to advance,* at a rapid rate. Researchers of every stripe have been scrambling to keep abreast of development strategies in an effort not only to provide detailed information for those individuals and agencies formulating policy in the region but also to identify and classify as much of the rapidly shrinking Amazonian biome as is possible. While anthropologists and cultural geographers have continued to study human populations in the Amazon Basin and their adaptive solutions to various environmental and ecological milieus, the results and lessons of these investigations have been largely overlooked, or ignored, by the larger scientific community and developmental theorists. As recent events have irrefutably demonstrated, rational development of the Amazon region will demand an intimate knowledge and understanding of the structure and dynamics of ecosystems as well as the complex heterogeneity that characterizes the region as a whole.

There is a sad irony in the realization that those who could most assist in our understanding of this remarkable region are rapidly disappearing as a consequence of modern development—Amerindian and *caboclo* knowledge systems are being lost to humanity at an alarming rate. There is thus a great urgency for the collection of ethnoecological information from as many diverse social groups, geographic areas, and ecological microzones in Amazonia as possible. It is extraordinary that *caboclos,* who are considered by some to be the dominant cultural force in Amazonia (Moran, 1974; Ross, 1978), have remained largely ignored by researchers. To date, there have been only two in-depth studies of *caboclos* in the Brazilian Amazon (Wagley, 1953; Parker, 1981). As *caboclos* are the principal inhabitants of rural Amazonia, and for all practical purposes the sole inhabitants of *várzea* environments, their knowledge and understanding of the various microenvironments they occupy represents a significant source of ethnoecological information.

The question is frequently heard: "What can be done about the destruction of Amazonia?" The answer may in part be linked to the development of an appreciation for the biological and resource diversity of the region *as perceived* by native peoples. Building upon this foundation, we can thus begin to elaborate development policies that are more socially and environmentally sound. There is a certain humility with which Western science must, most uncustomarily, encounter folk science in order to benefit from these rich systems of knowledge. The study of ethnoecology (including ethnobotany and ethnozoology, among others), provides a pathway to a productive linkage between these two systems of knowledge as, hopefully, this paper suggests. There exists enormous potential in ethnoecological inquiry for increasing our understanding of the natural world, and it is our hope that in the future there can be a fruitful collaboration between natural scientists and ethnoecologists in Amazonia as well as other areas of the world.

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REVISION OF THE WIND RIVER FAUNAS, EARLY EOCENE OF CENTRAL WYOMING.
PART 3. MARSUPIALIA

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ABSTRACT

Dental remains of three species of *Peratherium* (*P. comstocki, P. marsupium,* and *P. innominatum*), one species of *Peradectes* (*P. chesteri*) and two species in a new genus, *Armintodelphys* (*A. blacki, A. dawsoni*) are reported from the Wind River Formation, north-central Wyoming. This is the first Wasatchian record of *P. marsupium* and, with *P. innominatum,* the first record of marsupials from the Lysite Member. The range of *P. comstocki* is extended into the early Bridgerian. Review of other Eocene Didelphini indicates that: *Entomacodon minutus* and *Peratherium morrisi* belong in *P. knighti*; *P. innominatum* is a valid species of *Peratherium*; *P. macgrewi* is a subspecies of *P. innominatum*; and *P. knighti* occurs in Wasatchian deposits. Among Peradectini, *Peradectes chesteri* is distinct from *P. protinnominatus* and is morphologically and phylogenetically intermediate in a lineage that includes the latter and *P. minutus* (=*Nanodelphys minutus*); *Armintodelphys* is most closely related to *P. pauli.*

INTRODUCTION

Almost one hundred years ago Cope (1884:269) described *Peratherium comstocki* from the "badlands of the Wind River, Wyoming." Since then only three specimens have been added to the marsupial record from the Wind River Formation (Guthrie, 1971), all from the Lost Cabin Member—two were described as *Peratherium* cf. *P. chesteri* and one as *P. comstocki.* Subsequent work by field parties from the Carnegie Museum of Natural History and the University of Colorado

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Museum (see Stucky and Krishtalka, 1982) has yielded 47 specimens of didelphids that are referred to three genera and six species. Three are known species of *Peratherium* (*P. comstocki*; *P. marsupium* Troxell, 1923; *P. innominatum* Simpson, 1928), one belongs to *Peradectes (P. chesteri*) and two are new species in a new genus of Peradectini, *Armintodelphys*. Examination of material related to these studies has led to a review of the occurrences, systematics, and evolutionary relationships of Paleocene and Eocene North American didelphids, which will appear elsewhere (Krishtalka and Stucky, 1983*a*).

Abbreviations used in this paper are as follows: AMNH, American Museum of Natural History; CM, Carnegie Museum of Natural History; PM, Field Museum of Natural History; PU, Princeton University (Museum); UCM, University of Colorado Museum; UCMP, University of California Museum of Paleontology; USNM, U.S. National Museum; UW, University of Wyoming; YPM, Yale Peabody Museum; Fm, Formation; loc., locality; L, length; W, width.

LOCALITIES AND AGE

The didelphid material from the Wind River Formation was recovered by surface prospecting and underwater screening of sediments from seven localities in the Lost Cabin Member (CM locs. 34, 1039, 1040, 90, 1085; UCM locs. 79040, 80061), two in the Lysite Member (CM locs. 931, 932), and two in a previously unnamed sequence of strata that is not referrable to either of these members (UCM locs. 80062, 81008; Stucky and Krishtalka, 1982). This sequence is here termed the "Red Creek facies." One of us (Stucky, 1982; in preparation) has proposed that three of the localities in the Lost Cabin Member (CM loc. 34; UCM locs. 79040, 80061) are not Lostcabinian but Gardnerbuttean (Robinson, 1966), which is now thought to represent the earliest part of the Bridgerian, and is older than Bridger A (McGrew and Sullivan, 1970). Briefly, this conclusion is based on: (1) the restriction of *Lambdotherium* to localities in the Red Creek facies and lower part of the Lost Cabin Member of the Wind River Formation, and to localities in other basins in western North America that preserve Wasatchian faunas; (2) the first appearance of *Antiacodon, Trogosus, Palaeosyops, Hyrachyus,* and other taxa at localities in the upper part of the Lost Cabin Member; these localities are stratigraphically above those that record the last appearance of *Lambdotherium*; faunas with these taxa from other basins in western North America have traditionally defined the Bridgerian Land Mammal Age. For the same reasons, an early Bridgerian Age is assigned to faunas from the upper part of the Huerfano Formation (Huerfano B) and the Cathedral Bluffs tongue of the Wasatch Formation, a conclusion also advocated by West (1973), West and Dawson (1973), and Gingerich (1979). The Bridgerian age of taxa from localities in the upper part of the Lost Cabin Member is reflected in the systematics section below. In addition, we recognize that the Bridger Basin is structurally a part of the Green River Basin. We continue its use as a geographic reference in deference to historical tradition and greater geographic precision.

SYSTEMATICS

Family Didelphidae Gray, 1821

In the most recent review of Tertiary didelphids Crochet (1977, 1979) recognized five genera: *Peratherium* Aymard, 1850 (four species, early Eocene–Oligocene, Europe); *Amphiperatherium* Filhol, 1879 (four species, early Eocene–middle Miocene, Europe); *Herpetotherium* Cope, 1873 (six species, early Eocene–early Miocene, North America); *Peradectes* Matthew and Granger, 1921 (four species, late Paleocene–middle Eocene, North America; two species, early Eocene, Europe); and *Nanodelphys* McGrew, 1937 (two species, middle Eocene–middle Oligocene, North America). Bown and Rose (1979) subsequently named a new didelphid genus, *Mimoperadectes.*

The six species of *Herpetotherium* had long been included in *Peratherium* (Cope, 1884; Simpson, 1928, 1968; Setoguchi, 1975; Green and Martin, 1976), but Crochet (1977) resurrected the former on the basis of two diagnostic features—dominance of stylar cusp D on the upper molars (as opposed to B) and a less reduced talonid on the last molar. These features alone do not seem to warrant recognition of *Herpetotherium,* and are, in any case, variable within and among the North American Eocene species he attributed to *Herpetotherium.* Fox (manuscript; personal communication, 1982), however, recognizes *Herpetotherium* for the type species, *H. fugax,* based on unique features of the anterior dentition, as well as the characters outlined by Crochet (1977, 1979) for the upper and lower molars. Accordingly, *Peratherium* is retained here for five North American Eocene species (see below), at least until *H. fugax*-like anterior dentitions are recovered for these species. In agreement with Bown (1979), and as discussed elsewhere (Krishtalka and Stucky, 1983*a*), *Nanodelphys* is a junior synonym of *Peradectes.* Thus, recognized genera of North American Tertiary didelphids are: *Peratherium, Herpetotherium, Peradectes, Mimoperadectes,* and a new genus from the Wind River Formation, *Armintodelphys.*

Until most recently, identification of these genera relied primarily on features of the upper molars. Lower molars were thought to be of little diagnostic value until Setoguchi (1973, 1975) and Crochet (1977, 1979) distinguished *Peratherium* from *Peradectes* and *Nanodelphys* on discrete differences in the structure of the hypoconulid-entoconid complex. Bown (1979) and Rose (1981) also adopted these criteria. Crochet's (1979) two tribes of didelphines—Didelphini and Peradectini—can be distinguished by diagnostic characters on their lower molars, including the structure of the hypoconulid, entoconid, and entoconid notch, and the comparative size of the trigonid and talonid. Also useful on the upper molars is the size of the conules, stylar cusp C, and the paracone and metacone, the presence or absence of dilambdodonty, and the shape of the posterolingual area of the protocone.

Tribe Didelphini Crochet, 1979

North American Tertiary genera in this tribe are *Peratherium* and *Herpetotherium.* Unlike members of the Peradectini, these genera have tall, spire-like entoconids, much lower, posteriorly projecting hypoconulids, and deep, wide entoconid notches on M_{1-4}. M^{1-3} have a posterolingually expanded protocone, strong conules and stylar cusp C, dilambdodonty, and lower paracone than metacone.

Peratherium Aymard, 1850

Peratherium (and *Herpetotherium*) are distinct from other genera of North American Tertiary didelphids in three major features of the molar dentition. (1) On M^{1-3} the paracone is at least half the size and height of the metacone—often and in part a function of wear (in unworn specimens the paracone may be only slightly lower than the metacone; see Fig. 4); (2) the centrocrista is dilambdodont; (3) on M_{1-3} the entoconid is large, high and conical, whereas the hypoconulid is a much lower, flat, shelf-like cusp that projects posteriorly behind the entoconid. Although the two cusps are twinned, they are separated by a wide, deep valley (entoconid notch). In the other North American Tertiary didelphids, all of which belong to the Peradectini (except possibly *Thylacodon pusillus*; Krishtalka and Stucky, 1983*a*), the paracone and metacone are more nearly subequal and not dilambdodont; the entoconid and hypoconulid are smaller, subequal, and more closely twinned; the two cusps arise from a common internal talonid wall and are separated by a much weaker entoconid notch. *Peratherium* lacks the distinctive anterior dentition of *Herpetotherium.*

Our analysis has led to the recognition of five Eocene species of *Peratherium.* In order of decreasing size they are: *P. comstocki* Cope, 1884; *P. edwardi* Gazin, 1952; *P. marsupium* Troxell, 1923; *P. knighti,* McGrew, 1959; and *P. innominatum* Simpson, 1928.

Peratherium morrisi Gazin, 1962, from the Cathedral Bluffs tongue of the Green River Formation, southwestern Wyoming, is a junior synonym of *P. knighti*; the type of the former is indistinguishable from lower molars in McGrew's (1959) hypodigm of *P. knighti.* Setoguchi (1973), misled by Gazin's (1952) figure of *P. morrisi,* erred when he suggested that this species belonged in either *Peradectes* or *Nanodel-*

phys. The type of *P. morrisi* bears the entoconid-hypoconulid structure that is characteristic of *Peratherium* and is close in size to *P. knighti.*

The type of *Entomacodon minutus* Marsh, 1872, is, as suggested by Robinson (1968), a marsupial and is also conspecific with *Peratherium knighti. Peratherium* has priority over *Entomacodon,* as does *E. minutus* over *P. knighti,* but the resultant *P. minutum* (Marsh, 1872) is preoccupied by *P. minutum* (Aymard, 1846). In sum, *P. knighti* includes *E. minutus* and *P. morrisi.* We have identified two teeth (M_1, CM 42139; M_2 or M_3, UCMP 59131) of *P. knighti* from the Four Mile fauna (McKenna, 1960), extending the earliest known record of this species from the early Bridgerian to the early Wasatchian.

Peratherium chesteri Gazin, 1952, from the La Barge fauna, has been transfered to *Peradectes* (Setoguchi, 1973; Bown, 1979), an action with which we agree.

As discussed in detail below, *Peratherium innominatum* Simpson, 1928, belongs in *Peratherium* rather than *Peradectes* (contra Setoguchi, 1973; Bown, 1982), and *P. macgrewi* Bown, 1979 is a Graybullian subspecies of *P. innominatum.*

Finally, although Setoguchi (1973) and Bown and Rose (1979) advocated synonymy of *Peratherium edwardi* Gazin, 1952 with *P. comstocki,* we recommend at least tentative recognition of *P. edwardi.* The type, USNM 19200, and a referred specimen, USNM 19206, both from the La Barge fauna, are, as Gazin indicated, intermediate in size between *P. comstocki* and *P. marsupium*; until a larger sample of this species is recovered, allocation of *P. edwardi* to either *P. comstocki* or *P. marsupium* is unwarranted.

Peratherium comstocki Cope, 1884

(Fig. 1, 2; Table 1, 2)

Type.—AMNH 4252, partial left dentary with M_{2-3}.

Type locality.—Uncertain. Cope (1884) reported the type from the "badlands of the Wind River, Wyoming," and named the species for Professor Theodore D. Comstock, a geologist from Cornell University, who had explored the Wind River region. Matthew (1899:31) listed the type as "*Didelphys*" *comstocki* from the Bighorn Basin, and since then both basins have been cited as the type locality. Matthew (1909: 92), Osborn (1909:46), Troxell (1923) and Hay (1930) favored the Wind River Basin; Simpson (1928) and later students, the Bighorn Basin. Cope (1884) acknowledged his error (Cope, 1880) in describing a Bighorn Basin collection of Eocene vertebrates as coming from the Wind River Basin, but it appears that the three type specimens in that collection did not include AMNH 4252 (Gazin, 1953; Gingerich, 1980). Whatever the answer to this little mystery, *P. comstocki* has since been

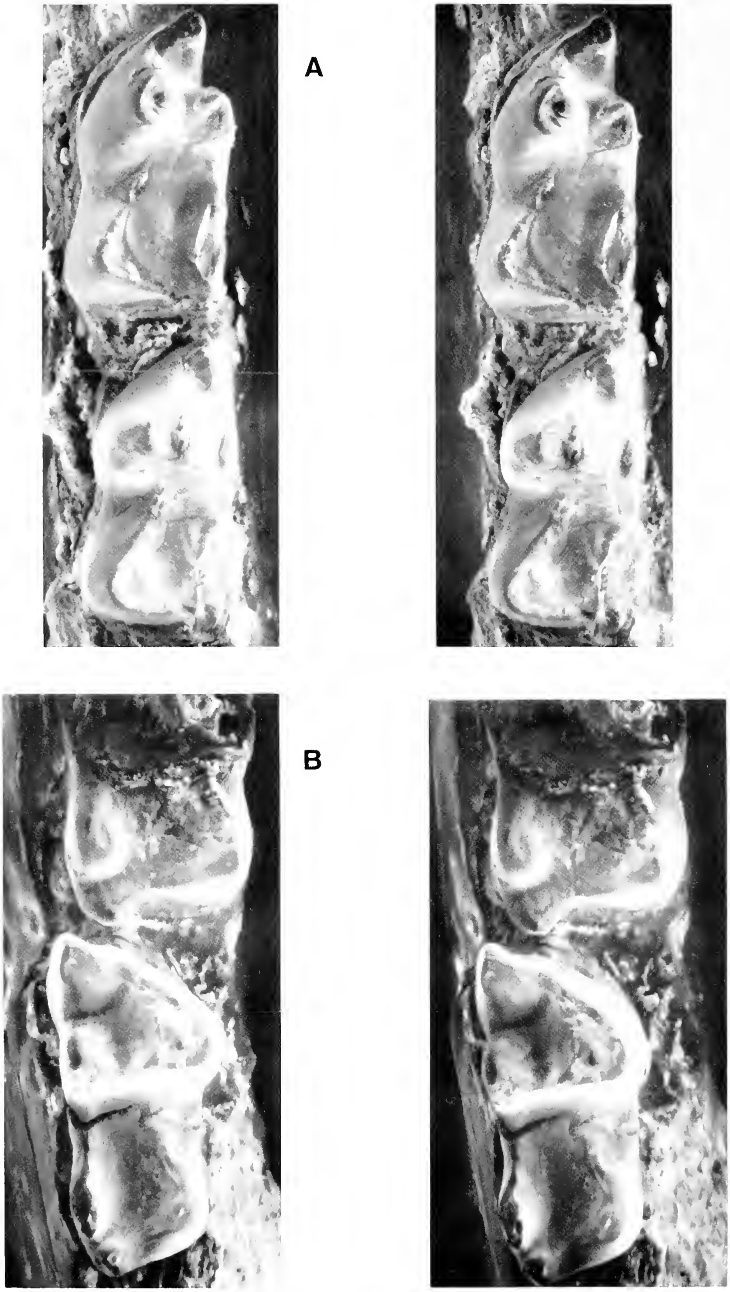

Fig. 1.—*Peratherium comstocki.* (A) CM 55562, LM$_{1-2}$; (B) CM 21126, LM$_{3-4}$; both approx. × 15.

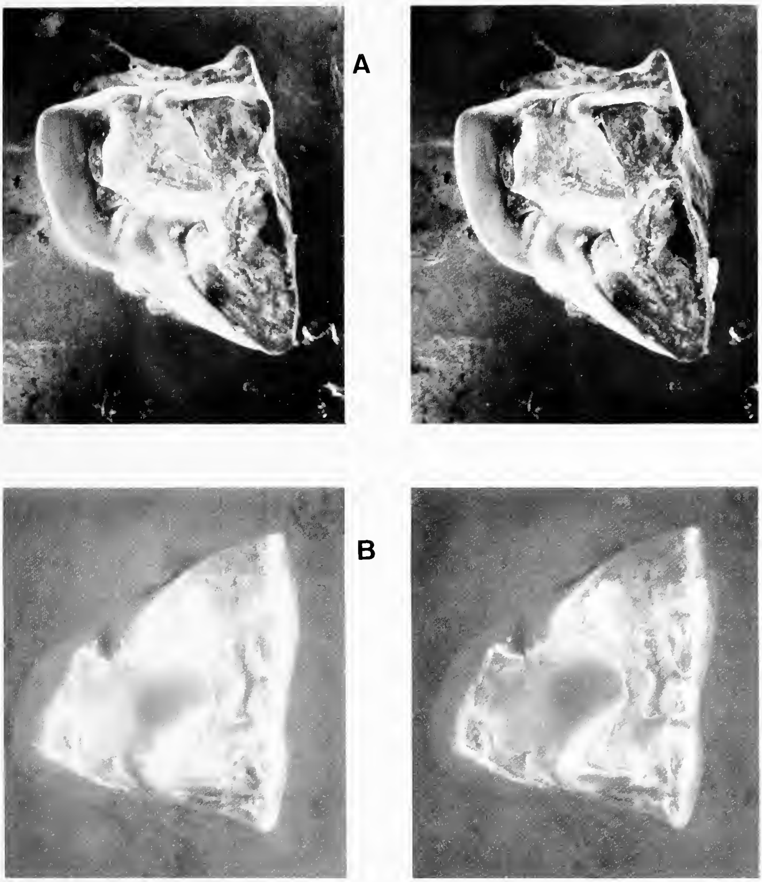

Fig. 2.—*Peratherium comstocki.* (A) CM 35842, LM^1; (B) UCM 44573, RM^2; both approx. × 14.

recovered from both the Bighorn and Wind River basins (Guthrie, 1971; Schankler, 1980; this paper).

Referred specimens.—M_{2-3}—CM 40078, 55567; M_{1-2}—CM 55562; M_{3-4}—CM 21126; M_1—CM 55561; M_4—CM 40079; M^1—CM 35842; M^2—UCM 44573; upper molar frag., UCM 45337.

Localities.—CM loc. 34 (Gardnerbuttean, Lost Cabin Member); UCM loc. 80062 (Lostcabinian, Red Creek facies); both in the Wind River Basin (Wind River Fm.), Wyoming.

Known distribution.—Wasatchian—Wind River Basin (Wind River

Table 1.—*Dimensions of lower molars of* Peratherium *and* Armintodelphys, *new genus, from the Wind River Formation, northcentral Wyoming.*

Museum and catalog no.	Locality	M_1		M_2		M_3		M_4	
		L	W	L	W	L	W	L	W
Peratherium comstocki									
CM 55561	34	2.7	1.6						
CM 55562	34	2.7	1.6						
CM 55567	34			3.1	2.0				
CM 55568	34			3.1	2.2				
CM 40078	34			3.0	2.0	3.0	2.0		
CM 21126	34						2.0	3.0	1.4
CM 40079	34							2.9	1.4
Peratherium marsupium									
CM 41157	34		1.3						
UCM 45234	79040			2.7	1.5				
CM 37099	931			2.6	1.6	2.7	1.6		1.2
UCM 42869	79040					2.9	1.7		
Peratherium innominatum									
UCM 44576	80062	1.6	0.8						
UCM 42864	79040	1.8	1.0						
UCM 44866	80061			1.7	1.0				
UCM 42870	79040			1.7	1.0				
UCM 42865	79040			1.9	1.1				
CM 22001	90			1.7	1.0				
CM 36531	34			1.7	1.1				
Armintodelphys blacki									
CM 41159 (Type)	1039					2.2	1.1	2.2	0.9
CM 41161	1040						1.0		
UCM 45252	80061			2.0	1.1				
Armintodelphys dawsoni									
CM 55560	34			1.5	0.9				
CM 55569 (Type)	34				0.8	1.5	0.8		

Fm.), Bighorn Basin (Willwood Fm.), Wyoming; ?San Juan Basin (San Jose Fm., Lucas et al., 1981), New Mexico. Earliest Bridgerian—Wind River Basin (Wind River Fm.), Wyoming; Huerfano Basin, (Huerfano Fm.), Colorado (*P.* cf. *comstocki,* Simpson, 1968). Late Bridgerian—Bridger Basin (Bridger Fm.), Wyoming. Late Bridgerian or early Uintan—Agua Fria (lower Buck Hill Group; West, 1982), Texas.

Emended diagnosis.—Largest known North American Eocene species of *Peratherium*; M^{1-2} with greatly enlarged stylar cusps; labial expansion of stylar cusps B and D create shallow ectoflexus; cusp C medial, equidistant and separate from B and D; lower molars with proportionately longer talonids.

Table 2.—*Dimensions of upper molars of* Peratherium *from the Wind River Formation, north-central Wyoming.*

Museum and catalog no.	Locality	M^1		M^2		M^3		M^4	
		L	W	L	W	L	W	L	W
Peratherium comstocki									
CM 35842	34	3.1	2.8						
UCM 44573	80062			2.8	3.3				
Peratherium marsupium									
CM 41165	1085	2.5	2.6						
UCM 44870	80061					2.7	2.5		
UCM 44580	80062					2.6	2.7		
UCM 44545	79040					2.7	2.9	2.3	2.8
Peratherium innominatum									
UCM 44869	80061	1.6	1.8						
UCM 42872	80061	1.6	1.6						
UCM 45285	80061			1.9	1.7				
UCM 44867	80061							1.3	1.9

Description.—On the first three lower molars the entoconid is large, high and conical, and is isolated from the proximal hypoconulid by a deep, wide notch. The hypoconulid, flat and shelf-like, juts posteriorly behind the entoconid. The talonid is longer and wider than the trigonid, the paraconid is the lowest of the trigonid cusps, and the metaconid is lingual and slightly posterior to the higher protoconid. The precingulid is strong but short, ending posteriorly at the base of the crown below the apex of the protoconid. The hypoconid is broader than the entoconid, but the two cusps are subequal in height. The cristid obliqua is slightly convex labially and meets the trigonid below and labial to the notch of the protocristid. The postcristid descends posterolingually from the apex of the hypoconid to the hypoconulid. From the latter a postcingulid extends labially to the posterior part of the base of the hypoconid.

M_1 is shorter and narrower than M_2 or M_3 and its paraconid leans more anterodorsally. M_4 differs from the other lower molars in having a more elongate talonid that is also narrower than the trigonid, a broader paraconid than metaconid, and in lacking a postcingulid.

The only known M^1 (CM 35842) bears a large metastylar wing and a weak ectoflexus, which is formed by the labial expansion of stylar cusps B and D. The protocone occurs anteriorly, in line with the paracone and stylar cusp B, so that the posterolingual face of the protocone is expanded and slightly "squared-off." The paracone and much higher metacone are subcrescentic and dilambdodont, with a buccally directed centrocrista. The stylar shelf is worn, but it appears that cusp D, elongate in shape, was dominant in the unworn condition, followed in size by cusp B and subequal cusps C and A. A ridge, perhaps developed through wear, joins cusp C to the buccal extension of the centrocrista.

On M^2 (UCM 44573) all of the stylar cusps appear hypertrophied. Cusp D, conical rather than elongate, is slightly larger than cusp B, and both are approximately twice as large as the subequal C and A cusps. Cusp C is equidistant from cusps B and D and directly buccal to the apex of the centrocrista. A slight ectoflexus between cusps B and D is more a function of the labial expansion of these cusps than a true emargination of the stylar shelf. Cusps B, C, and D are separated by acute notches, whereas a weak ridge connects cusps A and B.

Discussion.—The referred lower and upper molars bear the diagnostic features of *Peratherium* described above. These teeth are significantly larger than those assigned below and in other studies to either *P. marsupium, P. knighti,* or *P. innominatum.* M_2 and M_3 agree in size and structure with those on the type of *P. comstocki.* The first and second upper and lower molars referred here were previously unknown for this species. CM 21126, cited in Guthrie (1971) as M_{2-3}, preserves M_4 and part of M_3.

We agree with Simpson's (1968) allocation of UCM 26541, from the upper part of the Huerfano Formation, to *Peratherium* cf. *comstocki.* This specimen, and those from CM loc. 34 are the first records of this species from the early Bridgerian. CM 13901, M_{3-4} from the upper part of the Bridger Formation, extends the range of *P. comstocki* into the late Bridgerian, and the material from Agua Fria allocated to this species (West, 1982) may be late Bridgerian or early Uintan. Finally, AMNH 56307, originally described as an M_4 of *P. comstocki* from the early Eocene of the Powder River Basin (Delson, 1971), was subsequently identified as an M_2 of *Mimoperadectes* (Bown and Rose, 1979).

Peratherium marsupium (Troxell, 1923)
(Fig. 3; Table 1, 2)

Type.—YPM 13518, partial right dentary with P_3, M_{1-3}.
Type locality.—Bridger Basin, Wyoming.

Referred specimens.—M_{2-4}—CM 37099; M_1—CM 41157, 41158; M_2 or M_3—UCM 42869, 44336, 45234; M_4—UCM 46719; M^{3-4}—UCM 45545; M^1—CM 41165; M^3—UCM 44580, 44870; DP^3—UCM 44574.

Localities.—CM loc. 931 (Lysitean, Lysite Member); CM loc. 34, UCM locs. 80061, 79040 (Gardnerbuttean, Lost Cabin Member); UCM loc. 80062 (Lostcabinian, Red Creek facies); CM loc. 1085 (subage uncertain, Lost Cabin Member); all in the Wind River Basin (Wind River Fm.), Wyoming.

Known distribution.—Wasatchian through Duchesnean—Wind River Basin (Wind River Fm.; Wagon Bed Fm.), Wyoming. Bridgerian—Bridger Basin (Bridger Fm.), Bighorn Basin (Blue Point Member; Eaton, 1982), Wyoming; Uinta Basin (Green River Fm.), Utah (Krishtalka and Stucky, 1983*b*). Late Bridgerian or early Uintan—Sand Wash Basin (Washakie Fm.), Wyoming; Agua Fria (lower Buck Hill Group; West, 1982), Texas.

Emended diagnosis.—Larger than *P. knighti* and *P. innominatum*; smaller than *P. comstocki* and *P. edwardi*; unlike *P. comstocki,* stylar

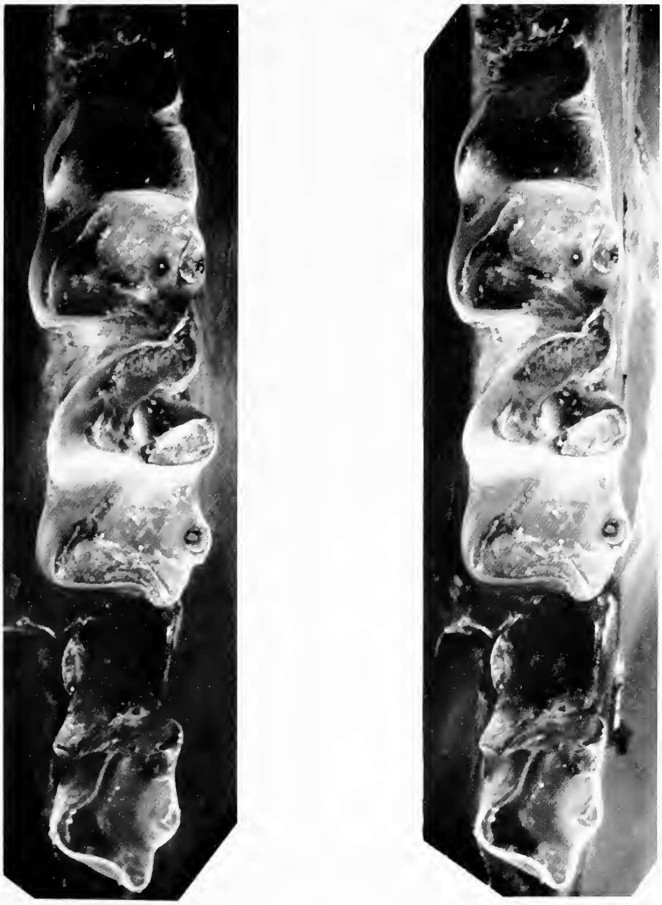

Fig. 3.—*Peratherium marsupium.* CM 37099, LM_{2-3}; approx. × 13.

cusps not bulbous labially; unlike *P. knighti,* ectoflexus deeper on M^2 and especially M^3.

Description.—The lower molars closely resemble those of *P. comstocki* except for two features also noted by Simpson (1928): smaller size and slightly shorter talonids in proportion to the trigonids. M^1, like that of *P. comstocki,* has a large metastylar salient, and M^{1-3} have an anterior protocone that is elongated posterolingually. On the only referred M^1—a worn specimen—stylar cusps B and D are subequal and small, followed in size by cusp A and a tiny cusp C. There is no evidence of a cusp E. On M^{2-3} cusp A is absent, cusp C is joined to D, and the metaconule is larger than the paraconule. Unlike on M^{1-3}, the paracone is dominant on M^4, cusp A is the only stylar cusp, and the crown is quadrate. A stylar ridge extends from posterior to cusp A to the area labial to the metacone. The DP^3 referred here (UCM 44574) lacks a stylar shelf and has a bulbous metacone.

Discussion.—The recovery of *P. marsupium* from the Wind River Formation represents the first Wasatchian record of this species and, with *P. innominatum,* the first known occurrence of marsupials in the Lysite Member. One of the specimens (CM 23194) that West and Dawson (1975) assigned to *P. marsupium* is closer in size and referred to *P. knighti.*

Peratherium innominatum Simpson, 1928
(Fig. 4; Table 1, 2)

Type.—AMNH 11493, partial left dentary originally preserving M_{1-4}.

Type locality.—Millersville, Lower Bridger, Bridger Basin, Wyoming.

Referred specimens.—M_1—UCM 44576, 42864, 44606; M_2 or M_3—CM 22001, 36531, 36967, UCM 44578, 42865, 42870, 42866; M_4—UCM 44575, 44577; M^1—UCM 42872, 44869; M^2, M^3—UCM 46614; M^2—UCM 45285; M^2 or M^3—UCM 44868, CM 22000, 55564; M^4—UCM 44881, 44867, 45255; upper molar fragment, UCM 44579.

Localities.—CM loc. 932 (Lysitean, Lysite Member); UCM locs. 80062, 81008 (Lostcabinian, Red Creek facies); CM loc. 90 (?Lostcabinian, Lost Cabin Member); CM loc. 34, UCM locs. 79040, 80061 (Gardnerbuttean, Lost Cabin Member); all in the Wind River Basin (Wind River Fm.), Wyoming.

Known distribution.—Wasatchian—Wind River Basin (Wind River Fm.), Bighorn Basin (Willwood Fm., record of *P. macgrewi,* see below), Wyoming; Four Mile area (Wasatch Fm.; see below), Colorado. Bridgerian—Wind River Basin (Wind River Fm.), Bridger Basin (Bridger Fm.), Bighorn Basin ("Aycross-like beds," Eaton, 1982), Wyoming; Uinta Basin (Green River Fm.), Utah. Uintan and Duchesnean—Wind River Basin (Wagon Bed Fm.), Wyoming.

Emended diagnosis.—Much smaller than *P. comstocki* and *P. marsupium*; consistently smaller than *P. knighti*; also differs from *P. knighti* in having distinct ectoflexus on M^2 and especially on M^3.

Description.—The lower molars referred here resemble the type, AMNH 11493, in size and in having tall entoconids, low, posteriorly projecting hypoconulids, deep, wide entoconid notches, and compressed trigonids. The upper molars have much higher metacones than paracones and posterolingually expanded protocones. On M^1 (UCM 42872) stylar cusp B is well-developed and equal in size to a twinned C + D cusp, which occurs labial to the premetacrista. The anterior border of cusp C is directly labial to the dorsal apex of the centrocrista and separated by a large gap from cusp B. The stylar shelf is indented by a weak ectoflexus between cusps B and C. Stylar cusp A is extremely weak; there is no cusp E. On M^2 (UCM 45285), B is the largest of the stylar cusps; cusps C and D—proximal but separate—and A are subequal and larger than E.

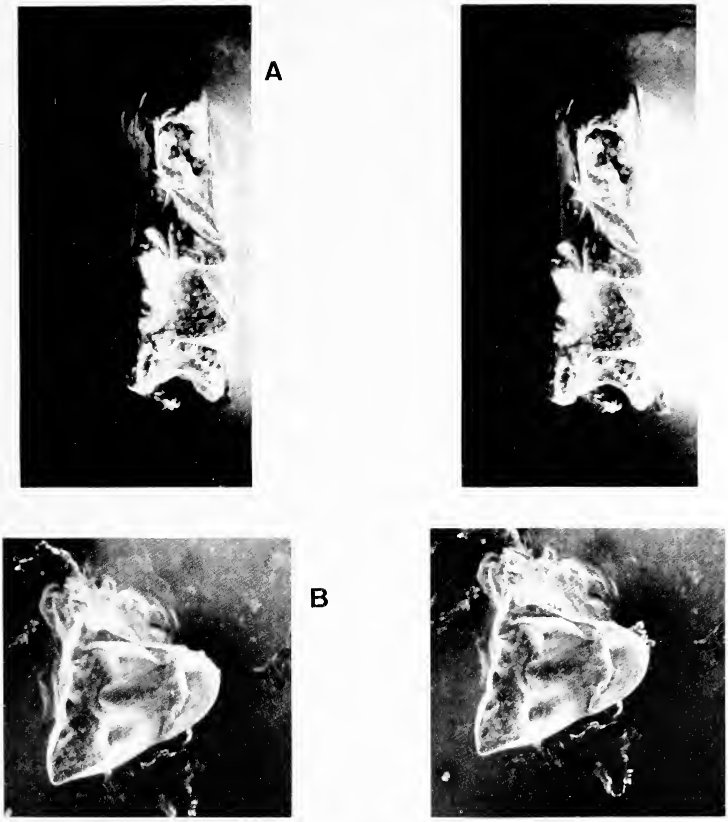

Fig. 4.—*Peratherium innominatum.* (A) CM 36531, RM$_2$ or M$_3$, approx. × 14; (B) UCM 45285, RM^2; approx. × 11.

Discussion.—Setoguchi (1973) and Bown (1982) allocated *Peratherium innominatum* to *Peradectes.* When Simpson (1928) described the type, AMNH 11493, it preserved M$_{1-4}$. Unfortunately, M$_1$ is now missing, and the entoconid and protoconid of M$_3$ are broken, apparently due to subsequent attempts at further preparation and/or casting of the specimen. Nevertheless, the size of the entoconid on M$_2$ and its broken base on M$_3$ is clearly *Peratherium*-like. In these diagnostic features, as well as in the size and morphology of M$_{2-4}$, AMNH 11493 is virtually identical to large samples of *Peratherium* from Powder Wash, Uinta Basin, and from the Wind River Formation. These samples are described here and elsewhere (Krishtalka and Stucky, 1983*b*) as *Peratherium innominatum.*

The two teeth (CM 22000, CM 22001) that Guthrie (1971) assigned to *Peratherium* cf. *P. chesteri* are referred here to *P. innominatum.* A lower jaw that West (1973, Pl. 1, Fig. B; PM 15320) figured and referred to *P. innominatum* may not be a marsupial; two other specimens (West, 1973: Pl. 1, Fig. C, D; PM 15682, PM 15866) he identified as *P. innominatum* are referrable to *Peradectes chesteri.* UW 984 from Tabernacle Butte, identified as *Peratherium* cf. *innominatum* by McGrew (1959), bears the diagnostic features of *Peradectes* and is referred below and elsewhere (Krishtalka and Stucky, 1983*a*) to *P. chesteri.* Our analysis of the Badwater late Eocene didelphids indicates that Setoguchi's (1975) sample of *Peratherium* cf. *P. knighti* includes specimens of *P. knighti* and *P. innominatum.*

P. innominatum is closest in size and morphology to *P. knighti* and *P. macgrewi.* The teeth are smaller than those of *P. knighti* and M^{2-3} have more distinct ectoflexi. Distinction of *P. innominatum* from *P. macgrewi* other than on mean size is not possible with the known material. Except for M_1, upper and lower molars of *P. innominatum* are slightly but consistently larger. The current stratigraphic record and the close similarity between the Graybullian *P. macgrewi* and the Lysitean through early Bridgerian *P. innominatum,* imply an ancestor-descendant relationship between the two that involved a slight increase in size. Similar anagenetic increase in size occurs between the Wind River Formation population of *P. innominatum* and that from Powder Wash, Green River Formation, Utah (Krishtalka and Stucky, 1983*b*). *P. macgrewi* is reduced in rank to a subspecies of *P. innominatum* for biostratigraphic purposes (Simpson, 1961:175).

Peratherium innominatum macgrewi (Bown, 1979), new rank

This temporal subspecies of *P. innominatum* is known only from Graybullian horizons in the Bighorn Basin and the Sand Wash Basin. We have identified an isolated M_2 or M_3 (CM 42137) of *P. i. macgrewi* from Sand Quarry, Four Mile fauna, Colorado. Also, as noted by McKenna (1960, Fig. 18a), UCMP 44095 from Kent Quarry is *Peratherium*-like. The disparity in height between the paracone and metacone on M^{1-2}, the dilambdodont centrocrista, and the expanded posterolingual area of the protocone distinguish this specimen from contemporaneous *Peradectes* in the Four Mile sample. The size of M^{1-2} on UCMP 44095 is within the range of these teeth in the hypodigm of *P. i. macgrewi* from the type area (Bown, 1979). Also, one of the upper molars in UW 9742 that Bown (1979, Fig. 40A, center) identified as *P. chesteri* is dilambdodont and belongs to *P. i. macgrewi.*

Tribe Peradectini Crochet, 1979

North American Tertiary genera in this tribe are *Peradectes* (including *Nanodelphys,* see Bown, 1979; Krishtalka and Stucky, 1983*a*), *Mimoperadectes,* and *Armintodelphys,* the new genus from the Wind River Formation. They differ from *Peratherium* in that M_{1-4} bear a low or very reduced entoconid, a closely twinned and dorsally projecting hypoconulid, and a weak or vestigial entoconid notch. Additionally, M^{1-3} have a V-shaped protocone (no posterolingual expansion), conules and stylar cusp C that are small to absent, no dilambdodonty, and a paracone that is as high as or slightly lower than the metacone.

Peradectes Matthew and Granger, 1921

Peradectes is much smaller than *Mimoperadectes* and has a larger metaconid than paraconid on M_{2-4}. Compared to *Armintodelphys,* lower molars of *Peradectes* retain subequal hypoconulid and entoconid and an entoconid notch.

Our revision of the systematics of Paleogene North American didelphids (Krishtalka and Stucky, 1983*a*) indicates that there are six discernable species of *Peradectes*: *P. elegans* Matthew and Granger, 1921; *P. pauli* Gazin, 1956; *P. protinnominatus* McKenna, 1960; *P. chesteri* (Gazin, 1952); *P. californicus* (Stock, 1936; see Lillegraven, 1976); *P. minutus* (McGrew, 1937). Of these, only *P. chesteri* has been found in the Wind River Formation. *Thylacodon pusillus* may also be a species of *Peradectes* (Clemens, 1979) and is under study elsewhere (see Archibald, 1982).

Peradectes chesteri (Gazin, 1952)

Type.—USNM 19199, right partial dentary with M_3.

Type locality.—Upper part of the Wasatch Formation (="Upper Knight beds"), La Barge, Wyoming.

Referred specimen.—M^1—UCM 45288.

Locality.—UCM loc. 80061 (Gardnerbuttean, Lost Cabin Member), Wind River Basin (Wind River Fm.), Wyoming.

Known distribution.—Late Wasatchian—Green River Basin (Wasatch Fm.), Wyoming. Bridgerian—Wind River Basin (Wind River Fm.), Green River Basin (Bridger Fm.), Wyoming; Uinta Basin (Green River Fm.), Utah.

Emended diagnosis.—Compared to *P. elegans*: teeth smaller; M_1 smaller than M_2; M_3 talonid narrower (basally) than trigonid; compared to *P. elegans* and *P. pauli*: P_3 lower than M_1 and with shorter talonid; M_4 talonid shorter than trigonid; compared to *P. elegans, P. pauli* and *P. protinnominatus*: M_{1-3} talonids with narrower occlusal width (hypoconid more internal); compared to *P. elegans, P. pauli, P. protinnominatus* and *P. californicus*: greater disparity in L/W ratio from M^1 to M^3; conules and stylar cusps vestigial; M^3 more transverse with a more highly compressed protocone; M_{1-3} narrower in proportion to length, with no labial emargination between trigonid and talonid; compared to *P. californicus*: P_3 talonid present; compared to *P. minutus*: M^{1-3} paracone higher than protocone and stylar cusp B; stylar cusp B not enlarged; M^3 and especially M^2 less transverse, with less compressed protocone; gap between M_4 and ascending ramus present.

Description.—The isolated M^1 ($L = 1.2$; $W = 1.1$) is abraded, but preserves the diagnostic features of the species. As in the sample of upper molars from Powder Wash (Krishtalka and Stucky, 1983*b*), the paracone is slightly lower than the metacone, but higher than the protocone and stylar cusp B. Conules and stylar cusps other than B are absent or were worn away.

Discussion.—Setoguchi (1973) and Bown (1979) correctly allocated *Peratherium chesteri* to *Peradectes,* based on the entoconid-hypoconulid configuration on the lower molars. These authors and Rose (1981) also considered *P. chesteri* a senior synomym of *P. protinnominatus,* a conclusion that is at odds with our analysis of the material. As discussed elsewhere (Krishtalka and Stucky, 1983*a*), *P. protinnominatus* is a valid species and includes the Clarkforkian and early Wasatchian material from the Bighorn Basin that Bown (1979) and Rose (1981) referred to *P. chesteri.*

The most complete known specimen of *P. chesteri* is UW 984, a lower jaw with P_3–M_4 from Tabernacle Butte, which was previously identified as *Peratherium* cf. *innominatum* (McGrew, 1959) and *Peradectes* sp. cf. *P. innominatus* (Bown, 1982). *P. innominatum* was shown above to be a species of *Peratherium* rather than *Peradectes,* and UW 984 bears the hypoconulid-entoconid complex of the latter. M_3 on UW 984, as on the type of *P. chesteri,* is smaller than that of *P. elegans* and has a narrower talonid than trigonid. It is also smaller than M_3 of *P. pauli* and *P. protinnominatus,* and the buccal contour at the base of the crown between the trigonid and talonid is less emarginate. In addition, the morphology of P_3–M_4 on UW 984 indicates that, in contrast to *P. elegans, P. pauli* and *P. protinnominatus*: molars of *P. chesteri* have lower trigonids; P_3 is lower than M_1, M_{1-3} are narrower in proportion to length, have narrower talonids and a more nearly straight buccal margin basally; and M_4 has a shorter talonid than trigonid. Unlike the condition in *P. elegans,* M_1 is smaller than M_2. *P. chesteri* differs from *P. californicus* in having a talonid on P_3 and from *P. minutus* in retaining the gap between M_4 and the ascending ramus.

Apart from the single upper molar referred here, upper molars of *P. chesteri* have been recovered from Powder Wash (Krishtalka and Stucky, 1983*b*) and the Green River Basin (West, 1973, Figs. C, D; PM 15682, PM 15866). They differ from upper molars of all North American species of *Peradectes* except *P. minutus* in having more transverse M^{2-3}, vestigial conules and stylar cusps C and D, and a more compressed protocone, especially on M^3. In contrast to *P. minutus,* in *P. chesteri* M^{1-3} have a higher paracone than protocone and stylar cusp B, and a smaller stylar cusp B, and M^2 is less transverse, with a less compressed protocone.

The features of the upper and lower dentition of *P. chesteri,* and its temporal distribution, suggest that this species is intermediate morphologically and phylogenetically between *P. protinnominatus* and *P. minutus.*

Armintodelphys, new genus

Etymology.—Arminto, a hamlet in Natrona County, Wyoming; *delphys,* Gr., womb, a common suffix for generic names of marsupials.

Type species.—Armintodelphys blacki, new species.

Included species.—Type species and *A. dawsoni,* new species.

Diagnosis.—Differs from all North American Tertiary didelphines as follows: 1) entoconid lower and smaller than the hypoconulid, with no entoconid notch; 2) talonid narrower (basally) than the trigonid on M_{1-2}. Smaller than *Mimoperadectes* and with smaller paraconid than metaconid on M_{2-4}.

Known distribution.—Latest Wasatchian to earliest Bridgerian—Wind River Basin (Wind River Fm.), Wyoming.

Discussion.—Armintodelphys is the fifth known genus of North American Tertiary didelphines and, along with *Peradectes* and *Mimoperadectes,* is included in the Tribe Peradectini Crochet, 1979 (as emended here).

Armintodelphys is more derived than species of *Peradectes* in having an entoconid that is much smaller and lower than the hypoconulid on M_{2-4}. *Peradectes* retains the primitive condition (for the Peradectini) of an entoconid that is slightly taller than or subequal to the hypoconulid. A revision of the species of *Peradectes* (Krishtalka and Stucky, 1983*a*) indicates that *Armintodelphys* most closely resembles *Peradectes pauli* in the buccal emargination of the base of the crown between the trigonid and talonid of M_{2-3}, the longer talonid than trigonid on M_4, and the narrower talonid than trigonid on M_3. These features imply that *Armintodelphys* evolved from or shared a common ancestry with *P. pauli.*

Armintodelphys blacki, new species
(Fig. 5; Table 1)

Etymology.—Named in honor of Craig C. Black for his contribution to the paleontology of the Wind River Basin.

Type.—CM 41159, partial left dentary with M_{3-4} and alveoli for P_3–M_2.

Type locality.—CM loc. 1039 (Buck Spring: Lost Cabin K-5), Lost Cabin Member, Wind River Formation, Natrona County, Wyoming.

Referred specimens.—Dentary fragment with M_3 talonid—CM 41161; associated P_3, M_1 trigonid, M_2, M_3 trigonid—UCM 45252.

Localities.—Type locality (Lostcabinian, Lost Cabin Member) and UCM loc. 80061 (Gardnerbuttean, Lost Cabin Member), both in the Wind River Basin (Wind River Fm.), Wyoming.

Known distribution.—Late Wasatchian to earliest Bridgerian—Wind River Basin (Wind River Fm.), Wyoming.

Diagnosis.—Largest species of *Armintodelphys*; no posterior cingulid on M_{2-3}.

Description.—Upper molars of *A. blacki* have not been recovered. The dentary, long and slender as in other didelphines, is 4.5 mm deep below M_4. The inflected angle begins just below the coronoid process and the mental foramen occurs directly below the posterior root of P_3. Alveoli preserved on the type specimen indicate that there were no diastemata between the anterior premolars. P_3 is premolariform. The single, dominant cusp—the protoconid—bears a posterolabial crest that extends from its apex to the labial border of the postcingulid, as in *Peradectes* and *Peratherium,* but in contrast to *Mimoperadectes* where this crest is posteromedial (Bown and Rose, 1979, Pl. 1, Fig. 2). No talonid cusps are present, but a talonid basin is developed posterolingual to the protoconid and anterior to the strong postcingulid.

The cusps on the trigonid fragment of M_1 are similar in size and position to M_1 of *Peratherium* and *Peradectes.* The paraconid is anterior and almost as high as the metaconid, which is directly lingual to and lower than the protoconid. Compared to M_1, the trigonids on M_2 and M_3 are wider and more compressed anteroposteriorly. A groove on the anterior face of the paraconid receives the hypoconulid of the anterior molar. On M_{2-4} the talonid is narrower than the trigonid and the cristid obliqua meets the posterior wall of the trigonid labial to the protocristid notch. The buccal base of the crown is excavated between the talonid and trigonid. A wear facet in the hypoflexid notch descends the posterior face of the trigonid to the dento-enamel border of the tooth, suggesting that, as in *A. dawsoni,* the paracone on the upper molars was as tall as the metacone. The entoconid, smaller than in *Peratherium, Peradectes,* and *Mimoperadectes,* and well-removed from the metaconid, occurs on a lingual ridge that runs from the metaconid to the hypoconulid. The latter is the tallest talonid cusp and lies posterolabial to the entoconid. On M_{2-3} the talonid notch is lower than the point at which the cristid obliqua meets the trigonid. M_4, known only in the type, resembles M_{2-3} but has a more elongate talonid, with a more medial and posteriorly projecting hypoconulid.

Armintodelphys dawsoni, new species
(Fig. 5; Table 1)

Etymology.—Named in honor of Mary R. Dawson for her contributions to the paleontology of the Wind River Basin.

Type.—CM 55569, partial dentary with talonid of M_2, M_3, and trigonid of M_4.

Type locality.—CM loc. 34 (Davis Ranch, also called Sullivan Ranch; "maroon shale" layer of Guthrie, 1971), Lost Cabin Member, Wind River Formation, Wind River Basin, Natrona County, Wyoming.

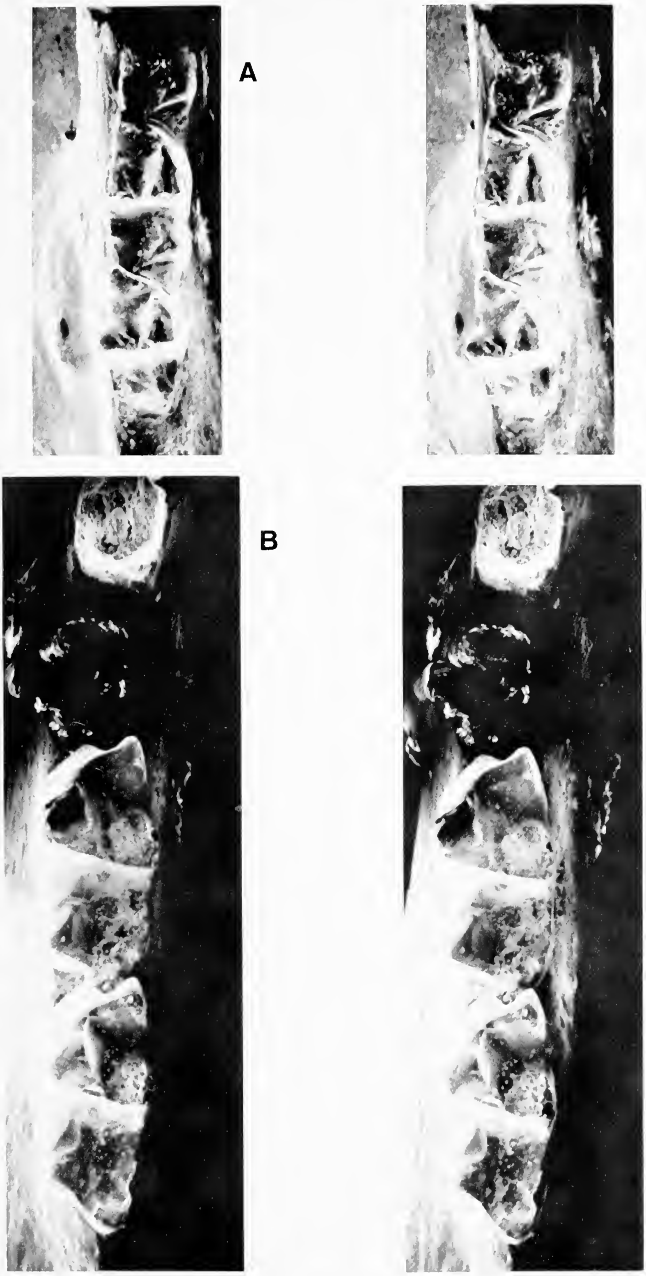

Fig. 5.—*Armintodelphys,* new genus. (A) *A. dawsoni,* new species, CM 55569, RM$_{2-4}$ (type); (B) *A. blacki,* new species, CM 41159, LM$_{3-4}$ (type); both approx. × 15.

Referred specimen.—M_2—CM 55560.

Localities.—Type locality (Gardnerbuttean) only.

Known distribution.—Early Bridgerian—Wind River Basin (Wind River Fm.), Wyoming; Uinta Basin (Green River Fm.), Utah.

Diagnosis.—Smallest species of *Armintodelphys*; differs from *A. blacki* in having a postcingulid on M_{2-3}.

Description.—The depth of the mandible below M_4 is 2.7 mm in the type specimen. Apart from the differences cited in the diagnosis, the lower molars compare favorably to those of *A. blacki* described above.

OCCURRENCES AND RELATIONSHIPS

Three lineages of *Peratherium*—*P. comstocki, P. knighti,* and *P. innominatum*—differing mainly in size, appear abruptly in the early Wasatchian; *P. comstocki* extends to the early Bridgerian, and the other two into the Duchesnean. A fourth, *P. marsupium,* ranges from the middle Wasatchian to the Duchesnean, and a fifth, *P. edwardi,* is known only from the late Wasatchian. Anagenetic change in these species is small or undetectable; four of the species are stable, whereas *P. innominatum* appears to undergo a slight increase in size. Three of these species (*P. innominatum, P. marsupium, P. comstocki*) are present in the Wind River Formation. They occur in lithosympatry at only two of the eleven localities that yielded marsupial material (CM loc. 34; UCM loc. 80062).

The Peradectini are represented in the Wind River Formation by two species in a new genus, *Armintodelphys* (*A. blacki* and *A. dawsoni*), and by *Peradectes chesteri. Armintodelphys* is most closely related to *Peradectes pauli. P. chesteri,* known from late Wasatchian to late Bridgerian horizons, appears to be morphologically and phylogenetically intermediate between *P. protinnominatus* and *P. minutus.* If this inference is correct, trends in the *P. protinnominatus-P. chesteri-P. minutus* lineage involved the development of more transverse M^{2-3} with a more compressed protocone, and reduction in the crown height of the upper and lower molars, in the conules and stylar cusps C and D, in the length and width of the talonid on the lower molars and in the buccal emargination between the talonid and trigonid on M_{1-3}.

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PALEOCENE AND EOCENE MARSUPIALS OF NORTH AMERICA

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ABSTRACT

North American Paleocene and Eocene marsupials compose two tribes of didelphines. The Didelphini contains five species of *Peratherium* (*P. comstocki, P. edwardi, P. marsupium, P. knighti, P. innominatum*). The Peradectini includes six species of *Peradectes* (*P. elegans, P. pauli, P. protinnominatus, P. californicus, P. chesteri, P. minutus*), two species of *Armintodelphys* (*A. blacki, A. dawsoni*), and one species of *Mimoperadectes* (*M. labrus*). Previous allocations of *Alphadon* and *Albertatherium* to the Peradectini, *P. innominatum* to *Peradectes, P. protinnominatus* to *P. chesteri,* and the latter to *Herpetotherium* are revised, as are the systematics of all of the species. The two tribes differ in the structure of the entoconid-hypoconulid complex on the lower molars and in the presence or absence of dilambdodonty on the upper molars. The five species of *Peratherium* show virtually no evolutionary change throughout their range in the Eocene. In contrast, the six species of *Peradectes* form a branching lineage that is characterized by cladogenetic speciation and anagenesis from the Paleocene through the Oligocene. *Armintodelphys* and *Mimoperadectes* appear to be early offshoots of that lineage.

INTRODUCTION

Marsupials occur in most early Tertiary North American faunas. The first such record was *Entomacodon minutus* Marsh, 1872, from the Bridger Basin, which was not identified as a marsupial until almost one hundred years after its original description (Robinson, 1968; Krishtalka and Stucky, 1983*a*). Similarly, *Peratherium comstocki* Cope, 1884,

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originally called a creodont, was first recognized as a didelphid by Simpson (1928), who also reviewed the systematics of *Peratherium* (=*Herpetotherium*) *marsupium* (Troxell, 1923), and named *Peratherium innominatum* from material that Matthew (1909*b*) had assigned to this genus. Matthew (1899, 1909*a,* 1909*b*) had debated the marsupial versus insectivore affinities of *E. minutus* (including *Centracodon delicatus* Marsh, 1872) and *P. comstocki* and opted for the latter. This position was colored by the late Nineteenth Century view, taken to its extreme by Wortman (1901), of a close relationship between marsupials, creodonts, and carnivores. Matthew (1909*b*:335–339) clarified the distinctions between marsupials and allegedly closely related placentals by identifying their "primitive" and "specialized" characteristics; he (p. 321) emphasized the relative importance of derived features in phylogenetic reconstructions. Indeed, Matthew's discussion, although devoid of cladistic terminology, presages what some current students believe to be the modern innovation in systematics.

In 1921, Matthew and Granger described the first records of North American Paleocene marsupials, *Peradectes elegans* and *Thylacodon pusillus.* In the next 60 years Stock (1936), McGrew (1937, 1959), Gazin (1952, 1956, 1962), McKenna (1960), Bown (1979), and Bown and Rose (1979) added six species of *Peratherium* (*P. californicum, P. knighti, P. chesteri, P. edwardi, P. morrisi, P. macgrewi*), two species of *Peradectes* (*P. pauli, P. protinnominatus*), and two new genera, *Nanodelphys* and *Mimoperadectes,* each with one species (*N. minutus, M. labrus*) to the North American Paleocene and Eocene didelphid record. Most recently, we (Krishtalka and Stucky, 1983*a*) named a new genus, *Armintodelphys,* with two species (*A. blacki, A. dawsoni*), from the early and middle Eocene of Wyoming.

Partial systematic reviews of some of these 19 species in nine genera have occurred only within the last ten years (Setoguchi, 1973, 1975; Bown, 1979, 1982; Lillegraven, 1976; Crochet, 1977, 1979), resulting in a confusing, and often conflicting, shuffling of species among *Peratherium, Herpetotherium, Peradectes,* and *Nanodelphys.* None of these studies encompassed all Paleocene and Eocene North American didelphids. In the course of describing the marsupials from the Wind River Formation (Krishtalka and Stucky, 1983*a*) it became apparent that such a study was necessary. Those didelphids recorded from the Wind River Formation (*Peratherium comstocki, P. marsupium, P. innominatum*; *Peradectes chesteri*; *Armintodelphys blacki, A. dawsoni*) were systematically revised. Remaining North American Paleocene and Eocene didelphids are revised here, except for *Thylacodon pusillus,* which is under study elsewhere (see Clemens, 1979; Archibald, 1982). Also included is a summary of the occurrences of these didelphids and a reconstruction of their evolutionary relationships.

Abbreviations used in this paper are as follows: AMNH, American Museum of Natural History; CM, Carnegie Museum of Natural History; KU, University of Kansas; LACM, Los Angeles County Museum; MCZ, Museum of Comparative Zoology, Harvard University; PM, Field Museum of Natural History; PU, Princeton University (Museum); TTU-P, Texas Tech University, Paleontology; UCM, University of Colorado Museum; UCMP, University of California Museum of Paleontology; UM, University of Michigan Museum of Paleontology: USNM, U.S. National Museum; UW, University of Wyoming; YPM, Yale Peabody Museum; Fm., Formation; L, length; W, width.

SYSTEMATICS

Family Didelphidae Gray, 1821
Subfamily Didelphinae (Gray, 1821)

Crochet (1979) separated known didelphines into two groups, the Didelphini and Peradectini, based, in part, on diagnostic features of the dentition that Setoguchi (1973) had identified earlier. These features, as well as those identified in another study (Krishtalka and Stucky, 1983*a*), indicate that members of the Didelphini have lower molars with a tall, spire-like entoconid, a lower, proximal and posterior hypoconulid, and a deep entoconid notch. Their upper molars are dilambdodont, with a lower paracone than metacone, strong conules and stylar cusps, and a posteriorly expanded protoconal base. In contrast, members of the Peradectini have lower molars with subequal and twinned entoconid and hypoconulid, and a weak or vestigial entoconid notch. Their upper molars are not dilambdodont and bear subequal paracone and metacone, a V-shaped protocone, and weak or vestigial stylar cusps and conules.

Both groups differ from known Cretaceous didelphines in having lower molars with shorter talonids and a cristid obliqua that meets the posterior wall of the trigonid labial to the protocristid notch. This implies a common ancestry for the Didelphini and Peradectini from a Cretaceous didelphine. These features, as well as those that are diagnostic of the Peradectini, also imply that *Alphadon* and *Albertatherium* do not belong in that tribe (contra Crochet, 1979).

Tribe Didelphini Crochet, 1979

According to Crochet (1979), *Herpetotherium* is the only North American Tertiary genus in this tribe and includes all North American species formerly referred to *Peratherium*. *H. fugax,* the type species, has a diagnostic anterior dentition (Fox, manuscript; personal communication, 1982). However, the characters of the molar dentition cited by Crochet (1977) in support of this synonymy are variable, at least within the North American Eocene species of Didelphini (Krishtalka and Stucky, 1983*a*)—species for which the anterior dentition is not known. Accordingly, these species are retained in *Peratherium*.

Peratherium Aymard, 1846

This genus is not known from North American Paleocene horizons. Based on the known material, the five North American Eocene species of *Peratherium* are, in decreasing order of size (Tables 1 and 3), *P. comstocki* Cope, 1884, *P. edwardi* Gazin, 1952, *P. marsupium,* (Troxell, 1923), *P. knighti* McGrew, 1959, and *P. innominatum* Simpson, 1928.

The systematics of three of these species—*P. comstocki, P. marsupium,* and *P. innominatum*—were reviewed in detail in a treatment of the marsupials from the Wind River Formation (Krishtalka and Stucky, 1983*a*), and are briefly summarized here.

Peratherium comstocki Cope, 1884

Referred specimens.—In addition to material referred elsewhere (Cope, 1884; Simpson, 1928, 1968; West, 1982; Krishtalka and Stucky, 1983*a*), CM 13901 (M_{3-4}), from the Bridger Fm., Twin Buttes, Bridger Basin, Wyoming.

Discussion.—*P. comstocki* is the largest known North American Eocene species of *Peratherium.* The referral of CM 13901 and material from Agua Fria, Texas (West, 1982) extends the known range of this species from the early Wasatchian to the late Bridgerian and perhaps into the earliest Uintan, during which time preserved dentitions of *P. comstocki* show no significant morphological change.

Peratherium marsupium (Troxell, 1923)

Referred specimens.—In addition to material referred elsewhere [Troxell, 1923; McGrew and Sullivan, 1970; West, 1973 (except PM 15864); West and Dawson, 1975 (except CM 23194); Setoguchi, 1975 (except CM 23793, 23803, TTU-P 1375, 1238); Eaton, 1982; West, 1982; Krishtalka and Stucky, 1983*a,* 1983*b*], CM 36533 (DP^3), TTU-P 5966, CM 29061 (both M^1), CM 15043, 15144, 15668, 15708, 29109, 51345, 53754, 51422 (all M^2), CM 28850, 29021 (both M^3), CM 15626 (M^4), CM 55938 (P_3–M_1), CM 55939 (P_3), CM 29045, 55940, 55941 (M_2 or M_3) from localities 5A, 5 Front, 6, Rodent, Wood and 20, Wagon Bed Fm., Wind River Basin, Wyoming.

Discussion.—This species is well-known from middle Wasatchian to Duchesnean faunas of the western interior of North America, and, like *P. comstocki,* undergoes no perceptible changes in preserved parts of the dentition during its geological extent.

Peratherium innominatum Simpson, 1928

Referred specimens.—In addition to material referred elsewhere [Simpson, 1928; Bown, 1979 (as *P. macgrewi,* except UW 10129); Eaton, 1982; Krishtalka and Stucky, 1983*a,* 1983*b*], UCMP 44095 (M^{1-2}), CM 42137 (M_2 or M_3), from Sand Quarry, Four Mile area, Wasatch Fm., Colorado; part of UW 9742 (M^2), from the Willwood Fm., Bighorn Basin, Wyoming; UCMP 109647 (M^3), from the Uintan of California; CM 23851, 23852 (both DP^3), CM 15728 (M^1), CM 15083, 23787, 23918, 51354 (all M^2), CM 23788, 51237 (both M^{2-3}), TTU-P 1349, CM 14644, 15034, 15035, 15049, (all M^3), CM 23832, 23893

Table 1.—*Dimensions of type specimens of species of* Peratherium.

Taxa and catalog no.	P_3 L	P_3 W	M_1 L	M_1 W	M_2 L	M_2 W	M_3 L	M_3 W	M_4 L	M_4 W
P. comstocki										
AMNH 4252					3.15	1.90	3.25	1.70		
P. edwardi										
USNM 19200							2.95	1.70	2.55	1.50
P. marsupium										
YPM 13518	1.90	1.00	2.25	1.20	2.70	1.50	2.70	1.50		
P. knighti										
YPM 13514 (*E. minutus*) PU 16115 (*P. morrisi*)					2.2	1.4	2.3	1.4	2.1	1.1
P. innominatum										
AMNH 11493					1.5	1.0	1.5	1.0		1.0

(both M^4), TTU-P 1360, CM 15676, 15682, 16004, 23935, 23936 (all DP_3), TTU-P 2420, CM 15121, 15132, 15692 (all M_1), TTU-P 2425, 2429, CM 15078, 15102, 15672, 15729, 23844, 23887, 23901, 23906, 23917, 51248 (all M_2 or M_3), CM 23846 (M_4), from localities 5, 5A, 5 Front, 5 Back, 6, Wood and 20, Wagon Bed Fm., Wind River Basin, Wyoming.

Discussion.—Unlike *P. comstocki* and *P. marsupium, P. innominatum* has been confused with other didelphines. This species was considered a species of *Peradectes* by Setoguchi (1973), Bown (1982), and Crochet (1979), due, perhaps, to a misinterpretation of the diagnostic (and damaged) features on the type specimen. M_2 on the latter (AMNH 11493) preserves a large, spire-like entoconid, a lower, posterior hypoconulid, and a deep entoconid notch. These features are also evident on the broken M_3 on the type and are diagnostic of *Peratherium* and other Didelphini. *P. innominatum* is closest in size to contemporaneous *Peradectes chesteri,* the type of which has an M_3 with subequal entoconid and hypoconulid and a weak entoconid notch. Upper molars of these two species from the same localities also show the diagnostic features of *Peratherium* and *Peradectes.* Unlike the latter, upper molars of *P. innominatum* are dilambdodont, with a much lower paracone than metacone, prominent stylar cusps and conules, and a posterior expansion of the base of the protocone.

Study of the sample of *P. innominatum* from the Wind River Formation (Krishtalka and Stucky, 1983*a*) and Powder Wash (Krishtalka and Stucky, 1983*b*) indicates that this species includes the Graybullian *P. macgrewi* Bown, 1979, as a temporal subspecies. Two of Bown's identifications are revised: one of the upper molars in UW 9742 (Bown, 1979, Fig. 40a, center) is dilambdodont and belongs in *P. innominatum* (rather than *P. chesteri*); UW 10129 (Fig. 40c) is not dilambdodont and is transferred to *Peradectes protinnominatus* (from *P. macgrewi*).

Remains of this species have also been identified (Krishtalka and Stucky, 1983*a*) in the early Eocene Four Mile, middle Eocene Carter Mountain (Eaton, 1982) and late Eocene Badwater samples of didelphids (part of Setoguchi's, 1975, *Peratherium* cf. *P. knighti* and *Nanodelphys* cf. *N. minutus*). Lillegraven's (1976) referred material of *Peratherium* sp. cf. *P. knighti* from the Uintan of San Diego County may include specimens of both *P. knighti* and *P. innominatum.* The range in size of the molars overlaps with that of both species, and the figured upper molars include two morphs: some have a shallow ectoflexus (Lillegraven, 1976, Fig. 1, 2), whereas one (Fig. 3c) has a deep ectoflexus, as is characteristic of *P. knighti* and *P. innominatum,* respectively.

Bown (1982) referred material from the Aycross Formation to *Peradectes* sp. cf. *P. innominatus* on the basis of their similarity to UW 984 from Tabernacle Butte (see McGrew, 1959). UW 984 is identified here and elsewhere (Krishtalka and Stucky, 1983*a*) as *Peradectes chesteri,* according to features discussed below; the Aycross material, by implication, may also belong to *P. chesteri.*

According to these observations, the known record of *P. innominatum* extends from the early Wasatchian to the Duchesnean of the western interior of North America, and possibly includes the Uintan of California.

Peratherium edwardi Gazin, 1952
(Fig. 1)

Type.—USNM 19200, partial left dentary with M_{3-4}.

Type locality.—12 miles north of Big Piney, in SW1/4 section 33, T. 32 N, R. 111 W, Sublette County, Wyoming.

Referred specimen.—USNM 19206 (M^{3-4}), from the type locality.

Known distribution.—Late Wasatchian—Green River Basin (Wasatch Fm.), Wyoming.

Discussion.—This poorly known species is intermediate in size between *P. comstocki* and *P. marsupium.* Allocation of this material to the former, as advocated by Setoguchi (1973) and Bown and Rose (1979), is not warranted until a larger sample is available.

Peratherium knighti McGrew, 1959
(Fig. 2)

Entomacodon minutus Marsh, 1872.
Centracodon delicatus Marsh, 1872.
Peratherium knighti McGrew, 1959.
Peratherium morrisi Gazin, 1962.

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

Type locality.—Locality 5, Tabernacle Butte, upper part of Bridger Formation, Wyoming.

Referred specimens.—In addition to material referred elsewhere [McGrew, 1959; West and Dawson, 1973; Bown, 1982; Setoguchi, 1975 (except TTU-P 1237, 1349, 2425, 2429, CM 23787, 23832, 23935, 23936—referred above to *P. innominatum*; TTU-P 5966—referred above to *P. marsupium*)], YPM 13514, partial dentary with M_4 (type of *Entomacodon minutus*), YPM 13508, dentary with $P_{1-3}M_{1-4}$ (type of *Centracodon delicatus*), both from Henry's Fork, Bridger Formation, Bridger Basin, Wyoming; UW 3003 (M_4), UW 2988 (M_{3-4}), from the lower part of the Bridger Fm., Bridger Basin, Wyoming; PU 16115, partial dentary with M_{2-3} (type of *Peratherium morrisi*), from the Cathedral Bluffs tongue of the Wasatch Fm., Washakie Basin, Wyoming; CM 42135 (M_{3-4}), from the type locality; CM 42139 (M_1), UCMP 59131 (M_2 or M_3), from the Wasatch Fm., Four Mile area, Colorado; PM 15864 (M^{2-4}), from the lower part of the Bridger Fm., Green River Basin, Wyoming; CM 23194 (M_2 or M_3), from the Washakie Fm., Sand Wash Basin, Colorado; CM 15600, 15601, 15606, 15656 (all DP^3), CM 15030, 15031, 15036, 15037, 15046, 15077, 15081, 15108, 15631, 15670, 23841 (all M^1), CM 55936 ($M^{1,2,3}$), CM 55937 ($M^{2,3}$), CM 15048, 15029, 15097, 15105, 15608, 15614, 15634,

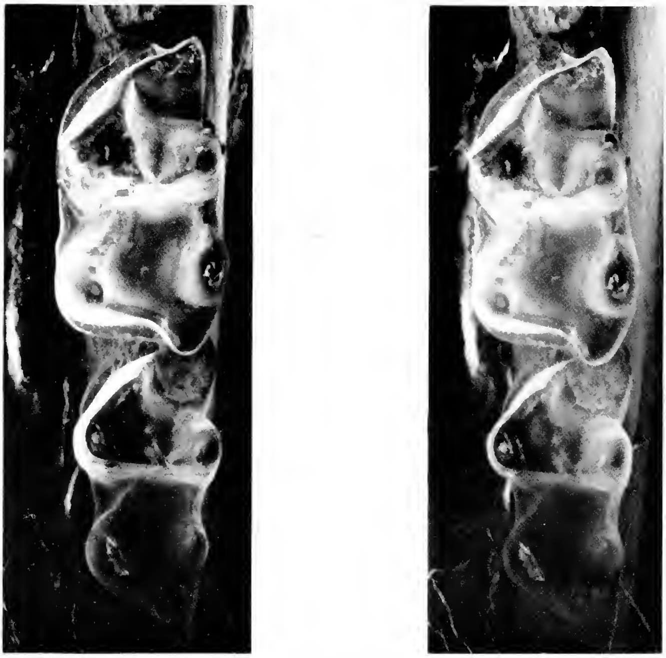


Fig. 1.—*Peratherium edwardi,* USNM 19200, LM$_{3-4}$, type; approx. × 14.

23803, 23888, 29069 (all M^2), CM 15027, 15032, 15050, 15059, 15101, 15118, 29110 (all M^3), CM 15033, 15079, 15080, 15143, 15636, 15678, 55963 (all M^4), CM 15134 (DP$_3$), CM 14642, 14645, 15028, 15058, 15114, 15119, 15150, 15741, 51202 (all M$_1$); CM 15040, 15042, 15044, 15057, 15659, 15689, 15710, 15720, 15742, 23894, 23911, 28832, 28893, 29024, 55942, 55964, 55969 (all M$_2$ or M$_3$), from localities 5, 5A, 5 Front, 5 Back, 6, Wood and 20, Wagon Bed Fm., Wind River Basin, Wyoming.

Known distribution.—Early Wasatchian—Four Mile area (Wasatch Fm.), Colorado. Bridgerian—Washakie and Green River basins (Cathedral Bluffs tongue of the Wasatch Fm.), Bridger Basin (Bridger Fm.), Green River Basin (upper and lower parts of the Bridger Fm.), Bighorn Basin (Aycross Fm.), Wyoming. Late Bridgerian or Uintan—Sand Wash Basin (Washakie Fm.), Colorado. Uintan and Duchesnean—Wind River Basin (Wagon Bed Fm.), Wyoming.

Emended diagnosis.—Smaller than *P. comstocki, P. edwardi, P. marsupium*; larger than *P. innominatum*; ectoflexus on M$^{2-3}$ much shallower than in *P. marsupium* and *P. innominatum.*

Discussion.—Three taxa are conspecific with *P. knighti*—*Entomacodon minutus, Centracodon delicatus,* and *Peratherium morrisi.* The first two were synonymized by Matthew (1909*b*) as *E. minutus* (which

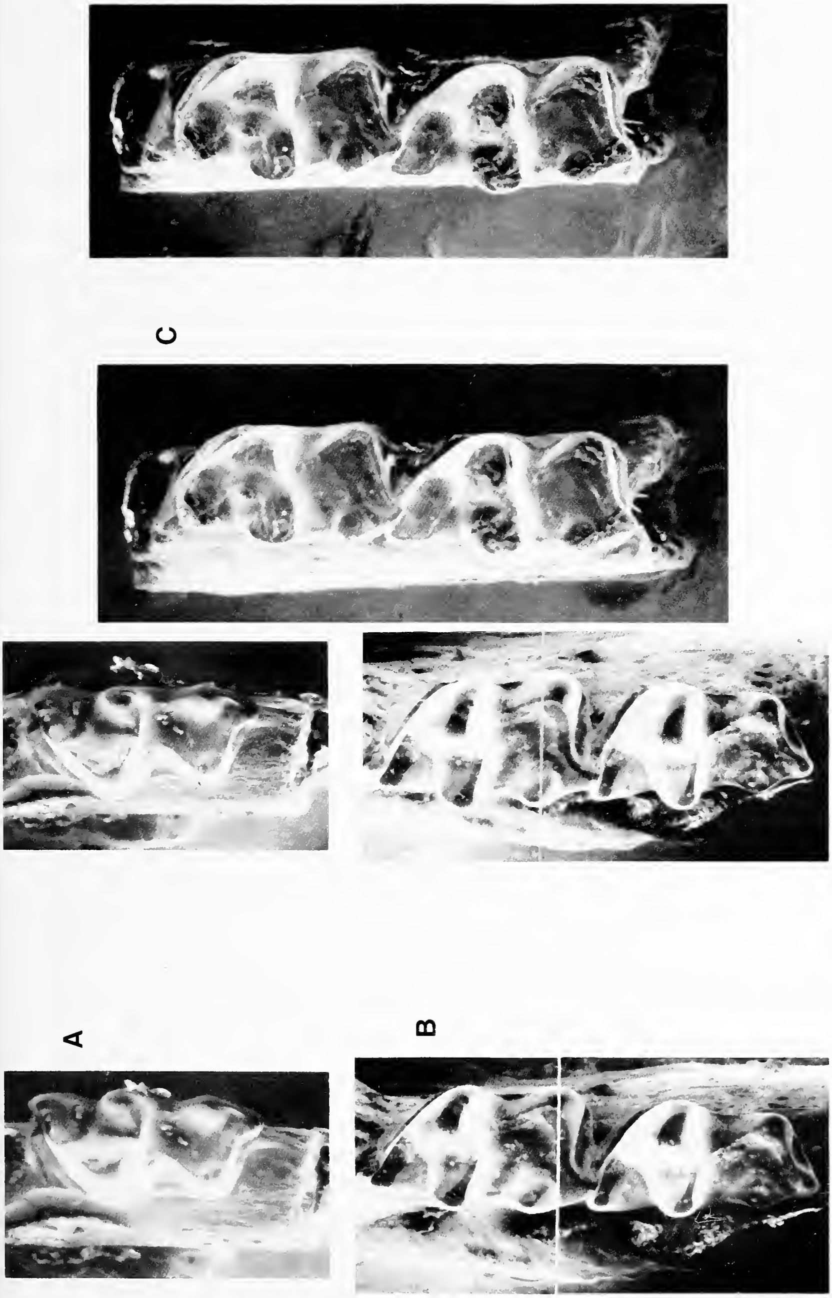


Fig. 2.—*Peratherium knighti.* (A) YPM 13514, M$_4$ (type of *Entomacodon minutus*); (B) CM 42135, RM$_{3-4}$ (from Tabernacle Butte, the type locality); (C) PU 16115, RM$_{2-3}$ (type of *P. morrisi*); all approx. × 15.

has page priority; Marsh, 1872:214–215), and the types of both were tentatively identified as marsupials by Robinson (1968). The types of *E. minutus* and *P. morrisi* are indistinguishable from lower dentitions in the hypodigm of *P. knighti* from Tabernacle Butte. *Peratherium* has priority over *Entomacodon,* as does *E. minutus* over *P. knighti,* but the resultant *P. minutum* is preoccupied by *P. minutum* Aymard, 1850. *C. delicatus* is a *nomen oblitum* according to the rules of zoological nomenclature (Art. 23b).

P. knighti is closest in size to the larger *P. marsupium* and the smaller *P. innominatum,* but known samples of these species do not overlap in size. Additionally, M^{2-3} of *P. knighti* have shallower ectoflexi. According to these criteria, we have identified *P. knighti* from material (see "Referred specimens") previously assigned to: *P. marsupium* from the lower part of the Bridger Formation, Green River Basin, Wyoming (West, 1973) and the Washakie Formation, Sand Wash Basin (West and Dawson, 1975); *Peratherium* sp. from Bridger A (McGrew and Sullivan, 1970); as well as from unpublished specimens from the Four Mile fauna, Colorado.

As discussed earlier, *P. knighti* may occur in the Uintan of California (Lillegraven, 1976). Analysis of late Eocene samples of *Peratherium* from Badwater indicates that material previously referred to *Peratherium* cf. *P. knighti* (Setoguchi, 1975) includes specimens of *P. knighti, P. innominatum,* and *P. marsupium.*

Based on these synonymies and reidentifications, *P. knighti* is known from the early Wasatchian to the Duchesnean in the western interior of North America, and possibly from the Uintan of California.

Tribe Peradectini Crochet, 1979

North American didelphines included here are *Peradectes, Mimoperadectes,* and *Armintodelphys. Nanodelphys* is congeneric with *Peradectes* (Crochet, 1978). As discussed under Didelphinae, and Evolutionary Relationships, *Alphadon* and *Albertatherium* lack the diagnostic characters of this tribe and (contra Crochet, 1979) are removed from the Peradectini.

The systematics of one of the species of *Peradectes* (*P. chesteri*) and both species of *Armintodelphys* (*A. blacki* and *A. dawsoni*) were treated elsewhere (Krishtalka and Stucky, 1983*a*), as part of a description of the didelphines from the Wind River Formation. The systematics of these taxa are briefly summarized here, and additional material is referred to *P. chesteri.*

Peradectes Matthew and Granger, 1921

Three North American species were originally assigned to *Peradectes*—the type species, *P. elegans* Matthew and Granger, 1921; *P.*

pauli Gazin, 1956; and *P. protinnominatus* McKenna, 1960. Subsequently, Setoguchi (1973) and Bown (1979) identified *Peratherium chesteri* Gazin, 1952, and *Peratherium innominatum* Simpson, 1928 as species of *Peradectes,* and *P. protinnominatus* as a junior synonym of *P. chesteri.* Setoguchi (1973) also advocated inclusion of *Peratherium morrisi* in *Peradectes,* and Bown (1979) noted a lack of sufficient morphological distance between *Nanodelphys minutus,* the type species, and *Peradectes chesteri* to warrant generic distinction. Lillegraven (1976) transferred *Peratherium californicum* Stock, 1936, to *Nanodelphys,* and opted for retaining *N. californicus* and *N. minutus* despite an apparent lack of morphological distinction. Crochet (1978) reduced *Nanodelphys* to a subgenus of *Peradectes* in which he included the North American species *P. minutus, P. californicus, P. innominatus,* and *P. protinnominatus. P. elegans* was referred to the subgenus *Peradectes, P. pauli* was considered too poorly known to be discussed, and *P. chesteri* was assigned to *Herpetotherium.* Lastly, Clemens (1979) and Archibald (1982) have suggested that *Thylacodon pusillus* is a species of *Peradectes.*

Review of the type and referred material of these taxa indicates that *Peradectes* is characterized by M_{1-3} with short talonids, labial cristid obliquas, and an entoconid and hypoconulid that are low, subequal, and closely appressed; these cusps are separated by a weak entoconid notch and share a common internal talonid wall. On M^{1-3} the paracone and metacone are subequal and not dilambdodont, the stylar cusps and conules are weak, and the posterolingual part of the base of the protocone is not expanded. These features are also diagnostic of the Peradectini. Compared to Cretaceous didelphines, the absence of dilambdodonty, and the V-shaped protocone are primitive retentions. Unlike *Mimoperadectes,* the metaconid is larger and higher than the paraconid on M_{1-3} of *Peradectes*; unlike *Armintodelphys,* the entoconid is subequal to the hypoconulid, rather than reduced to a nubbin. Measurements of these taxa are given in Tables 2 and 3.

Systematic conclusions implied by examination of the material are: (1) *Nanodelphys* is congeneric with *Peradectes*; as suggested by Bown (1979) and Crochet (1978), the morphological distinctions between *N. minutus,* the type species, and species of *Peradectes* are of specific magnitude and are minor compared to those that define other genera of didelphines; Crochet's (1978) subgenus *Nanodelphys* has no systematic utility; (2) there are six discernable North American species of *Peradectes*: *P. elegans, P. pauli, P. protinnominatus, P. chesteri* (=*Peratherium chesteri*), *P. californicus* (=*Peratherium californicum* and *Nanodelphys californicus*) and *P. minutus* (=*Nanodelphys minutus*); (3) neither *Peratherium morrisi* nor *P. innominatum* belongs in *Peradectes*; the former is a junior synonym of *Peratherium knighti* and the latter

Table 2.—*Dimensions of type and paratype specimens (lower dentition) of species of* Peradectes, Armintodelphys, *and* Mimoperadectes.

Taxa and catalog no.	P_3		M_1		M_2		M_3		M_4	
	L	W	L	W	L	W	L	W	L	W
P. elegans										
AMNH 17376 (right)	1.4	0.7	1.7	1.0	1.7	1.0	1.7	1.0	1.7	0.9
AMNH 17376 (left)	1.4	0.7	1.7	1.0	1.7	1.0	1.7	1.0	1.7	0.9
P. pauli										
USNM 20879 (type)							1.5	1.0	1.5	0.9
USNM 20880 (paratype)			1.55	0.80		0.90				
P. protinnominatus										
UCMP 45947 (paratype)			1.55	0.90	1.60	1.05				
UCMP 45948 (paratype)			1.55	0.90	1.60	1.00				
UCMP 45950 (paratype)	1.1	0.6	1.5	0.8						
P. californicus										
LACM (CIT) 202-1943	1.10	0.55	1.35	0.75	1.50	0.85		0.80		
P. chesteri										
USNM 19199							1.4	0.9		
A. blacki										
CM 41159							2.2	1.1	2.2	0.9
A. dawsoni										
CM 55569						0.8	1.5	0.8		
M. labrus										
UM 66144	2.70	1.45	2.97	1.76	3.07	1.83	3.20	1.77	3.05	1.84

Table 3.—*Dimensions of type and paratype specimens (upper dentition) of species of* Peradectes, Mimoperadectes, *and* Peratherium.

Taxa and catalog no.	M^1		M^2		M^3		M^4	
	L	W	L	W	L	W	L	W
Peradectes elegans								
AMNH 17369 (paratype)	1.60	1.50	1.60	1.70	1.40	1.90	1.05	1.95
Peradectes protinnominatus								
UCMP 44077	1.6	1.4	1.5	1.7	1.4	2.0		
Mimoperadectes labrus								
UM 66144	2.84		3.09	3.47	2.94	3.66	2.36	3.26
Peratherium knighti								
AMNH 55684	1.9	1.6	2.05	2.0	2.05	2.2		

is a valid species of *Peratherium* (see above); (4) *Thylacodon pusillus* may not belong in *Peradectes* or the Peradectini.

Peradectes elegans Matthew and Granger, 1921
(Fig. 3)

Type.—AMNH 17376, paired dentaries with RP_1, P_3–M_4 and LP_2–M_4.

Paratype.—AMNH 17369 (M^{1-4}).

Type locality.—Mason Pocket, Animas Formation (see Lucas and Ingersoll, 1981), Colorado.

Referred specimens.—In addition to the material referred elsewhere (Simpson, 1935; Gazin, 1956), UCMP 44767 (M_{2-4}), CM 42138 (M_3), from the Wasatch Fm., Sand Quarry, Four Mile area, Colorado; CM 41108 (M_{2-3}), UCM 46216 (M_{3-4}), from the Fort Union Fm., Saddle locality, Bison Basin, Wyoming: AMNH 17199 (M^{1-2}), from the type locality.

Known distribution.—Tiffanian—Bison Basin (Fort Union Fm.), Wyoming; San Juan Basin (Animas Fm.), Colorado. Early Wasatchian—Four Mile area (Wasatch Fm.), Colorado.

Emended diagnosis.—Differs from other species of *Peradectes* as follows: larger size; P_3 more trenchant with longer talonid; P_3 protoconid higher than that of molars; M_1 as large as M_2; M_{1-4} talonids broader and longer; M_3 talonid broader than trigonid; M^{1-3} with stronger stylar cusps and conules and with uncompressed protocone.

Discussion.—The oldest known material of *P. elegans,* from Bison Basin, includes M_{2-4} that are broad in proportion to length, with wider talonids than trigonids. Lower molars on the type of *P. elegans* from the Tiffanian Mason Pocket are similar; curiously, RM_3 on the type has a slightly narrower talonid than LM_3. M_1 on the type is as large as

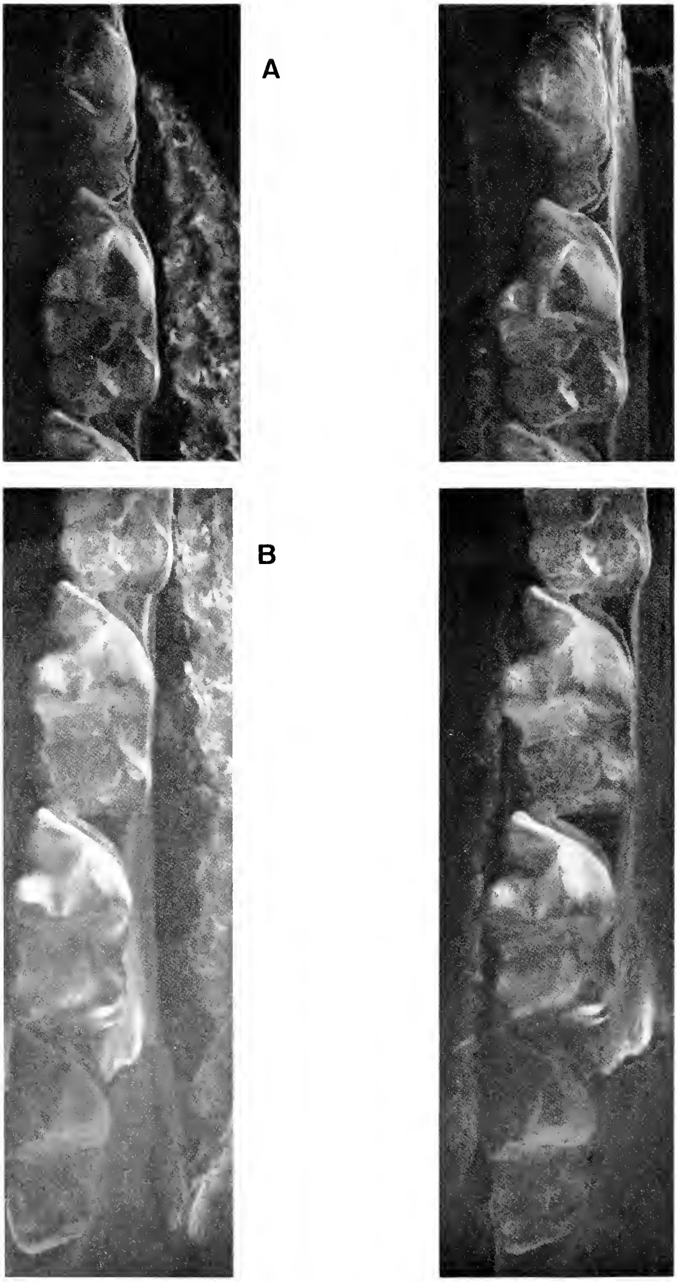


Fig. 3.—*Peradectes elegans.* (A) and (B) AMNH 17376, type, RP_3–M_1 and RM_{2-4}; × 16.5.

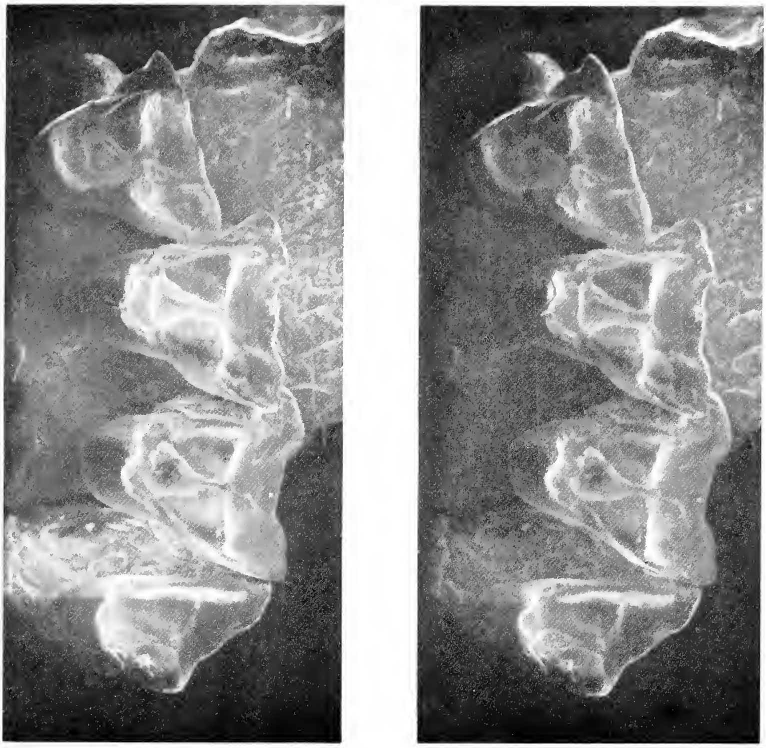


Fig. 3.—*Peradectes elegans.* (C) AMNH 17369, LM^{1-4}, paratype; approx. × 16.5.

M_2. P_3 is trenchant, higher than the molars and has a long talonid. On M_3 the talonid is broader than the trigonid. These characters distinguish the lower dentition of *P. elegans* from that of all other North American species of *Peradectes* and indicate that UCMP 44767, formerly identified as *P. protinnominatus* (McKenna, 1960, Fig. 17c), and CM 42138, both from Four Mile, represent *P. elegans.* M_3 in these specimens has a wider talonid than trigonid; M_{2-4} in UCMP 44767 are indistinguishable from *P. elegans* in size and structure, and the distance between the roots of M_1 implies that M_1 was as large as, if not larger than, M_2. This material represents the first Wasatchian record of *P. elegans.*

Upper molars of *P. elegans* from Mason Pocket are not transverse, but in occlusal view resemble an equilateral triangle. As noted by Simpson (1935), stylar cusps B, C, and D are present although variably developed, the conules are moderately strong and the paracone, slightly lower than the metacone, is higher than the protocone. In contrast, all other North American species of *Peradectes* have upper molars that are more transverse, with an anteroposteriorly compressed protocone and weaker or vestigial conules and stylar cusps C and D. Upper molars of *P. elegans* are not known from Four Mile.

Peradectes pauli Gazin, 1956
(Fig. 4)

Type.—USNM 20879, partial left dentary with M_{3-4}.

Paratype.—USNM 20880, partial left dentary with M_1 and part of M_2.

Type locality.—Saddle locality, Bison Basin, Fort Union Formation, Wyoming.

Referred specimens.—In addition to material referred elsewhere (Gazin, 1956), CM 41109 (M^3), MCZ 20793 (M^{2-3}), from the type locality.

Known distribution.—Tiffanian—Bison Basin (Fort Union Fm.), Wyoming.

Emended diagnosis.—Compared to *P. elegans*: smaller size; M_1 smaller than M_2; M_3 with narrower talonid than trigonid; M_4 with narrower talonid; M^{2-3} more transverse with compressed protocone. Compared to *P. protinnominatus, P. chesteri, P. californicus,* and *P. minutus*: bases of M_{3-4} more emarginate buccally between trigonid and talonid; M_4 talonid longer than trigonid. Compared to *P. californicus, P. chesteri,* and *P. minutus*: wider talonid occlusally on M_{1-3}. Compared to *P. chesteri* and *P. minutus*: M_{1-3} wider in proportion to length; less disparity in L/W ratio from M^2 to M^3; less compressed protocone on M^{2-3}; stronger conules and stylar cusps C and D. Compared to *P. minutus*: paracone proportionately higher than protocone and stylar cusp B.

Discussion.—Curiously, *P. pauli* has been ignored in recent important studies of early Tertiary didelphines (McKenna, 1960; Setoguchi, 1973; Bown, 1979; Crochet, 1978; Rose, 1981).

In contrast to *P. elegans,* on the type and paratype of *P. pauli* M_1 is smaller than M_2, M_{3-4} have narrower talonids, and the talonid on M_3 is narrower than the trigonid. As such, *P. pauli* is a distinct species from Bison Basin, where it occurs with *P. elegans* at the Saddle locality.

Analysis of the upper dentition leads to a similar conclusion. CM 41109, an isolated M^3, and MCZ 20793, M^{2-3}, both from Bison Basin, resemble one another and differ from *P. elegans* in being more transverse, with a narrower, anteroposteriorly compressed protocone and a deeper ectoflexus. Except for slightly larger size, they are closely similar to upper molars of *P. protinnominatus* from Four Mile and the Willwood Formation (see below; McKenna, 1960; Bown, 1979).

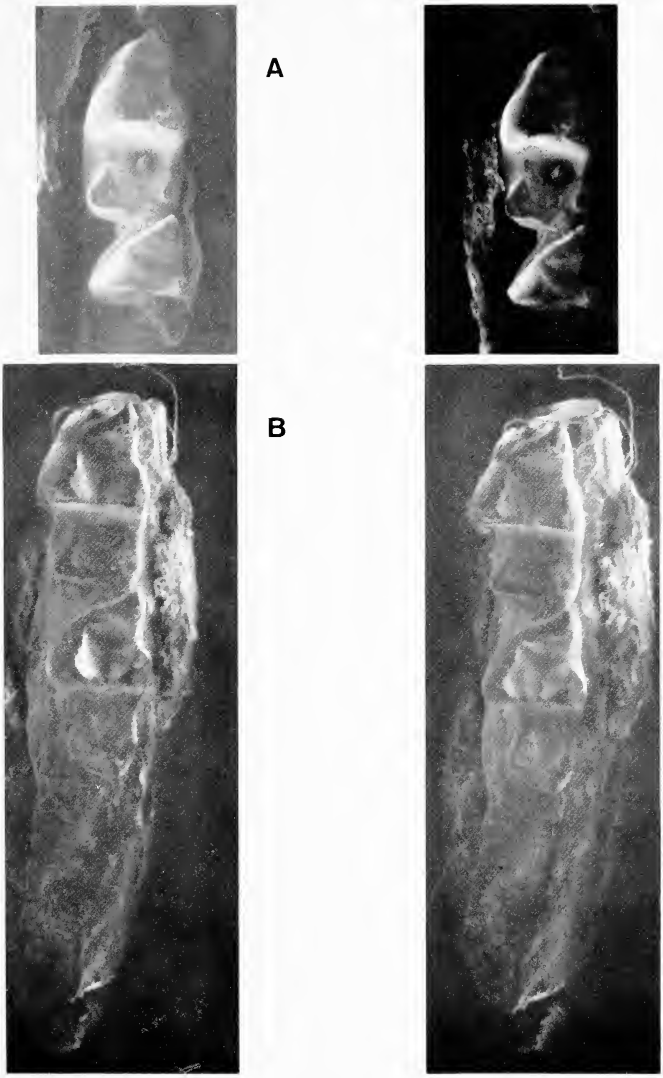


Fig. 4.—*Peradectes pauli.* (A) USNM 20880, LM$_1$ and trigonid of M$_2$, paratype; (B) USNM 20879, LM$_{3-4}$, type; both approx. × 16.5.

P. pauli is suitable morphologically and temporally to be basal to the branching lineage that includes *P. protinnominatus, P. californicus, P. chesteri,* and *P. minutus.*

Peradectes protinnominatus McKenna, 1960

Peradectes chesteri Bown, 1979.
Peradectes cf. *chesteri* Rose, 1981.

Type.—UCMP 44077, partial right maxilla with M^{1-3}.

Paratypes.—UCMP 45947 (M_{1-2}), UCMP 45948 (M_{1-2}), UCMP 45950 (P_3–M_1).

Type locality.—Alheit Pocket, Wasatch Fm., Four Mile area, Colorado.

Referred specimens.—In addition to material referred elsewhere (McKenna, 1960; Bown, 1979; Rose, 1981), CM 42138 (M_2), UCMP 59132 (M_3), UCMP 59130 (M^3), from the Wasatch Fm., Four Mile area, Colorado; UW 10129 (M^2), from the Willwood Fm., Bighorn Basin, Wyoming.

Known distribution.—Clarkforkian to early Wasatchian—Bighorn Basin (Willwood Fm.), Wyoming. Early Wasatchian—Four Mile area (Wasatch Fm.), Colorado.

Emended diagnosis.—Compared to *P. elegans*: smaller size; P_3 talonid shorter and trigonid lower than M_1; M_1 smaller than M_2; M^{2-3} more transverse, protocone compressed. Compared to *P. elegans* and *P. pauli*: M_4 talonid shorter than trigonid; M_{3-4} with weaker emargination between trigonid and talonid; M^{2-3} protocone more anterior. Compared to *P. californicus, P. chesteri,* and *P. minutus*: M_{1-3} with wider talonid occlusal width; M^{1-3} conules and stylar cusps C and D stronger. Compared to *P. chesteri* and *P. minutus*: less disparity in L/W ratio from M^1 to M^3; protocone on M^3 less compressed; paracone and metacone on M^{1-3} farther apart; M_{1-3} wider in proportion to length. Compared to *P. minutus*: M^{2-3} protocone less compressed; paracone higher than protocone on M^{1-3} and relatively higher than stylar cusp B.

Discussion.—Setoguchi (1973) and Bown (1979) synonymized this species with *P. chesteri.* However, the type of the latter, an M_3, can only be compared to UCMP 44767, the only specimen with an M_3 in the original material of *P. protinnominatus* from Four Mile (McKenna, 1960). UCMP 44767 is much larger than the type and referred material of *P. chesteri*; it has a wider talonid than trigonid on M_3, and subequal M_1 and M_2, and was referred above to *P. elegans.*

In contrast to *P. protinnominatus,* the type and other specimens of *P. chesteri* (see below) have lower molars that lack a buccal emargination between trigonid and talonid, and talonids that have a narrower occlusal width. As such, UW 9605 and UM 71663, from the Clarkforkian and early Wasatchian, respectively, of the Bighorn Basin, more closely resemble the paratypes of *P. protinnominatus.* Bown (1979) and Rose (1981) reached the same conclusion concerning these specimens (but allied them with *P. chesteri = P. protinnominatus*).

Upper molars of *P. protinnominatus* are also distinct from those of *P. chesteri.* Diagnostic differences involve the degree of compression of the protocone on M^3, the disparity in L/W ratio from M^1 to M^3, and the development of the conules and stylar cusps C and D. As also noted by Bown (1979), upper molars from his Bighorn Basin sample are indistinguishable from the type of *P. protinnominatus.*

Upper molars in UCMP 44095 from Four Mile (McKenna, 1960, Fig. 18a) and one of the upper molars in UW 9742 (Bown, 1979, Fig. 40a, center) are dilambdodont, and are reidentified here and elsewhere (Krishtalka and Stucky, 1983*a*) as *Peratherium innominatum.* UW 10129, originally identified as *Peratherium macgrewi* (Bown, 1979, Fig. 40c), is not dilambdodont and belongs in *P. protinnominatus.*

P. protinnominatus is intermediate in known dental morphology and temporal occurrence between *P. pauli* and *P. chesteri.* It is also closely related to *P. californicus,* which is more derived in the narrower occlusal width of the molar talonids, and in the weaker stylar cusps C and D and conules on M^{1-3}.

Peradectes californicus (Stock, 1936)

Peratherium californicum Stock, 1936.
Nanodelphys cf. *N. minutus* Setoguchi, 1975, in part.
Nanodelphys californicus (Stock, 1936), Lillegraven, 1976.
Peradectes californicum (Stock, 1936), Crochet, 1978.

Type.—LACM (CIT) 202-1943, partial right dentary with P_3–M_2.

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

Referred specimens.—In addition to material referred elsewhere (Lillegraven, 1976), CM 15664 (M_1), CM 52421, 23845 (both M_3), CM 52417 (M_4), CM 15138, 15612, 51367, 51250, 15611 (all M^1), CM 19748 (M^{2-3}), CM 15671, 15104, 15149 (all M^2), CM 15681 (M^3), from localities 5, 5 Front, 5 Back, 6, 20, Wagon Bed Fm., Wind River Basin, Wyoming.

Known distribution.—Uintan—San Diego County (Friars, Mission Valley, ?Santiago, Sespe Fms.), California. Uintan to Duchesnean—Wind River Basin (Wagon Bed Fm.), Wyoming.

Emended diagnosis.—Compared to *P. elegans*: teeth much smaller; P_3 smaller than M_1; M_1 smaller than M_2; narrower talonid than trigonid on M_3; M^{1-4} more transverse. Compared to *P. elegans* and *P. pauli*: protocone more anterior on M^{1-3}; shorter talonid than trigonid on M_4;

trigonids lower on M_{1-4}. Compared to *P. elegans, P. pauli,* and *P. protinnominatus*: P_3 without talonid (not known in *P. pauli*); M_{1-3} talonids with narrower occlusal width; M^{1-3} with weaker conules and stylar cusps C and D. Compared to *P. chesteri* and *P. minutus*: M^2 and M^{2-3}, respectively, less transverse, with a less compressed protocone; M^{2-3} with a shallower ectoflexus and stronger stylar cusps C and D; less disparity in L/W ratio from M^{1-3}.

Discussion.—Lillegraven (1976) recognized that Stock's (1936) type and referred material of *Peratherium californicum* represented an Uintan species of *Nanodelphys* that was morphologically indistinguishable from *Nanodelphys* cf. *N. minutus* from the late Eocene of Badwater (Setoguchi, 1973). He retained *N. californicus* and *N. minutus* on the basis of geographic and temporal disparity. The two species, as understood here, differ morphologically.

Setoguchi (1973) originally recognized two species of *Nanodelphys* from Badwater, *Nanodelphys* cf. *N. minutus* and *Nanodelphys* sp. nov., which he later (Setoguchi, 1975) combined in the former. Crochet (1978) and Bown (1979) independently suggested that *Nanodelphys* and *Peradectes* were congeneric, and Crochet allocated *N. minutus* and *N. californicus* to *Peradectes.*

From our analysis of the Badwater and Oligocene material it appears that *N. minutus* and *N. californicus* are discernable species of *Peradectes. P. californicus* includes some of the material that Setoguchi (1973, 1975) assigned to *Nanodelphys* cf. *N. minutus,* whereas Setoguchi's (1973) *Nanodelphys* sp. nov. is referred below to *Peradectes* sp. cf. *P. minutus.* Of Setoguchi's (1975) figured specimens of *Nanodelphys* cf. *N. minutus,* TTU-P 2426 (Fig. 9) is a DP^3 of *Peratherium innominatum* and CM 16007 (Fig. 12) is an M^2 of *Peradectes* sp. cf. *P. minutus.* The remainder are *P. californicus.* Some of his referred specimens (TTU-P 1360, 2420, CM 23846) also represent *Peratherium innominatum.*

In summary, *P. californicus* is known from the Uintan of California, and from the Uintan and Duchesnean of Wyoming where it occurs in lithosympatry with the smaller *Peradectes* sp. cf. *P. minutus* at five of the Badwater late Eocene localities. The *P. californicus* material from Wyoming shows a more restricted range in size than that from California, possibly because of the co-occurrence of the two species at Badwater and the implied character displacement. A larger sample of both species is needed to test this hypothesis.

P. californicus appears to have shared a common ancestry with the *P. chesteri-P. minutus* lineage from a *P. protinnominatus*-like peradectinine. The first three species are derived in having weaker conules and stylar cusps C and D on the upper molars (see Setoguchi, 1975, Fig. 11, 12; Lillegraven, 1976), and talonids on the lower molars with narrower occlusal widths between the cristid obliqua and the lingual border. The cristid obliqua runs posteriorly from the trigonid before turning labially to a more internal hypoconid, so that the occlusal width of the talonid is approximately one-half of the basal width. In contrast, other species of *Peradectes* retain the primitive posterolabial orientation of the cristid obliqua, a more buccal hypoconid, and an occlusally wide talonid on the lower molars, as well as stronger conules and stylar cusps C and D on the upper molars. M^3 in *P. chesteri* and M^{2-3} in *P. minutus* (and *Peradectes* sp. cf. *P. minutus*) are more advanced than in *P. californicus* in having a more anteroposteriorly compressed protocone and vestigial or absent stylar cusps C and D. Also, the disparity in L/W ratio from M^1 to M^3 is more marked.

Peradectes chesteri Gazin, 1952
(Fig. 5)

Referred specimens.—In addition to material referred elsewhere (Gazin, 1952; Krishtalka and Stucky, 1983*a*, 1983*b*), PM 15682 (M^{3-4}), PM 15866 (M^{2-3}), from Hawk and Fault localities, Bridger Fm., Green River Basin, Wyoming (see West, 1973); UW 984, (P_3–M_4), from Tabernacle Butte, Bridger Fm., Green River Basin, Wyoming.

Discussion.—The systematics of this species were treated elsewhere (Krishtalka and Stucky, 1983*a*). *P. chesteri* is known from late Wasatchian to late Bridgerian faunas. Material originally assigned to *P. chesteri* from the Clarkforkian and early Wasatchian of the Bighorn Basin (Bown, 1979; Rose, 1981) was referred above to *P. protinnominatus.*

Compared to *P. elegans, P. pauli,* and *P. protinnominatus,* diagnostic and derived features on the type of *P. chesteri,* an M_3, include an occlusally narrow talonid (the hypoconid is more internal), and an absence of the labial emargination between the trigonid and talonid. These characters are also preserved on UW 984, a partial right dentary with P_3–M_4 from Tabernacle Butte (see McGrew, 1959; Bown, 1982), and a lower molar from Powder Wash. Upper molars from Powder Wash, the Wind River Formation (Krishtalka and Stucky, 1983*a*, 1983*b*), and the Bridger Formation (West, 1973, Pl. 1, Figs. C, D) also bear distinctive features and are referred to *P. chesteri.* The morphology of these specimens indicates that this species is intermediate in molar structure between *P. protinnominatus* and *P. minutus. P. chesteri* has the basic features of the former, but is more derived in that: there is a greater disparity in L/W ratio from M^1 to M^3, so that M^1 is longer than wide, M^2 is more nearly equilateral, and M^3 is very transverse; the paracone and protocone are relatively lower and higher, respectively, and the paracone and metacone are closer to one another; the conules and stylar cusps C and D are vestigial or absent, and the protocone is

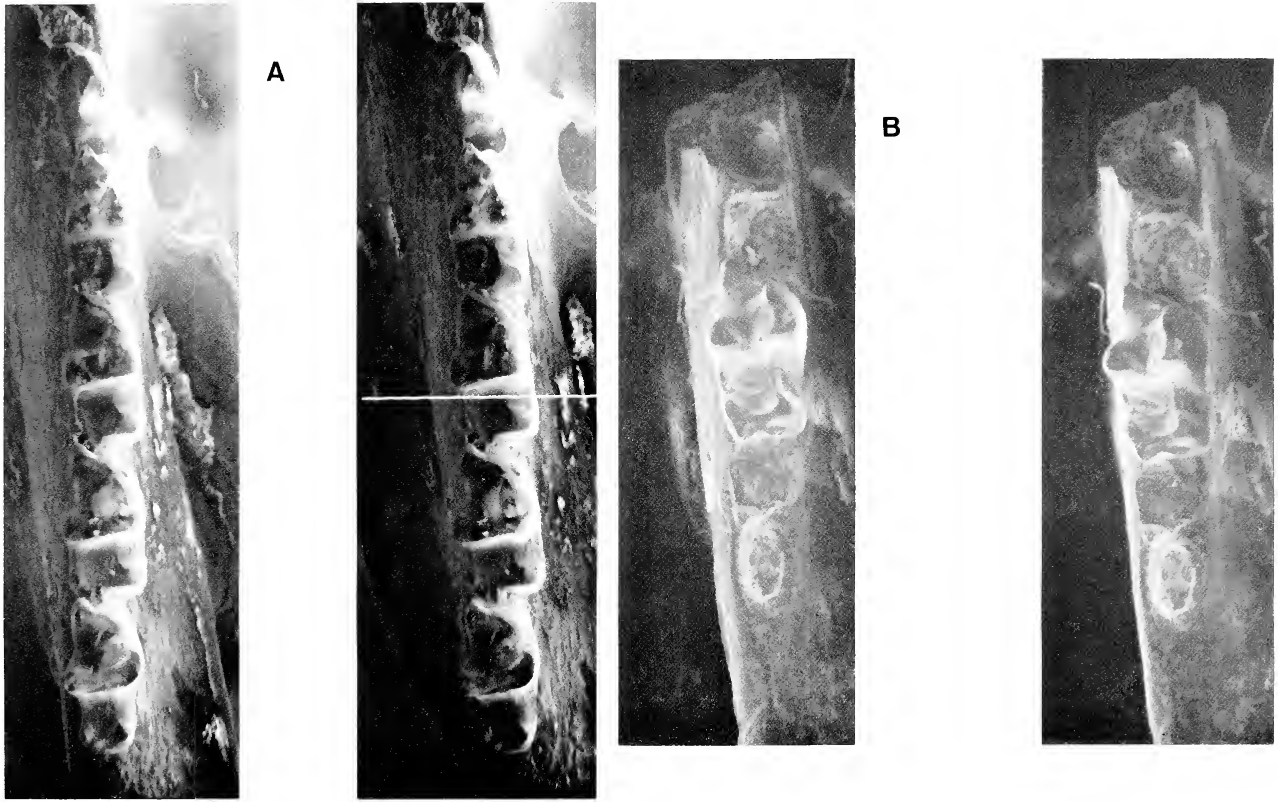


Fig. 5.—*Peradectes chesteri.* (A) UW 984, RP_3–M_4, approx. × 14; (B) USNM 19199, RM_3, type, approx. × 17.

more compressed anteroposteriorly on M^3; the lower molars are narrower in proportion to length, the talonids are narrower occlusally, and the buccal part of the base between the trigonids and talonids is not emarginate. These features are further modified in *P. minutus*: the protocone on M^{2-3} is more compressed anteroposteriorly and the paracone is reduced in height to that of the protocone and almost to that of stylar cusp B. On the type of *P. chesteri* a large gap occurs between the alveolus for the posterior root of M_4 and the ascending ramus of the dentary. This gap is absent from lower jaws of *P. minutus,* indicating a shortening of the jaw in the latter. *P. chesteri* is divergent from *P. californicus* in having a more compressed protocone on M^3, greater disparity in L/W ratio from M^1 to M^3, and in lacking conules and stylar cusps C and D. Their inferred common ancestry was discussed above.

Peradectes sp. cf. *P. minutus*

Nanodelphys sp. nov. Setoguchi, 1973.
Nanodelphys cf. *N. minutus* Setoguchi, 1975, in part.

Referred specimens.—CM 15091, 15628, 15687, 51369 (all M^1), CM 16007, 15094 (both M^2), CM 15047, 15618 (both M^3), CM 18216 (DP_3), CM 52415 (M_1), CM 15016, 15006, 15087, 15082, 29484, 52413, 52416 (all M_2), CM 15666, 15685, 23843, 23847, 52418 (all M_3), from localities 5, 5A, 5 Front, 5 Back, 6, Wood, 20, Badwater Creek area, Wagon Bed Fm., Wind River Basin, Wyoming.

Discussion.—Setoguchi (1973) was correct in recognizing the occurrence of two peradectines at the late Eocene Badwater localities. For reasons not given, he later (1975) emended this conclusion and combined the two species as *Nanodelphys* cf. *N. minutus.* The latter is a composite of two taxa, one of which is *P. californicus* (see above). The remaining part of the sample represents a primitive variant of *P. minutus,* which is here given tentative taxonomic recognition. The few M^2s and M^3s are somewhat less transverse than those of *P. minutus* and have a somewhat higher paracone in relation to the protocone and stylar cusp B. Also, parts of the dentition that preserve other diagnostic features of *P. minutus* (the short talonid on M_4; loss of the gap between M_4 and the ascending ramus of the dentary) are not represented in the Badwater sample. As such, it seems prudent to distinguish this material from *P. minutus* until more conclusive evidence for referral to the latter is available.

Peradectes sp. cf. *P. minutus* occurs with *P. californicus* at five of the Badwater localities. Teeth of the former are smaller, M^{2-3} are more transverse and have more compressed protocones, and, as a result, the disparity in L/W ratio from M^{1-3} is greater. Also, M_{1-3} are narrower in proportion to length. Although these two species differ in size at Badwater, their combined range in size is encompassed by the samples of *P. californicus* from the Uintan of California. As discussed above, this may be an example of character displacement in lithosympatric species, but larger samples are needed to test this inference.

Peradectes minutus (McGrew, 1937)

When McGrew (1937) named the Orellan *Nanodelphys minutus* the Tiffanian *P. elegans* was the only known species of *Peradectes.* Large differences in size and morphology implied generic distinction. However, the morphology of other species of *Peradectes* recovered since then from Paleocene and Eocene horizons indicates that *N. minutus* is the most derived species of a branching lineage that includes *P. pauli, P. protinnominatus,* and *P. chesteri* (and *Peradectes* sp. cf. *P. minutus*). Its advanced dentition appears to be the result of incremental and cumulative changes in that lineage, and generic distinction is no longer warranted. Crochet (1978) and Bown (1979) reached a similar conclusion.

Earlier suggestions by Galbreath (1953) and Setoguchi (1973) that "*N.*" *minutus* may be conspecific with *Peratherium huntii* are in error. Cope (1884) and Galbreath (1953) noted the large size of the entoconid on the type of *P. huntii*—a diagnostic feature of the Didelphini—and, partly on this basis, Hough (1961) allocated *P. huntii* to *Herpetotherium fugax.*

P. minutus is most closely related to *P. chesteri.* However, M^3 and especially M^2 are more transverse, with a more highly compressed protocone. On M^{1-3} the reduced paracone and the protocone are subequal in height and slightly higher than an enlarged stylar cusp B (see McGrew, 1937, Fig. 3; Setoguchi, 1978, Fig. 7A). *P. minutus* also lacks the gap on the mandible between M_4 and the ascending ramus that is evident on the type of *P. chesteri* (Fig. 5).

P. minutus is known from Oligocene horizons of the western interior of North America. Late Eocene material that Setoguchi (1975) referred to *Nanodelphys* cf. *N. minutus* was assigned above to *Peradectes* sp. cf. *P. minutus, P. californicus,* and *Peratherium innominatum.* As discussed above, recognition of *Peradectes* sp. cf. *P. minutus* is tentative. It has most of the derived features of *P. minutus* and, with recovery of additional material, may prove to be conspecific with the latter.

Setoguchi's (1978) sample of "*Nanodelphys* new species" from the Orellan of Badwater is also a composite of numerous taxa. Much of the material represents a small species of *Peratherium* or *Herpetotherium,* which explains his attribution of dilambdodonty to this species. Of the specimens he referred, only CM 19802, 19804, 21697, 33557, 33570, 33574, 33577, 33582, 33589, 33590, 33595, 33598, 33600, 33613, 33619, 33621, 33625, 33628, 33631, 33632, 33642, 33647 belong to the Peradectini, and specifically *P. minutus.* To these should also be added CM 33599 (M^{1-3}) and KU 16611 (M^{1-3}).

Armintodelphys Krishtalka and Stucky, 1983

The two species in this genus—*A. blacki* and *A. dawsoni*—are known from the late Wasatchian to early Bridgerian and from the early Bridgerian, respectively, of the Wind River Formation. *A. dawsoni* is also known from the early Bridgerian Powder Wash locality, Utah (Krishtalka and Stucky, 1983*b*). The systematics of the two species were treated in detail elsewhere (Krishtalka and Stucky, 1983*a*). Briefly, *Armintodelphys* is derived over other North American Peradectini in having M_{2-4} with a reduced, nubbin-like entoconid that is smaller and lower than the hypoconulid, and M_2 with a narrower talonid than trigonid. Otherwise, the two species most closely resemble *P. pauli* in retaining high molar trigonids, long talonids, a buccal emargination between the trigonids and talonids, a longer talonid than trigonid on M_4, and a narrower talonid than trigonid on M_3. More derived species of *Peradectes* have an M_4 with a shorter talonid than trigonid, as well as other advanced features. Accordingly, *Armintodelphys* may have evolved from or shared a common ancestry with *P. pauli.*

An M^2 from Powder Wash, tentatively referred to *A. dawsoni* (Krishtalka and Stucky, 1983*b*), differs from that of known species of *Peradectes* in having a weak, compressed protocone, an enlarged stylar cusp C, more closely approximated paracone and metacone, and expanded stylar salients. As in other Peradectini, the M^2 is not dilambdodont.

Mimoperadectes Bown and Rose, 1979

The only described species in this genus, *M. labrus,* occurs in early Wasatchian faunas from the Bighorn and Powder River basins. Apart from being the largest known species in the Peradectini, *M. labrus* is specialized in having a paraconid on M_{2-4} that is larger and higher than the metaconid. It shares with species of *Peradectes* the morphology of a low, subequal, and closely appressed entoconid and hypoconulid on the lower molars. It differs from all species of *Peradectes* except *P. elegans* in retaining an M_1 that is as large as M_2, an M^3 that is not transverse, and M^{2-3} with comparatively strong conules and stylar cusps C and D, and an uncompressed protocone. As such, *Mimoperadectes* most closely resembles *P. elegans,* but is more derived in having an M_3 with a narrower talonid than trigonid. These features imply that *Mimoperadectes* originated in common with *P. pauli* from a Paleocene species of *Peradectes* that had developed the narrow M_3 talonid. As Bown and Rose (1979) noted, the enlarged paraconid on the lower molars is convergent on the condition in stagodontid marsupials. Unlike the latter, *M. labrus* lacks the enlarged, specialized posterior premolars, and compressed trigonids on the lower molars.

EVOLUTIONARY RELATIONSHIPS

The depiction of relationships (Fig. 6) among *Peratherium, Herpetotherium, Peradectes, Mimoperadectes,* and *Armintodelphys* is based on current thought (Clemens, 1966, 1968, 1979; Fox, 1979) that an *Alphadon*-like dentition represents the primitive condition among didelphines. Accordingly, the following molar characters are primitive for Tertiary North American didelphines: on M_{1-3}, the talonid is equal in width to, but much longer than, the trigonid; the cristid obliqua meets the posterior wall of the trigonid medially, below the ventral apex of the protocristid; the entoconid is high and conical; the hypoconulid is subequal or lower than, and posterior or posterolabial to, the entoconid; the entoconid notch is moderate or large; the metaconid is larger than the paraconid; on M_4, the talonid is much longer than the trigonid; on M^{1-3}, the paracone and metacone are subequal; the centrocrista is straight (not dilambdodont) or weakly directed toward the stylar shelf (incipiently dilambdodont); the stylar cusps and conules are well developed.

In comparison, Tertiary North American didelphines are advanced dentally in having a shortened talonid on M_{1-3} and a more labial cristid obliqua on the lower molars (Fig. 6, node 1)—features that imply their common ancestry. Dental characters among these genera suggest a subsequent divergent radiation: on the one hand, members of the Didelphini—*Peratherium* and *Herpetotherium*—retain one variant of the primitive *Alphadon*-like hypoconulid-entoconid complex, but are specialized in having dilambdodont M^{1-3}, with a reduced paracone in comparison to the metacone and a reduced ectoflexus (Fig. 6, node 2). On the other hand, members of the Peradectini—*Peradectes, Mimoperadectes, Armintodelphys*—appear united by a different suite of derived features: on M_{1-3}, a reduced entoconid and hypoconulid that are closely appressed, subequal, and separated by a weak entoconid notch, and arise from a common internal talonid wall; on M^{1-3}, reduced stylar cusps and conules (Fig. 6, node 3). These genera retain the primitive, non-dilambdodont, structure of the upper molars.

Although the common ancestry of the Didelphini and Peradectini is implied by their possession of a shorter talonid and a labial cristid obliqua on M_{1-3}, their origin is difficult to decipher. The derived characters of each group appear to be variable among the species of *Alphadon* (see Clemens, 1966; Lillegraven, 1969; Fox, 1971, 1979). For example, published figures of the dentition indicate that dilambdodonty does not occur among species of *Alphadon*. However, incipient dilambdodonty, where the centrocrista or just the premetacrista is directed toward the stylar shelf, is evident on some upper molars of *A. marshi, A. lulli, A. rhaister,* and *A. russelli.* Some species of *Alphadon*

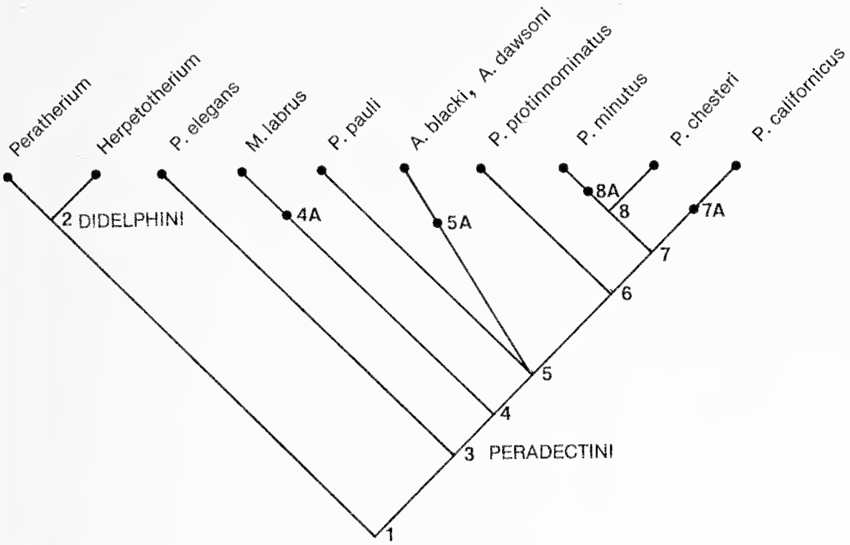


Fig. 6.—Relationships among Paleocene and Eocene North American marsupials. Node 1: shorter talonid on M_{1-3}; cristid obliqua meets trigonid labially, below protoconid on M_{1-3}; Node 2: M^{1-3} dilambdodont, paracone much lower than metacone and ectoflexus reduced; on M_{1-3}, entoconid taller and spire-like, hypoconulid much lower and posterior, entoconid notch very deep; Node 3: on M_{1-3}, reduced entoconid and hypoconulid subequal, closely appressed and share common internal talonid wall; entoconid notch weak; on M^{1-3}, stylar cusps C and D and conules reduced; Node 4: M_3 talonid narrower (basally) than trigonid; Node 4A: large size, M_{2-4} paraconid larger and higher than metaconid; Node 5: M_1 smaller than M_2; M^{2-3} more transverse, with moderately compressed protocone; Node 5A: M_{2-4} entoconid and entoconid notch vestigial; M_2 talonid narrower (basally) than trigonid; Node 6: M_4 talonid shorter than trigonid; P_3 with shorter talonid; P_3 lower than M_1; protocone more anterior on M^{1-3}; Node 7: M_{1-3} talonids with narrower occlusal width (hypoconid more internal, cristid obliqua runs posteriorly from trigonid); M^{1-3} with reduced conules and stylar cusps C and D; Node 7A: P_3 talonid lost; Node 8: greater disparity in L/W ratio from M^1 to M^3; conules and stylar cusps C and D vestigial; M^3 more transverse with a more highly compressed protocone; loss of labial emargination between trigonid and talonid on M_{1-3}; M_{1-3} narrower in proportion to length; Node 8A: M^{1-3} paracone reduced to height of protocone and almost to that of enlarged stylar cusp B; M^3 and especially M^2 more transverse, with a more highly compressed protocone; loss of gap between M_4 and ascending ramus (shortening of jaw).

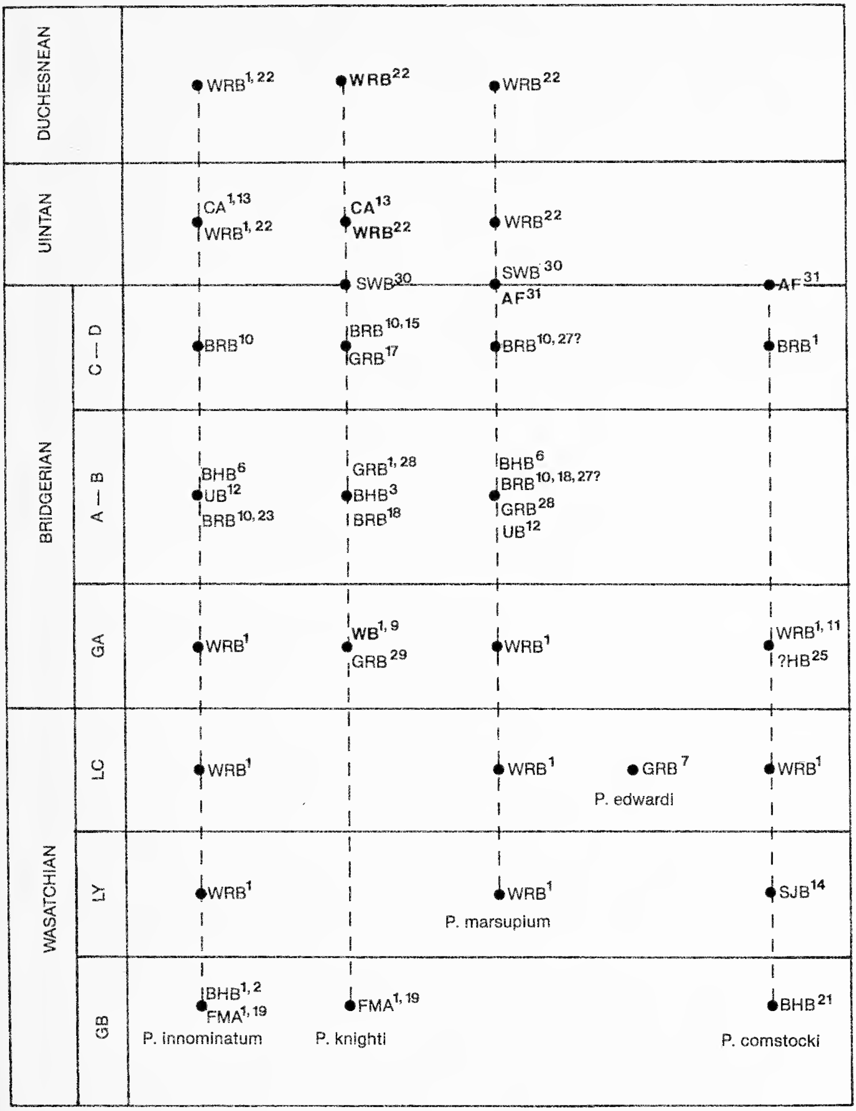
appear to have a tall entoconid, a lower and posterior hypoconulid, and a strong entoconid notch on some of the lower molars. Others have a subequal entoconid and hypoconulid and a weak entoconid notch. Compared to other species of *Alphadon, A. russelli* (Fox, 1979) seems to most closely resemble the Peradectini in having M_{2-3} with short talonids, a labial cristid obliqua, closely appressed, low and subequal entoconid and hypoconulid, and a weak entoconid notch. Similarly, some specimens of *A. rhaister* (see Clemens, 1966) and *A. marshi* (see Lillegraven, 1969) show affinity to the Didelphini in the greater development of dilambdodonty.

These observations cannot, as yet, suggest specific evolutionary relationships. The distribution of these features within and among species of *Alphadon* have not been emphasized, nor, perhaps, found taxonomically useful by students of Cretaceous didelphines. Conversely, diagnostic features cited for Cretaceous didelphines have not proven useful in distinguishing among the Tertiary ones. Given this state of affairs, the only evolutionary conclusion warranted at this time is that the species of *Alphadon* display a range of morphology that encompasses some of the distinctive features of Tertiary Peradectini and Didelphini. The divergence of the two tribes will be better understood when the distribution of these features among the species of *Alphadon* are documented.

One corollary of this conclusion is that Cretaceous didelphines, specifically *Alphadon* and *Albertatherium,* cannot be included in the Peradectini (contra Crochet, 1979) or Didelphini; none of the Cretaceous species has, as yet, been demonstrated to have the suite of diagnostic and derived features of either tribe. A second is that *Thylacodon pusillus* may not be a species of *Peradectes* nor the Peradectini, if figures of *Peradectes* cf. *P. pusillus* (Archibald, 1982, Figs. 42, 43), from the Puercan of Montana, accurately represent the morphology of the species. They indicate that M^1 and M^2 have large stylar cusps C and D, and M_{1-3} have elongated talonids, very high trigonids, large entoconids, and deep entoconid notches. None of the figured specimens exhibits the derived features of *Peradectes* or the Peradectini. A third corollary is that the common supposition of an ancestral-descendant relationship between *Peradectes* and *Peratherium* (Clemens, 1968) is unsupportable; at its earliest appearance *Peradectes* (ss) is too derived in features of the lower dentition.

→

Fig. 7.—Occurrences of North American Eocene species of *Peratherium.* Distance between ages and subages (GB—Graybullian; LY—Lysitean; LC—Lostcabinian; GA—Gardnerbuttean), and placement of occurrences (black dots) are diagrammatic. Letter abbreviations denote areas of occurrences; numbers refer to original sources for identifications and occurrences. AF—Agua Fria; BHB—Bighorn Basin; BRB—Bridger Basin; BSB—Bison Basin; CA—California; FMA—Four Mile area; GRB—Green River Basin; HB—Huerfano Basin; PRB—Powder River Basin; SJB—San Juan Basin; SWB—Sand Wash Basin; WB—Washakie Basin; WRB—Wind River Basin; UB—Uinta Basin. 1—this paper, Krishtalka and Stucky, 1983*a*; 2—Bown, 1979; 3—Bown, 1982; 4—Bown and Rose, 1979; 5—Delson, 1971; 6—Eaton, 1982; 7—Gazin, 1952; 8—Gazin, 1956;



9—Gazin, 1962; 10—Gazin, 1976; 11—Guthrie, 1971; 12—Krishtalka and Stucky, 1983*b*; 13—Lillegraven, 1976; 14—Lucas et al., 1981; 15—Marsh, 1872; 16—Matthew and Granger, 1921; 17—McGrew, 1959; 18—McGrew and Sullivan, 1970; 19—McKenna, 1960; 20—Rose, 1981; 21—Schankler, 1980; 22—Setoguchi, 1973, 1975; 23—Simpson, 1928; 24—Simpson, 1935; 25—Simpson, 1968; 26—Stock, 1936; 27—Troxell, 1923; 28—West, 1973; 29—West and Dawson, 1973; 30—West and Dawson, 1975; 31—West, 1982.

The five known Eocene species of *Peratherium* in North America differ principally in size (Tables 1 and 3), and bear the diagnostic trademarks of the genus at their earliest appearance. Thus, their preserved morphology does not provide any clues to the relationships among the five species. *Peratherium* is unknown from pre-Wasatchian faunas in North America (Fig. 7). Three species (*P. comstocki, P. knighti, P. innominatum*) appear penecontemporaneously in the early Wasatchian. This may imply that *Peratherium* immigrated to the western interior of North America near the onset of the Wasatchian. If so, this may have involved one species, with subsequent diversification, or a multiple immigration.

Three of the five species of *Peratherium* (*P. comstocki, P. marsupium, P. knighti*) show no detectable morphologic change throughout their stratigraphic extent, which according to West et al. (manuscript), corresponds to approximately 7, 9, and 11 million years, respectively. *P. innominatum* shows a gradual and slight anagenetic increase in size from the early Wasatchian to the Duchesnean (Krishtalka and Stucky, 1983*a*), a period of approximately 11 million years. This long-term stasis in the preserved dental morphology of these species is in sharp contrast to the evolutionary tempo and mode of North American species of *Peradectes,* as well as many placentals, during this period of time.

The six known North American Tertiary species of *Peradectes* differ in aspects of dental morphology other than size. *P. elegans* (Fig. 6, node 3) exhibits the primitive features of the Peradectini. *P. pauli* and remaining species of *Peradectes* (Fig. 6, node 5) are more derived in having a smaller M_1 than M_2, an M_3 with a narrower talonid than trigonid, and a more transverse M^3 with a compressed protocone. *P. protinnominatus* and remaining species (Fig. 6, node 6) are advanced over *P. pauli* in having a shorter talonid than trigonid on M_4, a reduced P_3, and a more anterior protocone on M^{1-3}. *P. californicus, P. chesteri,* and *P. minutus* (Fig. 6, node 7) are further derived in having reduced conules and stylar cusps C and D on M^{1-3}, and narrower talonids occlusally on M_{1-3}. *P. chesteri* and *P. minutus* (Fig. 6, node 8) have a greater disparity in the L/W ratio from M^1 to M^3, more compressed protocones, vestigial or absent stylar cusps C and D and conules, narrower lower molars in proportion to length, and no emargination between the molar trigonids and talonids. *P. minutus* (Fig. 6, node 8A) seems most advanced in the hypertrophy of stylar cusp B, the reduction in height of the paracone, and the severe compression of the protocone on the upper molars.

In summary, the primitive features of the Peradectini, expressed in *P. elegans,* are modified in *P. pauli* and, in turn, in *P. protinnominatus, P. californicus, P. chesteri,* and *P. minutus.* The major and discrete modifications are: reduction of P_3, M_1, the molar talonids, and the conules and stylar cusps C and D; compression of the protocone on the upper molars; and an increase in the disparity of L/W ratio from M^1 to M^3. Other modifications are less discrete. They are variable within a species to the point of near overlap with another species. For example, the progressive reduction in the buccal emargination on the lower molars, in the relative height of the trigonids, and in the height of the paracones on the upper molars appear to be part of a morphocline. They are valuable as diagnostic criteria (and are only used as such) in species that express disparate parts of that morphocline.

When the reconstruction of relationships among the species of *Peradectes* is superimposed on their stratigraphic record (Fig. 8), the polarity of morphologic change is consistent with the increasingly younger temporal occurrence of these species. Accordingly, these species appear to form a branching lineage that is characterized by speciation and gradual morphologic change. An ancestral-descendent relationship is implied in the *P. pauli-P. protinnominatus* lineage, with subsequent cladogenetic divergence of a *P. chesteri-P. minutus* lineage and *P. californicus.* Juxtaposition of the stratigraphic record and dental morphology of these species implies that each of the lineages is characterized by incremental and gradual morphologic change, and the appearance, anagenetically, of new, discrete phena, here termed species. None of these species has uniquely derived features that would preclude such a phylogenetic reconstruction. None of these lineages form an evolutionary species (sensu Simpson, 1961). To combine the species within them as such would deny the current paleontological evidence of the appearance of discrete and incremental evolutionary novelties in a temporal succession of progressively younger species. Gaps in the geologic record (and in our knowledge) of these species between their successive first and last occurrences are not evidence against the inferred lineages, nor evidence for an alternative interpretation. When those gaps are filled, that new evidence will lend support, demand modification, or refute the lineages inferred from current evidence.

Armintodelphys (Fig. 6, node 5A) may have evolved in common with *P. pauli*; it has the derived features of the latter, but is specialized in having a vestigial entoconid on M_{2-4} and a narrower talonid than trigonid on M_2. The affinities of *Mimoperadectes* are less clear. Except for an M_3 with a narrower talonid than trigonid, the dentition of *M. labrus* (Fig. 6, node 4A) most closely resembles that of *P. elegans,* and lacks the derived features of other species of *Peradectes.* It may have evolved in common with *P. pauli* from a Paleocene species of *Peradectes* with a reduced talonid on M_3. *M. labrus* is specialized in its large size, and in having a larger paraconid than metaconid on M_{2-4}.

The fossil record of North American early Tertiary didelphines reveals contrasting evolutionary histories. Species of the Didelphini ap-

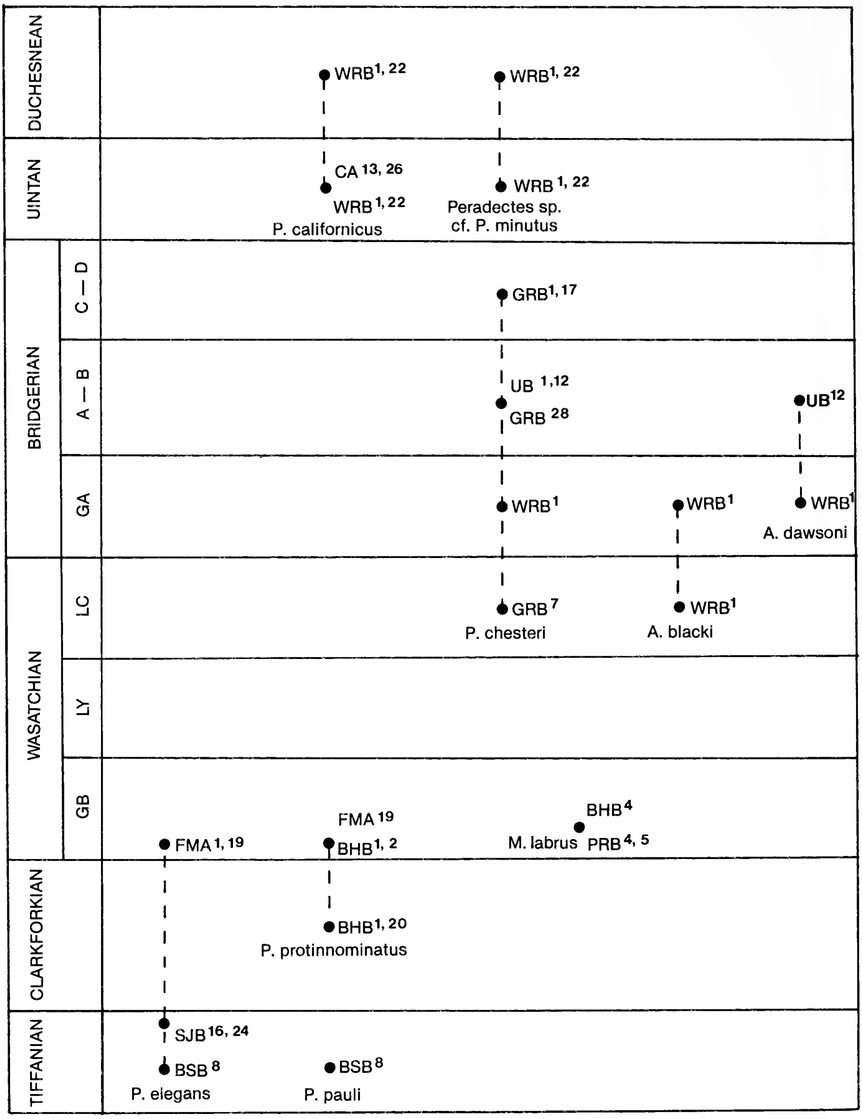


Fig. 8.—Occurrences of North American Paleocene and Eocene species of Peradectini. For explanation of symbols see legend for Fig. 7.

pear abruptly and penecontemporaneously, and remain virtually unchanged throughout their temporal extent. Among the Peradectini, species of *Peradectes* appear sequentially, exhibit cumulative modifications, and apparently form a branching lineage that is characterized by anagenesis and cladogenesis. *Armintodelphys* and *Mimoperadectes,* are offshoots of that lineage.

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THE CHIRA BEACH RIDGES, SEA LEVEL CHANGE, AND THE ORIGINS OF MARITIME ECONOMIES ON THE PERUVIAN COAST

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Abstract

The Chira beach ridges have been radiocarbon dated and provide the best available evidence for the establishment of the north Peruvian coast at 5000 B.P. The stabilization of sea level coincides with a change in the east Pacific Ocean current patterns. These two natural events are seen as major causal factors in the subsequent rise of complex preceramic maritime societies on the coast of Peru.

Introduction

The question of the origins and development of maritime societies on the Peruvian coast has engendered heated discussions by the archaeological community. However, little attention has been paid by archaeologists to the various disciplines, especially oceanography, that are able to provide many of the answers that have been posed concerning this crucial juncture in Peruvian cultural development. Changing environments and biological systems are key to our understanding of man's adaptation to this coast through time. Geological, tectonic, environmental, and oceanographic changes and the El Niño perturbation, all must be an integral part of any discussion centering upon the emergence of Peruvian maritime societies.

There are two environmental factors that are crucial to any discussion concerning the emergence of maritime based societies on the Peruvian coast: the date of the establishment of the modern climate and the

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formation of the present coastline. A major change in the east Pacific current patterns takes place prior to 5000 B.P., which, in turn, is responsible for the northward shift the cold Peru current that brings with it the major fishery that was intensively exploited by late preceramic populations (Rollins et al., 1981; Sandweiss et al., 1983). This event coincides with the formation of the present coastline of Peru at the time when modern sea level was reached. The beach ridges of the Chira River of northwest Peru, provide the best information of the date when modern sea level was attained. Both these two events occurred at circa 5000 B.P. and it is after this date that maritime oriented societies develop on the coast.

HOLOCENE ENVIRONMENTAL CHANGE

In 1981, I presented a model to explain the emergence of maritime societies on the Peruvian coast (Richardson, 1981). A main causal factor was seen to be the rise of sea level to present levels by 5000 B.P. It was demonstrated that the use of maritime resources can be traced as far back as 10,000 B.P. and that the evidence for early maritime exploitation lies submerged on the continental shelf, because the Peruvian coast was many times wider during the Holocene. Complex maritime societies were established when modern sea level and essentially modern distributions of molluscan and fish resources was attained. The developments leading up to the establishment of sedentary maritime societies on the Peruvian coast is to be found on the continental shelf, for the origin of maritime subsistence patterns was not an abrupt transition from hunting and gathering to littoral resources as so often stated, but rather a gradual process of adaptation that preceded the pre-cotton preceramic by several thousand years.

Prior to 5000 B.P., the coastal environment was also markedly different from that of the present. Campbell (1982) reconstructs the environment of northwestern Peru as one with annual monsoon rains, savannas, forests, lakes, and marshlands at 14,000 B.P. The mangrove molluscan fauna from archaeological sites, north of Lambayeque point to continued wetter conditions as late as 5500 B.P. (Richardson, 1978; Cardenas, 1979).

Recent studies in the Santa Valley region has resulted in the identification of an extensive warm water molluscan fauna in a series of preceramic sites (Rollins et al., 1981; Sandweiss et al., 1983). This fauna suggests that the ocean current system of the eastern Pacific was different from that of today. Dating to 5000 B.P., these shellfish species now inhabit the warm water Panamic-Province north of 7.5° south latitude. This study and corroborating evidence from marine sediments off the Central Peruvian Coast also points to a warm water regime prior to 5000 B.P. (DeVries, 1979).

This ever-growing body of evidence now suggests that we can only extend our present day model of the current pattern of this portion of the east Pacific Ocean back about 5000 B.P. The evidence strongly suggests that from at least 11,000 B.P. to about 5000 B.P., the central and northern coasts of Peru were bathed by warm Panamic Province-type waters, which today are found only north of Paita, about 5° south latitude. If the Equatorial warm water current was a yearly visitor to the coast or a year around phenomena, it would have major implications for a different climate and resource base available to pre-5000 B.P. coastal populations. Rainfall would have fallen on coast seasonally and land based resources may have been more abundant. If this senario is valid, the coast of Peru, from Lima northward, would have had a warm water current bathing its shores. The northern extension of the Peru Current with its upwelling and its abundance of resources would have been south of Lima, moving northward and becoming established in its present position after 5000 B.P. The hunters, gatherers, and maritime resource users would have enjoyed a higher abundance of land based resources in grasslands/forests across the wide expanse of the continental shelf prior to 5000 B.P. The warm water ocean resources, may have been markedly less than those enjoyed by post-5000 B.P. populations subsisting on cold water faunas. The dramatic change from the warm water to a cold water ocean regime prior to 5000 B.P. decreased rainfall on the coast to the point of turning the landscape into its current desert environment. The implacement of the cold water current by 5000 B.P. across the widest expanse of the continental shelf between 6° and 15° south latitude, provided the resource base for the succeeding rise of complex maritime societies on the Peruvian coast. The modern weather patterns of the eastern Pacific was established by 5000 B.P. and at the same time, sea level attained its present position. It is with the establishment of the modern coastline and climate that large archaeological sites appear in profusion in this area of the Peruvian coast.

THE CHIRA BEACH RIDGES

The best evidence to date for the establishment of the modern coastline on the western South American coast are the beach ridges of the Peruvian north coast. There are three sets of Holocene ridges, one situated north of the mouth of the Piura River and sets south and north of the Chira River (Fig. 1). Only the set north of the Chira River will be presented in detail.

The research into the Pleistocene marine terraces and Holocene Beach ridges has a long history in northwest Peru, stemming back to Thomas Bosworth's *Geology of the Tertiary and Quaternary Periods in the North-West Part of Peru* (1922) in which he discussed the Pleistocene tablazo

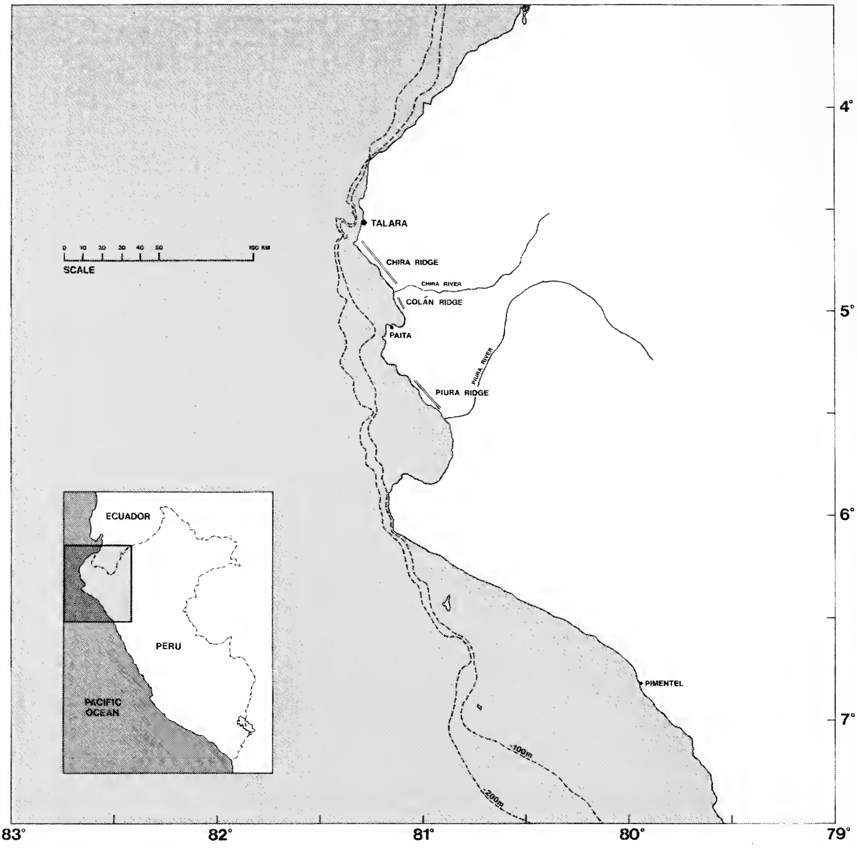

Fig. 1.—Location map of the Chira and Piura River beach ridges.

systems and the Holocene deposits of the Talara area. Other investigators, notably Horace Richards (1962), Lemon and Churcher (1961), Chotowski (manuscript), Woodman and Polia (1974), Nestor Chigne (1975), and Campbell (1982) have made studies of the Pleistocene and Holocene deposits. The archaeological research on the occupation of the Chira ridges began in 1965 in conjunction with a major research program on climate change and cultural development in the Chira and Piura River valleys. The twelve unpublished radiocarbon dates from these beach ridges provide the best sequence of Holocene beach ridge succession in Peru.

There are three raised Pleistocene marine floors fronting the Amotape Mountains—the Mancora (61–330 m high), the Talara (49–90 m high) and the latest, the Lobitos Tablazo (14–41 m high). These former marine floors overlie a truncated surface of the Cenozoic and the rocks of the Pennsylvania Amotape formation and are composed of a thick sequence of marine quartz sands, shelly and calcareous sands, marls, coquinas, and pebble beds. Each of these tablazos represent a period of marine encroachment, followed by vertical uplifts along the Pacific fault line, bordering the continental shelf.

Of interest to this discussion is the Lobitos Tablazo, little of which remains at present. The main section, still extant, is a thin ridge fronting the Holocene beaches acting as a barrier behind which mangrove vegetation, during the late Pleistocene and early Holocene, thrived (Richardson, 1978). The Lobitos ridge consists of a wave cut beach on its western margin. The mollusks of the western edge, facing the ocean are salt water species, whereas the mollusks on the eastern face consist of mangrove and other warm species reflecting a shallow lagoonal environment.

The nine beach ridges emanate out of the Chira River and stretch 30 km to Punta Balconas and Punta Pariñas at the modern town of Negritos. Parallel to the Lobitoas Tablazo, there are nine Holocene beach ridges which can be divided into two groups. The first four, with sharply defined profiles, are separated by broad swales and which are easily discernable, whereas the second group of five, presents a complex series of hummocky ridges with intermittent swales upon which there are active barcan dunes. In the central section of their distribution, the oldest four ridges are continuous, but as they near Punta Pariñas, the first two disappear and the remaining two become a series of isolated mounds. During this first episode of Holocene beach ridge development, Punta Balcones and Punta Pariñas were islands off the coast and only during the emergence of the second group of ridges did these two islands become landlocked.

These nine beaches were formed by the carrying of sediments from the mouth of the Chira River, northward with the prevailing direction of the current which were then implanted by wave action shoreward. The rate of discharge of the Chira is second only to the Santa and the Tumbes rivers and the sediment grains are uniform in size and have the same constituents as the Chira River alluvial deposits (Chigne, 1975). The beach ridges were then raised by tectonic uplift and as a consequence, a stranded beach system of 2.7 km wide resulted (Fig. 2).

The archaeological sequence for the Piura-Chira Region has been detailed elsewhere and the cultural associations of each ridge will be briefly discussed but not elaborated upon (Lanning, 1963; Richardson, 1973, 1978). The following cultural sequence, based on forty radiocarbon dates, will be used in this presentation: Amotape (11,500–

8000 B.P.); Siches-Estero (8000–5000 B.P.); Honda (5000–3500 B.P.); Paita (3500–2500 B.P.), Sechura (2500–1200 B.P.); and Piura (1200–1532 B.P.).

The shell capping of the beach ridges is the product of both natural and human agencies. On all ridges there are fireplace units and small middens of heated and discarded shells. On ridges 2–7, sherds are present, and on ridges 8 and 9 lithic tools prevail. Many of these ceramic fragments represent the breakage of whole vessles, due to wind erosion. All of the complete vessels recovered were placed mouth downward and buried, presumably for later reuse, and these are continually being uncovered by the wind and rapidly eroded. Except for a market basket handled Sechura pot and a badly eroded section of a Piura stirrup spout, all of the pottery represents utilitarian ware; water storage jars and a small percentage of wide mouthed cooking vessels. All of the utilitarian ceramics have been tied into the ceramic assemblages of each phase by comparison with nearby village sites and encampments.

The present population in Negritos and a small settlement on the present beach dunes at the southern edge of the ridges, still exploit the shellfish resources. Offshore fishing is also a major economic mainstay of San Pedro, the small fishing village outside of Negritos (Sabella, 1974). Sabella (personal communication) has made the following comments on the shellfish utilization by the Negritos population:

> The main mollusk gathered is the concha blanca (*Tivela hains*) and when they are in abundance, one man can fill an entire burlap sack in 45 minutes, Concha blanca is gathered at low tide, gatherers move into the shallows, first feeling for the shells with their feet. Once located, they reach down and dig them out by hand, often pulling several out at a time. The shells are relatively close to the surface, in two or three inches of sand . . . these small clams are the preferred bait for almost all types of fish, offshore as well as inshore species. The second type of shell is very small and is referred to as rique (*Donax peruvianis*). They are gathered with a "cafan" (a simple frame scoop with a net bag attached, much the same as the "muy muy" or sand crab scoop). The "cafan" is raked through the sand at low tide several times, and then the bag is agitated to remove the sand, leaving only the rique shells.

The beach ridges have been in continuous use since circa 5000 B.P., (Fig. 3). Prior to the beach ridge formation, the Lobitos Tablazo was occupied by the preceramic Siches populations exploiting the mangrove mollusks in the protected lagoon on the east side of the tablazo. The small Siches site below Petro Peru marker 280 on the tablazo should date between 8000–7000 B.P., because a Siches site (PV9-31) on the

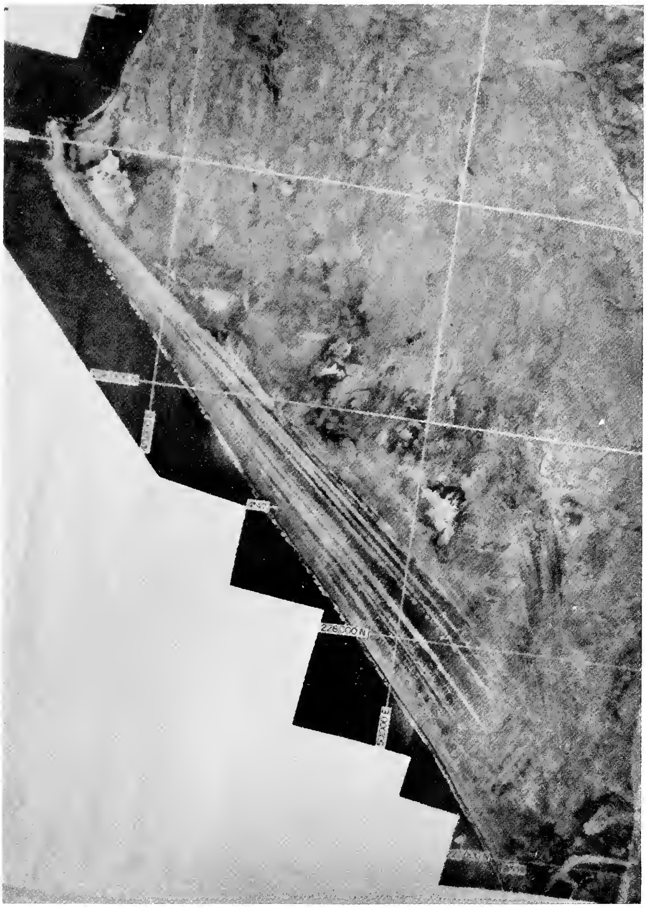

Fig. 2.—Air photo of the northern set of the Chira beach ridges. Photo courtsey of Sevicio Aerofotografico Nacional del Peru, negative number 1662-D-1, 1946.

Talara Tablazo near the mouth of the Chira River is dated to 7485 ± 120 (SI-1416) B.P.

With the emergence of the first Holocene shore line, the oldest ridge was utilized by preceramic populations after the disappearance of mangrove vegetation in the Talara region (Richardson, 1973, 1978). The dates on ridge 9 are 3985 ± 80 (SI-1456) B.P., 4485 ± 90 (SI-1450) B.P., and 4255 ± 65 (SI-1420) B.P., which places the occupation of this earliest ridge in the preceramic Honda phase. The base camp sites

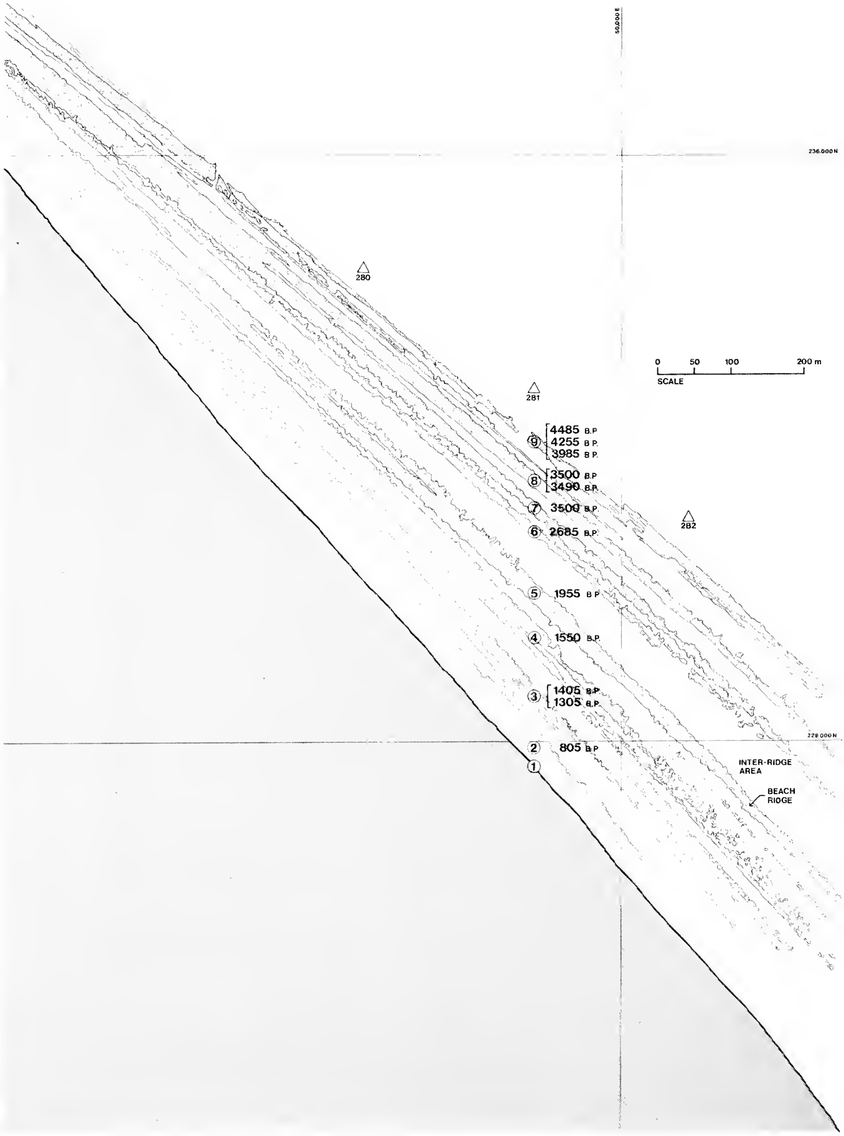

Fig. 3.—The Chira beach ridges and associated radiocarbon dates.

(PV7-16 and PV7-19) are situated on the Mancora Tablazo, north of Quebrada Pariñas and although no major Honda sites have been discovered in the Chira Valley, they were certainly present and may have been subsequently destroyed by later intensive irrigation farming.

Of the next three oldest ridges, ridge 6 is definitely correlated with late Paita ceramics, 2685 ± 105 (SI-1422) B.P. and on ridge 7 and 8 dates of 3500 ± 160 (GX1565) B.P. and 3490 ± 80 (SI-1421) B.P. are fully acceptable for early Paita. Two dates, 3610 ± 145 (GX1136) B.P. and 3390 ± 125 (GX1003) B.P. from the enormous Paita (PV8-7) site at the south end of the ridges supports this interpretation. The hearth, on ridge 8, from which the charcoal sample was secured, contained two sherds of the Paita period, probably representing the reuse of this ridge by Paita inhabitants of ridge 7. It is probable that ridge 8 may also prove to be preceramic in its occupation.

The dates on the four oldest ridges, of course, refer to the period of occupation and *not* to the date of the building or emergence of the former beaches. The temporal formation for the first set of four ridges spans over 3000 years.

Between this group of older ridges there is a 175 m wide separation before encountering the youngest group (Fig. 4). The five youngest ridges, including the present standline, begin their ceramic history during the Sechura period. Ridge 5, first of this group, associated with Sechura ceramics dates to 1955 ± 100 (SI-1423) B.P., whereas ridge 4 dates to 1550 ± 110 (GX1556) B.P. and ridge 3 at 1405 ± 75 (SI-1424A) and 1305 ± 100 (SI-1424B) B.P. It is interesting to note that the Sechura ridges were as intensively occupied as the Piura ridges, but that few village sites are known for the region versus the hundreds of sites known for the Piura period. The Sechura sites on the Chira River have most probably been destoryed through river channel changes and modern agriculture in the floodplain zone. Ridge 2 dates to the Piura phase at 805 ± 60 (SI-1457) B.P. A *circa* 2000 year period is indicated for the formation of this younger beach series. The width of these ridges as compared to the older set are between 125 and 225 m wider, which can be interpreted as the consequence of the Chira sediment load spreading northward in conjunction with the development of dune formations, not present on the older 4 ridges (Fig. 4).

The point to be stressed here is that the Chira beach ridges began forming only when modern sea level was attained at circa 5000 B.P. Certainly, beach lines were formed prior to 5000 B.P., but these were either submerged as the ocean rose or were destroyed by wave action as the sea encroached landward.

The beach ridges south of the mouth of the Chira River at Colán are composed of pebbles which were distributed from a small canyon

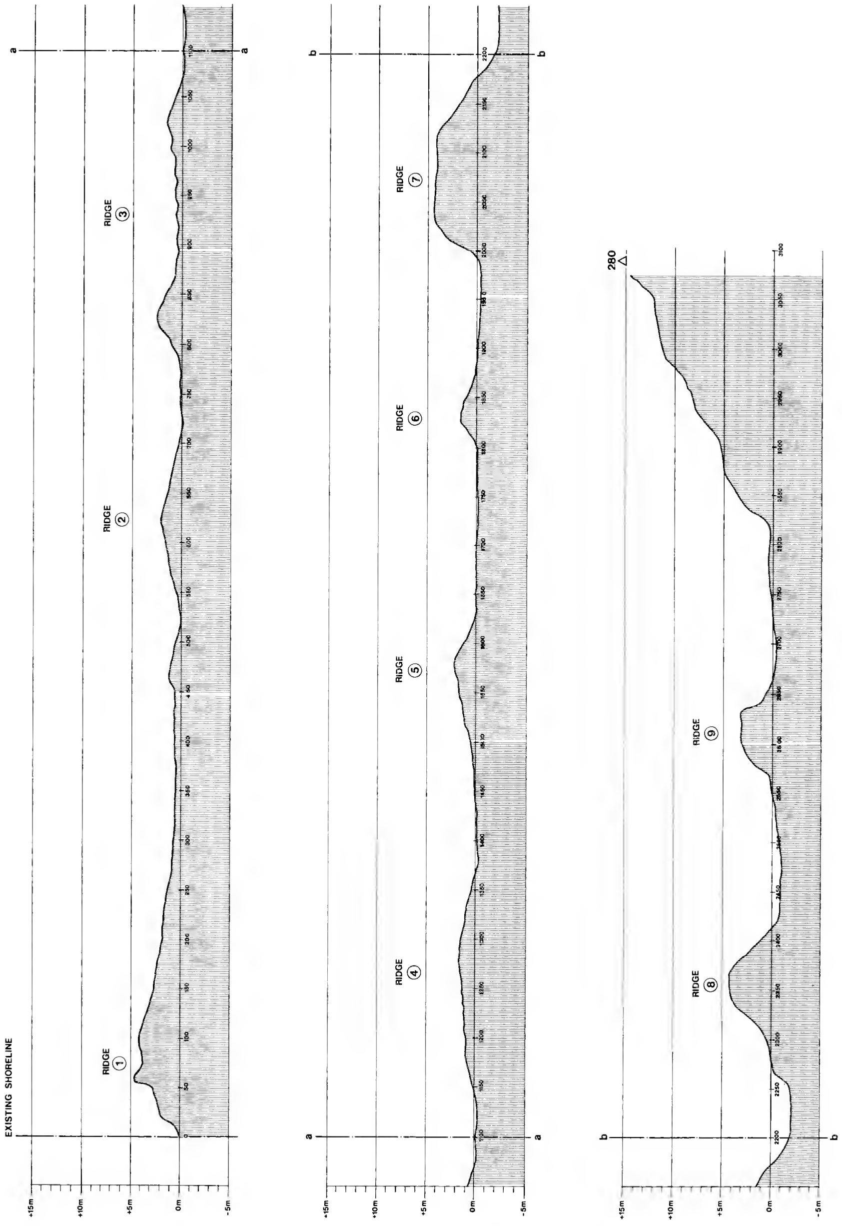

Fig. 4.—Cross section of the Chira beach ridges at survey marker 280. Adapted from Chigne (1975).

cutting into the Talara Tablazo. The pebbles from the Talara formation were eroded from the Canyon into the ocean at the southern edge of the present Holocene deposits at Colán and distributed northward by the current. The only mechanism of massive erosion in this desert region are the El Niños and there is a distinct possibility that the Colán ridges were formed by flooding as a result of catastrophic El Niños, yet to be dated.

CONCLUSIONS

Our knowledge of the impact that natural forces had upon prehistoric Peruvian cultural development is practically nil and until extensive oceanographic, geological, and paleoclimatological work is done in the Central Andes, the explanatory value of reconstructing Peruvian cultural development, strictly from the archaeological record, may prove misleading.

The date of 5000 B.P. is crucial to our understanding of the rise of complex maritime societies on the coast of Peru, for it is at this time that modern climate patterns had been established and modern coastlines formed. It was at this point in Peruvian cultural development that complex maritime adapted societies were established. It is now time for landlubbers to adapt themselves to the ocean and to interpret maritime origins from a seaward position rather than to continue to explain the establishment of maritime societies on the Peruvian coast, strictly from a landward position.

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LANDSCAPE ALTERATION AND PREHISTORIC HUMAN OCCUPATION ON THE NORTH COAST OF PERU

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ABSTRACT

A series of uplifted bays and former shorelines in the Chimbote region are discussed in relation to tectonic uplift during the Peruvian preceramic period. The molluscan fauna from a series of these preceramic sites are warm-water species, which the authors interpret as evidence for a warm-water current prior to 5000 B.P. This indicates that the east Pacific Ocean currents were markedly different from the modern current patterns. This date has a major implications for the pre-5000 B.P. climate of the north coast of Peru.

INTRODUCTION

Interdisciplinary studies have long been recognized as essential in understanding mankind's prehistory. Archaeologists have increasingly relied on the integration of many different branches of knowledge in the attempt to interpret the past. In this article, the techniques and contributions of archaeology, geomorphology, and molluscan paleoecology have helped us to delineate the relationships between man and a rapidly shifting physical environment during the preceramic epoch on the north coast of Peru.

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Geologic Setting

The Pacific Coast of Peru is tectonically active due to subduction of the Nazca plate beneath the South American plate. The distribution of earthquake hypocenters and volcanic activity suggest a large scale segmentation into subunits with varying amounts of inclination beneath the South American plate (Barazangi and Isacks, 1976). Beneath central and northern Peru, the Nazca plate is shallow and flattened and is associated with a high level of shallow (50 km deep) seismic activity but very little volcanic activity. In contrast, the Nazca plate beneath southern Peru and northern Chile is steeply inclined with concomitant deeper-focus seismic activity and increased volcanism. The boundary between the two segments may represent a tear in the Nazca plate. The shallow seismic zone beneath central and northern Peru may be the most active of the world's subduction zones (Barazangi and Isacks, 1976).

Human occupation of the Peruvian coast during the Holocene has been accompanied by episodically intensive tectonism including occasional cataclysmic earthquake activity (Moseley et al., 1981; Ortloff et al., 1982; Sandweiss et al., 1981) and in some areas, volcanism. The configuration of the subducting Nazca plate has not been geologically stable. Although the region of central and northern Peru has not been active volcanically during man's habitation of the area, volcanic rocks of Miocene and Pliocene age are common.

Tectonism, Molluscs, and Archaeology

Tectonism along the western margin of Peru has highly modified coastal morphology, profoundly affecting the history of human occupation in this region by altering natural and artificial environments and the essential resources, which these environments contain. Many changes visible in the archaeological record can be explained by reference to these environmental alterations. This paper details some preliminary investigations into the relationships between landscape alteration and human occupation on the north coast of Peru.

In order to understand changes in the resource base and settlement patterns of prehistoric populations on the Peruvian coast, it is necessary to temporally correlate tectonic episodes with archaeological sites. Marine molluscs, which are often very habitat-specific and have long been exploited by coastal populations, provide a valuable index of changes in coastal geomorphology and ecology and therefore provide powerful chronostratigraphic and paleoecologic tools.

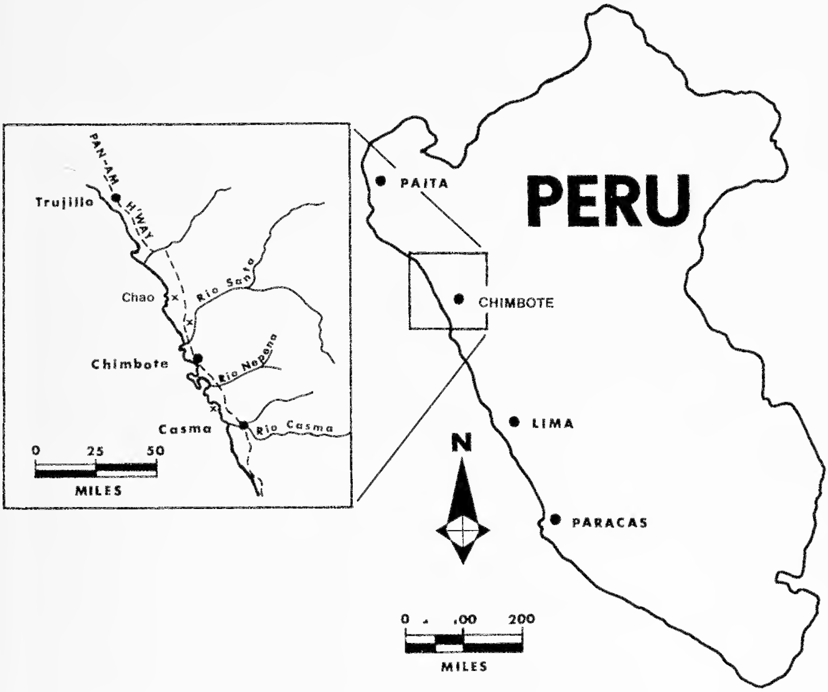

Fig. 1.—Project location. The Pampas las Salinas and Salinas de Chao sites are indicated by X's on the inset map.

The results of our investigation of preceramic sites on the northwest coast of Peru support a tectonic model for the area which involves relatively small, but distinct, blocks, possibly bounded by major fault systems trending approximately east–west (perpendicular to the coast). The rivers along the Peruvian coast also run east–west and may be controlled by these faults. Each block appears to have had a different tectonic history, decipherable by the study of molluscs in prehistoric midden deposits and in living position on uplifted beaches and bay floors, in conjunction with the study of relict geomorphic features visible in the field and on aerial photographs. The sparsely vegetated arid region of coastal Peru is an ideal setting for preservation and observation of such features.

This study focuses on two elevated relict bays in the Chao and Santa valleys (Fig. 1) and draws comparisons with other uplifted bays at Ventanilla on the central coast (Moseley, 1975) and at Otuma on the south coast (Craig and Psuty, 1971) and with the still-active bay of Huaynuna, between the Casma and Nepeña valleys to the south of the Santa River. The relict bays of Santa and Chao are only 15 km apart. Although both have evidence of preceramic occupation prior to uplift, the ancient strandline collectors of Chao gathered a diversity of cool-water molluscs indigenous to the present-day Peruvian coast, whereas the Santa strandlopers exploited an anomalous molluscan fauna.

The very different setting of Huaynuna Bay, also with associated preceramic middens, suggests the presence of a tectonic province boundary between Huaynuna and the Santa-Chao area to the north.

LANDSCAPE ALTERATIONS AND HUMAN OCCUPATION

Pampa las Salinas, Santa Valley

Situated to the north of the modern Santa River mouth, the present-day Pampa las Salinas area is a barren desert zone characterized by windswept beach ridges, salt flats, and rocky foothills (Fig. 2). The area has no natural source of surface water, and human habitation is restricted to a few dwellings in the irrigated southern portion of the Pampa along with several chicken ranches located further to the north, on top of relict beach ridges. The beach ridges provide access roads to the shore and a source of beach cobbles for construction. The salt flats are currently worked with heavy machinery.

A few thousand years ago, this region was geomorphically, and possibly climatically, quite different. The shoreline at that time was situated about 5 km to the east of its present position and formed a long, curving bay at the base of the foothills (Fig. 2). Fronted by an ancient sea cliff 5 to 10 m high, this relict bay represents the highest shoreline stand in the region. Sedimentary deposits on top of the sea cliff consist of culturally accumulated shell middens on top of colluvium naturally derived from the adjacent foothills. Below the cliff, the ancient *in situ* beach deposits are preserved as a white band of largely broken and size-sorted shell material, visible even on aerial photographs.

Preceramic shoreline collectors deposited refuse in middens along the top of the sea cliff and maintained a base camp on lower ground at the southern end of the bay. The largest of the cliff-top middens, the Ostra site, is situated on and around a rocky promontory overlooking the ancient beach.

Excavation of a small test pit revealed 60 to 70 cm of unstratified shell debris, some fish remains, and charcoal. No artifacts were found. Two C-14 assays on shell material from the Ostra midden yielded uncorrected dates of 5400 ± 60 years B.P. (SI-4954) for the bottom of the deposit and 5160 ± 60 years B.P. (SI-4955) for the middle of the deposit. The molluscan assemblage consisted entirely of warm-water, species, most of which are now only found 500 km or more to

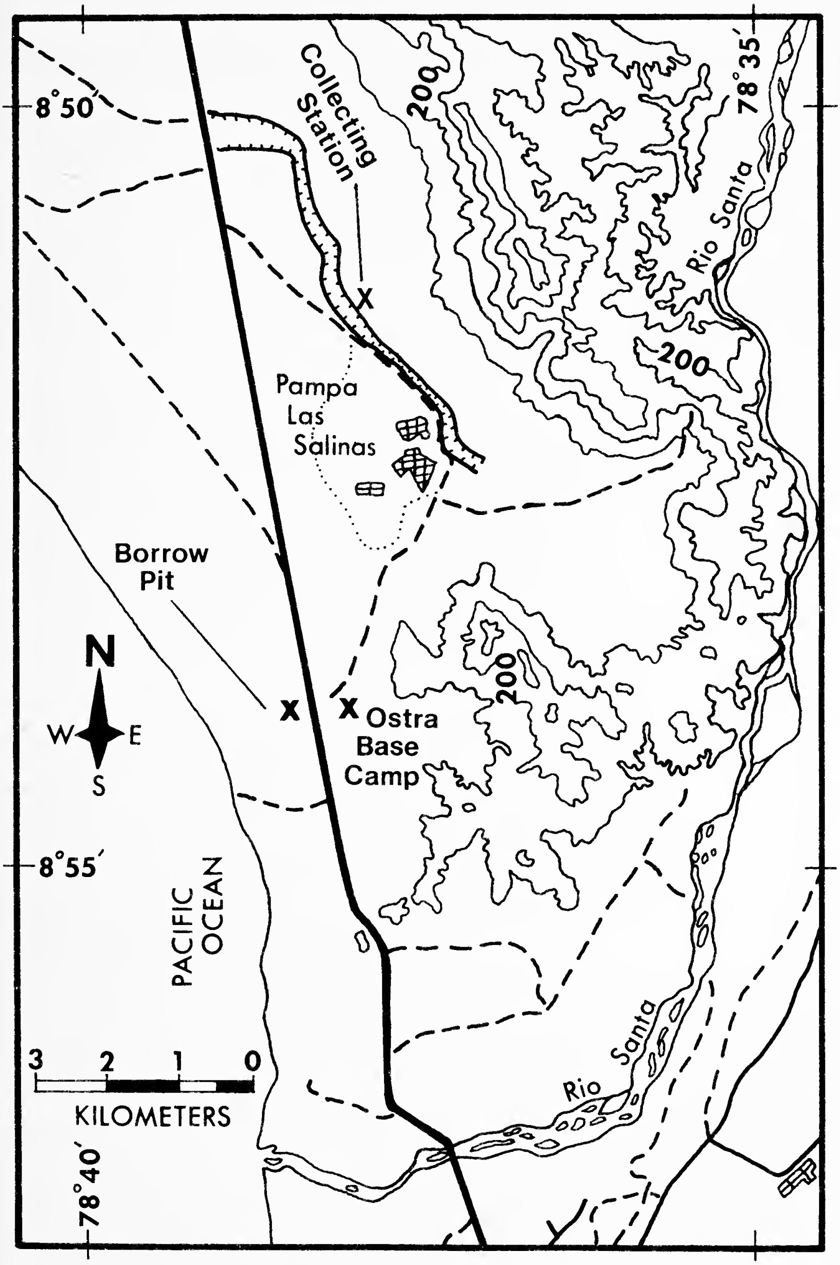

Fig. 2.—The Pampas las Salinas preceramic sites. The Ostra base camp and collecting station and the borrow pit are denoted with X's. The contour interval is 100 m.

Table 1.—*Molluscan species recovered from the Ostra Site, Pampa las Salinas.*

Species	Modern distribution
Argopecten circularis (scallop)	north of Paita, Peru
Ostrea chilensis (oyster)	entire coast, mostly north of Paita
Anomia sp. cf *A. peruviana*	north of Paita
Trachycardium procerum (Clam)	entire coast
Chione (*Lirophora*) *discrepans* (Clam)	north of Islay
Protothaca (*Colonche*) *ecuadoriana* (clam)	north of Tumbes
Anadara bifrons (clam)	north of Paita
Cerithium (*Thericum*) *stercusmuscarum* (snail)	northern Peru
Cerithidea mazatlanica (snail)	north of Peru
Nassarius (*Arcularia*) *tiarula* (snail)	north of Peru

the north of the Santa Valley (see Table 1). Most abundant were oyster and scallop shells, neither of which had previously been reported from any other archaeological site along the Humboldt-washed Peruvian coast. Subsequent to our work at Pampas las Salinas Pozorski and Pozorski (n.d.) have found an undated assemblage of warm-water molluscs at the preceramic Almejas site near Huaynuna bay.

The cockle *Trachycardium procerum* was the only mollusc species at the Ostra site that has also been found at other sites within the cold-water Peruvian province. *T. procerum* is quite temperature tolerant and was noted by Olsson (1961:247–248) to occur in both the warm-water Panamic and cool-water Peruvian provinces. Over its current geographic range, it displays the often-noted trend among molluscan species of increased size in colder waters. Olsson (1961) stated that "Peruvian specimens are as a rule larger than those from more northerly stations." The Ostra specimens are smaller than those from other Peruvian sites, in accordance with other evidence of warm-water conditions.

All of the mollusc species found in the Ostra site were also collected from the relict beach area directly below the site. Frequency distributions were, as expected, different in the two assemblages, reflecting human selection for economically more important (that is, larger) species. Some of the species were in living orientation in the relict beach area. Oysters, for example, were found cemented to isolated, often partially buried rocks. Excavation of shallow trenches at right angles to the paleo-strandline displayed typical flaser interbedding of intertidal and shoreface sands.

This undisturbed preservation of the beach facies mosaic, with no overlying sedimentary sequence, attests to either very rapid tectonic uplift of the area or a sudden sea level drop. The evidence demands a rapidity of change that is difficult to attribute to non-tectonic causes. Moreover, strandline retreat via sedimentary progradation would have most likely buried or destroyed the integrity of the facies mosaic by erosional reworking. The relative uplift of the Ostra site and concomitant westward migration of the strandline will hereafter be referred to as the Salinas Event. We believe that the suddenness of the Salinas Event is most compatible with a tectonic cause of cataclysmic nature.

The presence of a warm-water molluscan fauna at the Ostra site invites further speculation (Rollins et al., 1981). There is a substantial literature dealing with thermally anomalous molluscan assemblages, herein referred to as TAMAs (see Zinsmeister, 1974, for a recent review). In each described TAMA occurrence, the anomalous assemblage consists of a very few species and very few specimens of any particular species. With its moderately high diversity of Panamic (warm-water) species (see Table 1), the Ostra occurrence is a unique TAMA. Moreover, it obviously persisted at the Ostra site long enough to become a local resource base for a preceramic population. All previously described TAMAs, such as those of the early Pleistocene of California, can be attributed to individual years when warm (or cold) currents varied in intensities and positions. This permitted pelagic larvae, especially the planktotrophic forms with extended planktonic stages, to temporarily extend their ranges. All such TAMAs would be short-lived, incapable of becoming a significant food resource of the kind indicated by the Ostra remains. The Ostra occurrence requires an explanation which would permit the displaced fauna to spawn and increase population size sufficiently to allow profitable harvesting. All other described TAMAs involved species being transported into water where normal temperatures prohibited reproduction. The Ostra site and associated relict beach indicate the persistence of warmer (reproductively compatible) water conditions for at least several years—multiple age-classes of the transitional, warm-water species are preserved in the relict beach assemblage.

The coast of Peru certainly provides ample opportunity for current displacement of molluscan larvae. The sporadic El Niño current brings warm water down the Peruvian coast from the Gulf of Guayaquil area. Maximum El Niño events can reach as far south as the Paracas peninsula, although such events occur on the average only several times per century. A live *Spondylus* mollusc was reported from Callao Harbor on the central coast following the strong El Niño occurrence of 1925 (V. Valdiviezo, personal communication). *Spondylus* is a Panamic province mollusc normally limited to the warm waters north of Paita.

One explanation for the Ostra TAMA occurrence would involve closely-spaced, multiple El Niño events bringing warm-water molluscan larvae into the Ostra Bay, which might have been shallow enough to be heated by the sun. This explanation, however, requires that El Niño currents operated in the past in ways significantly different from what is indicated by their known history.

We believe that the Ostra TAMA occurrence is best explained as the result of a radically different organization of currents along the Peruvian shore prior to about 5000 B.P. According to our reconstruction, a southward-flowing Equatorial Countercurrent system formerly washed the coast of north-central Peru and supported a warm-water, Panamic-Peruvian molluscan fauna. Only after 5000 B.P. did the boundary between the Humboldt-dominated, cool-water current system and the warm-water system shift 400 km north to its present location near Paita. Alterations in the Quaternary distributions of ocean-floor phosphorite deposits and land-based guano-derived phosphate deposits support the TAMA evidence of permanent warm-water conditions along the early Holocene Peruvian shore (Burnett, 1980). The arguments for the postulated oceanic and climatic alterations are detailed in Rollins et al. (n.d.)

Paleoenvironmental relationships of the preceramic Ostra base camp site are more difficult to determine, due to later wall and road construction, cultivation, and extensive looting. Surface observations indicate that the base camp middens contained a molluscan fauna similar to that at the Ostra site, as well as fish and sea mammal remains and a crude lithic industry composed of cores, hammerstones, and unifacial scrapers made from beach cobbles. Mortars are also present and may have been used to process fish and molluscan resources.

The increased diversity of resource species coupled with the presence of artifacts suggest that this site was actually a base camp for the preceramic people who maintained a string of collecting stations such as the Ostra site along the bay shore to the north. The base camp was thus situated on the bay as near as possible to the mouth of the Santa River. This location would have maximized access to both bay shore and riverine environments and their respective resources.

The Salinas Event displaced the shoreline several kilometers to the west, probably causing the destruction of the warm-water mollusc beds and the abandonment of both the Ostra site and the Ostra base camp. There is no indication at either site of a shift in harvested species from warm water to cold water shellfish. This fact supports the argument that the sites were abruptly abandoned prior to the shift in coastal currents, probably following and as a result of the Salinas Event.

The Salinas Event also triggered two related geomorphic processes in the Pampa las Salinas area—the progressive southward migration of the Santa River mouth and the westward progradation of the coast due to sequential beach ridge formation. Prior to the uplift, the Santa River may have entered the ocean through the ancient bay itself (Moseley, personal communication). Evidence for this course is slight at present, but the suggestion deserves serious consideration. The presence of an active river mouth in the bay would affect interpretations of Ostra settlement patterns.

Immediately after the uplift, the Santa entered the ocean from behind a hill on the southern end of the Pampa. This mouth (Mouth 1) may have been the pre-uplift course as well. In any event, Mouth 1 was the basal focus of the first series of beach ridges visible in aerial photographs of the Pampa las Salinas. Later, the river mouth shifted several hundred meters south to exit behind another hill (Mouth 2), generating a second series of beach ridges. Mouth 1 is cut across the base, presumably by the river when it flowed from Mouth 2. This fact, along with the implications of the east to west (early to late) temporal gradient of the beach ridges, indicates that Mouth 1 predates Mouth 2.

More recently, the river has continued it southward migration to its present position 3 km south of Mouth 1. The lack of beach ridge formation in the area between Mouth 2 and the present mouth suggests that this last shift has occurred fairly recently. A few small, incipient ridges have formed to the north of the present mouth. Decreased flow due to bleeding of the Santa for irrigation may have affected the river's capacity to carry material for beach ridge consturction; progressive stabilization of the drainage system following the Salinas Event also might have caused a systematic reduction in the amount of material available for transport and incorporation in new ridges.

The southward migration of the Santa River following the Salinas Event can be explained by several models. The Salinas Event may have caused (or emphasized a pre-existing) south-dipping tilt of the coastal plain in the Santa Valley region. Alternately, if the Santa River runs along a major fault line perpendicular to the coast, uplift of the northern block relative to the southern block could have caused the river to move southward off the higher northern block. Further field work is necessary to test these various hypotheses.

Beach ridge formation is closely related to the actions of the river. The ridges all originate at river mouths and flow northward in the direction of the prevailing, wave driven longshore current. At least nine ridges run the length of the coast on the westward margin of Pampa las Salinas. Each ridge is composed of marine sand and river cobbles. Active marine involvement in the formation process is shown by the presence of several small, intertidal gastropods (*Prisogaster niger* and *Tegula atra*) still associated with their opercula[1]. Each ridge, as it was

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[1] Opercula are small discs used by certain gastropods to seal off the entrance to their shells. Because they are attached only by soft parts and become automatically disarticulated after death, the proximity of the opercula to the shells is a strong indication that the gastropods have not been transported since death and that the deposit is therefore primary.

constructed, must have been right on the beach front. The construction of a new ridge would deactivate the preceding one, creating a time transgressive, horizontally stratified sequence moving from east (earliest) to west (latest). Shell material from a borrow pit in one of the earliest ridges yielded an uncorrected C-14 date of 4235 ± 115 years B.P. (SI-4957). This date falls nearly one thousand years and many standard deviations later than the most recent date for the uplifted Ostra site, confirming the geomorphic observation that the ridge formation began subsequent to the Salinas Event.

Two processes may be involved in the sequential formation of the Santa beach ridges. Grolier et al. (1974) feel that the multiple ridges resulted from episodic seismic events, with each ridge representing a new, minor uplift. The other possible process is lateral accretion, the way in which beach ridges prograde seaward in tectonically stable areas (see for example, King, 1973). The beach ridge borrow pit mentioned above revealed a diagnostic sedimentary sequence. A thick layer of poorly sorted, relatively fine material with a few poorly rounded large clasts was overlain by a well sorted layer of well rounded cobbles. The following scenario would account for this sedimentary sequence:

1. A strong El Niño event accompanied by abnormal precipitation washed large quantities of loose material into the river from the normally inactive, unvegetated, arid region of the lower Santa drainage basin, while simultaneously increasing the competence of the river. Imbalances in the drainage system caused by tectonic episodes such as the Salinas Event would have increased still further the amount of material available for transport. The normal lack of rain means that the drainage system only adjusts itself much more rapidly to landscape alterations of tectonic origin during the rare El Niño events accompanied by heavy rains than at other times.
2. The rapid efflux of material out of the river mouth caused rapid progradation of the coast to the north of the river as the material was transported and deposited by the longshore current. This material was essentially unmodified and poorly sorted, similar to the lower layer found in the beach ridge.
3. After the El Niño rains ceased and the coastal system was no longer swamped with sediment, wave action again dominated coastal processes. The result was that fine sediment was removed and larger clasts were rounded and thrown up on the shore as a lag-type deposit. The upper layer of the beach ridge represents this kind of deposit. After each ridge reached a threshold height, material no longer reached the top and a new ridge formed on the seaward side with the next El Niño.

Both episodic, minor uplift and lateral accretion relating to major El Niño events may have been involved in the observed sequential formation of beach ridges in the Pampa las Salinas area. Further field testing will be required in order to evaluate the contribution of each of these processes. If the El Niño hypothesis proves valid, then the Santa beach ridges encode data on the history of major El Niño occurrences over the last 4000 years. Each major El Niño could be dated by C-14 analysis of marine gastropods incorporated in the diagnostic, El Niño-derived sedimentary sequence. These studies would supply information on intensity and periodicity of strong El Niño events. Such information is of considerable consequence in understanding the development of coastal Peruvian societies (Sandweiss, n.d.b.).

The Pampa las Salinas beach ridges have almost no evidence of premodern human use. The only abandoned structures on the ridges are a few slightly curved lines of stones opening away from the prevailing southwesterly winds; these lines may have been the foundations of windbreaks. They have no associated artifacts and could as easily be modern as ancient. The lack of sites in the Pampa las Salinas following the Salinas Event suggests a dwindling resource base related to the large magnitude uplift and perhaps to the postulated shift in coastal current regimes.

Salinas de Chao, Chao Valley

The other raised bay under consideration lies 15 km north of Pampa las Salinas, at Salinas de chao. Prior to uplift, this relict feature was a deep, arcuate bay fronted by a 5 to 10 m high sea cliff and anchored at the south end by a large, rocky promontory. While active, the Salinas de Chao Bay must have resembled the modern situation at Guañape, 40 km north in the Viru Valley. We refer to the uplift which stranded the Salinas de Chao as the Chao Event[2].

Today, the outlines of the relict bay are clearly visible in aerial photographs. Massive dunes stretch across the former floor, which now contains commercially exploited salt flats. A faint set of beach ridges intervenes between the flats and the modern shore. As in the Pampa las Salinas, the Salinas de Chao ridges must have formed after the uplift and are probably an actual extension of the southern (Santa) ridges. The Santa River is the nearest source of raw material upcurrent from the Salinas de Chao; the distance from this source accounts for the diminished size and definition of the Chao ridges.

A number of archaeological sites are located in the Salinas de Chao area. Most are preceramic. Based on surface collections of molluscs and the postulated effects of the Chao Event on the natural molluscan association, we proposed a relative chronology for four of these sites.

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[2] Thomas J. DeVries (personal communication) believes that there may have been two episodes of uplift at Salinas de Chao, separated by decades or even several hundred years. Again, further fieldwork will be necessary to evaluate this possibility.

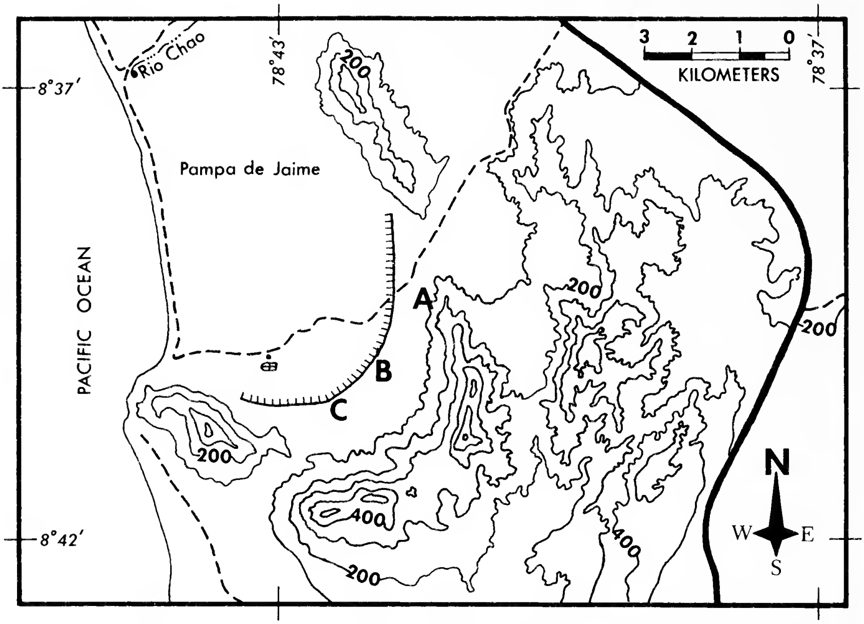

Fig. 3.—Location of the Salinas de Chao preceramic sites. Contour interval is 100 m.

Radiocarbon dating of shell material from three of the sites has partially confirmed our analysis.

Called Los Morteros by Cardenas (1979) and referred to here as Site B, the earliest site is a large mound on the edge of the former sea cliff (Fig. 3). A rocky knoll may underlie the mound. Architectural remains at Site B consist of several crude, round foundations. Two C-14 dates on shell material from the surface of this site yielded uncorrected dates of 4380 ± 75 years B.P. (SI-49598) and 4040 ± 75 years B.P. (SI-4959A), while a charcoal sample was assayed at 4010 ± 85 years B.P. Cardenas (1979:28) reports two dates for the site, 4560 ± 60 and 4660 ± 60 years B.P. The earlier date is on charcoal from a depth of 1.20 m and the later date is on charcoal at a depth of .40 m in the same pit (Cardenas, 1977–1978:26–27).

Molluscs found on Site B cover a broad spectrum of cool-water species from both sandy and rocky habitats (see Table 2). Many molluscs are habitat-specific, and sand-dwelling species are usually limited to sandy beaches, whereas rock-dwelling species live on rocky promontories and similar zones. Finer habitat distinctions than the basic sand/rock dichotomy are possible, but are unnecessary for the present analysis. Food is the only indicated use of molluscs in the Salinas de

Table 2.—*Molluscan species recovered from Site B, Salinas de Chao.*

Species	Modern distribution
Argopecten purpuratus (scallop)	south of Paita, Peru
Donax peruvianus (Clam)	Ecuador to Chile, rare north of Paita
Mesodesma donacium (clam)	south of Paita
Barbatia (*Acar*) *pusilla* (clam)	south of Paita
Trachycardium procerum (clam)	entire coast
Chormytilus chorus (mussel)	south of Paita
Concholepas concholepas (snail)	south of Callao
Sinum cymba (snail)	Ecuador to Chile
Thais (*Stramonita*) *haemastoma* (snail)	Peruvian-Panamic province
Thais (*Stramonita*) *chocolate* (snail)	entire coast
Mitra (*Atrimitra*) *orientalis* (snail)	south of Paita
Fissurella crassa (limpet)	south of Galapagos
Scurria parasitica (snail)	south of Paita
Polinices (*Polinices*) *intermeratus* (snail)	Baja California to Peru (14°14′S)
Crepidula cf. *C. onyx* (snail)	southern California to Chile

The following additional species were identified at Site B, Salinas de Chao by Thomas J. DeVries (personal communication):

Xanthochorus buxea (snail)
Perumytilus purpuratus (mussel)
Aulacomya ater (mussel)
Diloma nigerrima (snail)
Tegula atra (snail)
Polinices uber (snail)
Amphineurid spp. (chitons)

All of these species are Peruvian.

Chao sites, so it is safe to assume that the shellfish were collected live from their respective habitats (rather than as beach detritus) and therefore indicate the range of microenvironments exploited at the time of site occupation.

According to our molluscan model, Site B was occupied prior to uplift, while the bay was still active. The site's location gave it direct access to the sandy littoral zone in both directions, whereas a rocky shore environment lay within easy walking distance to the southwest. The modern fishing hamlet of Puerto Moorin on Guañape Bay in the Viru Valley is similarly situated; fishermen routinely walk to the rocky headlands to collect molluscs and to fish (Sandweiss, n.d.a.).

Various factors may have influenced the choice of site location on the bay shore some distance from the interface between the rocky and sandy littoral. The following criteria were probably significant:

1. The location of fresh water must have been important. Unfor-

tunately, we have no information on the location of water sources in the Salinas de Chao.

2. The rocky littoral zone has a more limited spatial distribution than the sandy shore, thus concentrating species available on or from rocky headlands into a higher density biomass. Mosely (1975:14) has written that "for early populations, one of the richest of all local economic complexes" was the rocky shore. Sandy shore resources are more spread out; sand-dwelling mollusc beds have a tendency to move from place to place. This kind of shifting, extended distribution necessitates a large collecting range. Site B may have been located to allow access to the maximum possible amount of sandy littoral zone while still keeping the rocky shore resources within practical exploitation range.

3. The rocky knoll suspected to underlie the site is the only such feature along the shore of the relict bay. Considering the similar situation of the Ostra site, it seems likely that rocky knolls overlooking the beach were the preferred settlement locations of preceramic strandline collectors. Advantages of a raised dwelling site along the coast include a better view of the surroundings and approaches, protection from waves and extra-high tides, and exposure to the sea breezes which drive off mosquitos.

4. Site B is located on that section of the relict bay which lies closest to the most obvious access route to the Chao Valley and to the interior in general. This fact suggests that the site may have been occupied seasonally by people moving down from more inland regions.

Site B occupation terminated with or before the stranding of the bay by the Chao Event. No other site has as large a variety of molluscs, either in terms of number of species or of exploited microenvironments; destruction of molluscan resources by a tectonic event is implicated in the decrease in diversity. The Chao Event therefore dates after about 4000 years ago, more than 1000 years after the Salinas Event. The Pampa las Salinas displays no evidence of a major uplift following the Salinas Event. Therefore, the time gap between the two named events indicates that the two zones have distinct Holocene tectonic histories despite their geographic proximity.

Following the malaco-chronologic model, the next site in the sequence is Site C, on the shore of the relict bay to the southwest of Site B. The molluscan assemblage consists almost exclusively of two sand-dwelling beach clams, the small *Donax peruvianus* and a larger bivalve. Only a very few specimens of rock-dwelling shellfish (*Fissurella* sp. and *Conchelepas conchelepas*) are present, despite the location of Site C closer to the rocky headlands than Site B. Architectural remains consist of crude, round foundations of stone, similar to the surface architecture of Site B.

The following scenario may explain the transition from Site B to Site C, if the two sites really are sequential. First, the Chao Event uplifted the bay, displacing the shoreline to the west. At the same time, the rocky promontory at the southwest end of the bay was uplifted sufficiently to strand the intertidal zone and kill the resident rock-dwelling molluscs. The Site B occupants, perhaps after a short hiatus, moved to the Site C location to be closer to the new shoreline and its concomitant marine resources. Destruction of the intertidal mollusc populations accounts for the lack of rock-dwelling species in the site. Because rocky headlands on the Peruvian coast are discrete units separated by large expanses of sandy beach, it is difficult for rock-dwelling molluscs to recolonize a rocky zone immediately following destruction of the resident population. The loss of variety in the sand-dwelling species may have resulted from destruction of the bay bottom shellfish beds and from differential speeds of recolonization—beach clams are fast colonizers and would be the first species to appear in quantity following a catastrophic uplift. Water source remains an unknown factor. The decision to relocate on the now-stranded sea cliff fronting the relict bay rather than the open bay bottom nearer to the shore may be explained by the apparent preference for raised dwelling sites and the probable instability of the immediately post-uplift bay floor.

The one radiocarbon date for Site C contradicts the details of the above scenario. A sample of shell material from the surface of the site yielded an uncorrected date of 2980 ± 115 years B.P. (SI-4958), a thousand years after the dates for Site B. Either the date is in error (possibly the dated shell was dropped by a later collector passing over the site long after it was abandoned) or else our reconstruction must be revised. Even if the date is correct, Site C still post-dates Site B and the loss of variety in mollusc species can still be explained by tectonic destruction of the local rocky habitat.

The third site in the sequence (Site D) is located on the ancient sea cliff about 100 m to the north of Site B. The molluscan fauna at this site are the same as in Site C, with the addition of another sand-dwelling clam, *Mesodesma donacium*. Building remains at this site consist of well constructed, rectangular stone foundations. We consider this site to be later than Site C on account of the addition of *M. donacium* to the molluscan assemblage and because the architecture differs from that of Site B and Site C but is similar to that of the Las Salinas site (Site A, see below). Comparison of the molluscan assemblages reveals a temporal discontinuity between Site B and Site D, despite their spatial proximity. If the sites had been contemporaneous, they would not have had such a marked difference in the number and kind of exploited molluscan species. No radiocarbon dates are available for Site D.

Called Las Salinas by Cardenas (1979), Site A is a large preceramic center with complex architecture including rectangular rooms and plazas, a sunken circular court, and platforms (Alva, 1978). Cardenas (1979:28) has obtained 6 C-14 dates for this site; the dates range from 3570 ± 60 B.P. to 3300 ± 150 B.P. and average about 3400 years B.P. These dates fall over 500 years after the Site B dates, at the very end of the Preceramic period.

Site A lies about 1 km to the east of the raised bay and is built on and around a rocky spur at the entrance to the Salinas de Chao. The molluscan remains show a greater variety of species than either of the other post-uplift sites, but fewer species are present here than in the pre-uplift Site B. The increase over earlier post-uplift times reflects in part a restablization of the local mollusc populations. The increase in site size and complexity evident in the layout of the Las Salinas site must reflect an increase in both the size and the organizational complexity of the Salinas de Chao population. These changes would support an increased exploitation range, which may account in part for the greater diversity of molluscan species. Considering modern conditions, it seems unlikely that the rocky promontory nearest to the Salinas de Chao provided a suitable habitat for rock-dwelling shellfish at any time following the uplift, so the presence of rocky shore molluscs in Site A strongly supports the hypothesis of expanded exploitation range. Because Site D lies on the direct route from Site A to the shore, the fact that Site D has the lesser variety of molluscs suggests that the two sites are not contemporaneous. An alternate explanation is that the two sites were occupied at the same time but that only Site A commanded the necessary labor or territorial rights to exploit or acquire resources from outside the immediate Salinas de Chao vicinity.

The size and complexity of the Las Salinas site and its location away from the shore but strategically placed to control access to the Salinas de Chao suggests the presence of some important resource in this area. Not far from the site is a wall, now partly destroyed, which blocks the entire access route from the interior. The most obvious candidate for the controlled resource is salt from the stranded bay floor. Access to salt was very important and strickly regulated among Andean groups at the time of the Spanish conquest and probably for many years before that time. If this interpretation is correct, it demands a post-uplift date for Site A: the key resource, salt from the salt flats, was only available after the Chao Event cast the bay floor up from the sea.

In summary, Site A is differentiated from the other three sites on the basis of the molluscan assemblages, the relative size and complexity, the location away from the shore of the relict bay, and the C-14 dates. Site A is the largest site of any period in the Salinas de Chao region. Later sites include an Early Intermediate shell midden near the modern shore containing great quantities of the sand-dwelling clam *Mesodesma donacium,* but no visible architectural remains. This site is interpreted as a specialized shellfish collecting (and drying?) station. Site A had a late reuse by squatters who left some pots and scatters of the small beach clam *Donax peruvianus* on top of several of the platforms. The pottery is in the Casma Incised style and dates to the Late Intermediate period (C. Daggett, 1983).

Huaynuna, Casma-Nepeña Valleys

Fifty km south of the Santa River, the active bay of Huaynuna lies between the Casma and Nepeña Valleys. A preceramic midden is situated only a few meters above and behind the bay shore. The midden contains abundant organic remains including the shells of cool-water molluscs. Sand-dwelling species predominate, but rock-dwellers are also present. The site in underlain by alluvium, beach sand, and an indurated sandstone (beach rock) containing large scallop valves (*Argopecten purpuratus*). The scallop valves were deposited on a bay floor and are C-14 dated at 3635 ± 80 years B.P. uncorrected (SI-4956). Because the indurated sandstone lies near the present sea-level and because the alluvial deposits on top of it are of non-marine origin, Huaynuna Bay seems not to have been significantly uplifted during the last 3500 years. In fact, none of the indicators of massive uplift seen in the Santa-Chao region are present here—no raised beaches or sea cliffs, no stranded shellbeds, and no beach ridges are found at Huaynuna. The presence of a midden so close to the modern shore shows that the coastal configuration has not changed significantly since the site was occupied during preceramic times. The hills around Huaynuna appear more rounded than those in the Santa-Chao region, indicating a longer term of stability and erosion in the drainage system of the former area (J. Donahue, personal communication).

Dating of the major Holocene tectonic events in the Santa and Chao zones shows that the two areas differ in terms of the chronology of seismic activity. Comparison of Holocene uplift features in the Santa and Chao zones with the lack of such features around Huaynuna indicates notably divergent tectonic histories, an order of magnitude greater than the differences between Santa and Chao. This fact suggests that the Huaynuna and Santa-Chao areas belong to different tectonic blocks. The boundary between these provinces may be a major fault. The Santa River may lie along such a boundary; the Cañon del Pato, a narrow gorge where the Santa comes through the Cordillera Negra, is highly suggestive of a major fault. A smaller fault may separate the Santa and Chao regions and may be indicated by the rocky spur which shears off from the coastal range to form the headland south of Salinas de Chao.

Other Uplifted Bays

Several other raised bays with associated preceramic middens have been reported on the Peruvian coast. Pozorski and Pozorski (1979: 337–341) use settlement pattern data and subsistence remains to suggest a date of around 0–200 A.D. for major tectonic activity at Salaverry in the north coast Moche Valley. They go on to list a number of segments of the Peruvian coast possibly uplifted during the late Holocene. These segments range from the far north coast to the south coast, and all have associated archaeological sites.

Moseley (1975) has discussed a number of sites on the shore of the raised bay at Ventanilla, to the north of the Chillon Valley on the central coast. He feels that the bay was gradually stranded by a "marine regression" which "left the rocky habitat dry and stranded" (1975:23). "When the waters receded, vast beds of clams were left stranded on the sand flats where they remain to this day" (1975:25). This situation recalls Pampa las Salinas and Salinas de Chao.

Moseley (1975:51) goes on to discuss two sites which lie within 2 km of each other but contain distinct molluscan assemblages. The Camino site has exclusively sand-dwelling species, while at the Pampa site, rock-dwellers predominate although sand-dwellers are also present. Radiocarbon dates "suggest overlapping occupations." Because the two sites are close together and have similar access to both sandy and rocky littoral resources, Moseley considers them to represent "the earliest possible suggestions of differential resource accessibility," perhaps "the result of the imposition of jural rights through which the residents of each settlement controlled access to resources in their immediate vicinity." As an alternative, he suggests that "the occupational overlap between Pampa and Camino implied by the radiocarbon dates is more apparent than real, in which case differences in subsistence patterns probably reflect factors other than jural rights."

Moseley is probably correct that "factors other than jural rights" are the cause of the observed differences in molluscan assemblages. A sudden uplift such as occurred in the Santa and Chao areas would have stranded the rocky habitat instantaneously, necessitating an immediate shift to the exclusive exploitation of sand-dwelling species. The rapidity of this change would explain the similarity in C-14 dates. According to the uplift hypothesis, the two sites are sequential rather than overlapping, with Pampa preceding Camino. This situation parallels the apparent sequence in the Salinas de Chao.

Craig and Psuty (1971) discuss a raised bay and associated preceramic shell middens at Otuma on the south coast of Peru. Their report presages many of the concerns of the present study. At Otuma, 31 out of 32 mounds of scallop (*Argopecten purpuratus*) valves are

> "situated at the crest of a raised sea cliff that nearly encircles the stranded Otuma embayment . . . stratigraphic analysis of midden contents indicates the Otuma lagoon was stranded by a sudden uplift that destroyed its shellfish beds. Abrupt abandonment of the locale by the aboriginal inhabitants followed" (1971, 152).

Limited isotopic dating of shell carbonate gave five dates between 3100–3600 B.P. (Craig and Psuty, 1971:130). The situation at Otuma is quite similar to that at the other raised bays, the closest parallel being with the Pampa las Salinas.

CONCLUSIONS

Both the data and interpretations presented in this paper are preliminary in nature and serve mainly to raise questions and suggest new ways of approaching prehistoric phenomena in coastal regions of intense tectonic activity. Molluscan analysis not only indicated a significant paleoclimatic anomaly, but also proved to be a useful tool for studying the relationships between human occupations and coastal landscape alterations. In the Santa and Chao areas, the presence of shell middens some distance from the modern shoreline was the key to recognizing the Holocene date of drastic changes in coastal morphology.

We have identified three major, interrelated processes of landscape alteration operating in the Santa-Chao region during the last 5000 years. Tectonic uplift, river mouth migration, and beach ridge formation all necessitated adjustments by local human populations and are therefore of particular archaeological importance.

Powered by tectonic forces, uplift stranded whole bays and altered the physical landscape, the availability and location of coastal resources, and hence the pattern of human settlement. We have found evidence of two major episodes of uplift, the Salinas Event at about 5000 B.P. and the Chao Event at about 4000 B.P. The Salinas Event coincides with the termination of a warm-water molluscan association that indicates coastal climate conditions very different from the modern, cool-water regime. Because this uplift occurred just at the time when sea level was stabilizing (Richardson, 1981), it preserved shell middens and ancient beach deposits which might otherwise have been submerged beneath the rising sea. This fortuitous preservation may explain the lack of warm-water molluscs in other early strandline occupations and further suggests that the postulated shift from warm-water to modern cool-water conditions was temporally if not causally related to the stabilization of sea level.

Uplift also set the stage for subsequent beach ridge formation by providing abundant sediment and a sufficiently straight coastline to allow cobble deposition and ridge construction. By constantly prograding the coast as well as by determining the physical characteristics of the intertidal zone (thereby controlling intertidal resources), ridge formation also affected human occupation. In the Pampa las Salinas area, where beach ridges became prominent features following the uplift, maritime-oriented occupation ended after the Salinas Event. In the Salinas de Chao area, beach ridges are much less significant and marine resources continued to be exploited long after both the Salinas and Chao Events.

Beach ridge formation depends not only on the direct effects of uplift, but also on the direction of the prevailing longshore current (to the north), river mouth (sediment source) location, and quite probably on the presence and intensity of rains accompanying major El Niño events. If the El Niño correlation is correct, then the Santa beach ridges are of tremendous potential importance in studying the history of the El Niño phenomenon.

Finally, the Salinas Event probably triggered the southward migration of the Santa River mouth. A shift in the lower course of the river meant a shift in the location of drinking water, irrigation water, and the floral and faunal resources of the riverine microenvironment. Each of these changes required adjustments by the local human populations.

Uplift, beach ridges, river mouth migration, changing climate, human occupations, alterations in settlement pattern, mollusc exploitation, and changes in molluscan assemblages are all observable in the Santa-Chao area. The correlations between these phenomena suggested here still require rigorous testing in the field and in the laboratory, but it is hoped that our observations will contribute to the growing awareness of the importance of such processes in understanding coastal cultures both in Peru and in other areas where similar processes occur.

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PRINCIPLES OF AGRARIAN COLLAPSE IN THE CORDILLERA NEGRA, PERU

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Abstract

The amount of land under cultivation on the arid north coast of Peru has decreased by 35 to 40% during the last 1000 years. Two physical processes are implicated in this agrarian collapse. The basic contributory process is uplift along the Peruvian continental margin, which causes ground slope changes, The second process involves rare but recurrent rains caused by El Niño perturbations of the normal marine and meteorological conditions. Uplift leads to river entrenchment, and El Niño rains aggravate erosional downcutting. Downcutting strands canal intakes, forcing abandonment of irrigation systems in favor of newer, lower canals which irrigate less land.

Introduction

The largest irrigation reclamation projects ever put into operation in South America are sophisticated pre-Columbian canal delivery sys-

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tems designed to feed highland runoff from the Pacific watershed of the Cordillera Negra to arid lands along the desert coast of Peru between ca. 6° and 9° south latitude (Kosok, 1965; Schaedel, 1951). Built principally after A.D. 500, but abandoned prior to European arrival, these networks, discovered four decades ago with the advent of systematic aerial photography, include multi-valley canal linkages (Kus, 1972; Ortloff et al., 1982; Eling, 1981; Shimada, 1981) as well as intra-valley canal systems, remnants of which surround and enclose the 30 to 40% smaller confines of contemporary irrigation agriculture (Moseley and Deeds, 1982). Significantly, financing and technology imported from industrialized nations are presently employed to erect large-scale reclamation projects within the ruins of these abandoned networks without knowledge of why the older and larger agrarian systems collapsed.

Within the lower Rio Moche valley (8° south latitude), between 1976 and 1980, 578 excavations were opened in abandoned canals and related agricultural structures (Pozorski and Pozorski, 1982). Hydraulic analyses of channel configuration and engineering parameters indicate that pre-Hispanic canal systems constructed during the past millennium employed essentially modern hydrological concepts of critical and sub-critical flow design techniques (Ortloff et al., 1982, 1983*a*, 1983*b*). This is not to imply either that native hydraulic engineering is well explored, or that all abandoned canals are free of design errors. However, these analyses support the contention that the roots of agrarian collapse do not lie with human error or technological inadequacies of the societies which built the reclamation works (Ortloff et al., 1982, 1983*b*). Proceeding from this position, it is possible to analyze irrigation agriculture as an artificial extension of the natural hydrological regime and to identify the long-term principles of agrarian collapse within the Moche Valley and adjacent river basins.

Both regional processes have been implicated and local causes identified in the break-down of irrigation systems between 6° and 9° south latitude (Ortloff et al., 1982; Eling, 1981; Shimada, 1981; Kus, 1972, 1983; Ericksen et al., 1970; Plafker, Ericksen, and Concha, 1971; Nials et al., 1979; Moseley et al., 1981).

Steep-gradient rivers of the watershed are eroding in response to two regional processes. The basic contributory process is uplift related to high rates of tectonic activity along the continental margin, which can cause ground slope change. The second process entails rare, but recurrent torrential rainfall on the otherwise completely arid coastal desert caused by El Niño perturbations of the normal Pacific marine and meteorological conditions. When the rare, major rains do fall—as last transpired in 1925—it is upon steep, unvegetated land surfaces covered with accumulated debris. As a result, the drainage system is flooded and extensive and intensive erosion and mass wasting occurs.

Canal intakes physically tie irrigation to the drainage systems. As rivers downcut and alter course, canal intakes loose efficiency and become stranded above the entrenched stream channel. Intakes may be reworked, but bedrock obstacles in the valley necks eventually curtail recutting, leading to final intake stranding and channel abandonment.

Due to the lack of annual precipitation below ca. 1500 m, the lower 48% of the watershed lies within the world's driest desert (Lettau and Lettau, 1978) so the water table of the coast land can only be recharged by river runoff. As uplift and river downcutting proceed, the water table falls and agriculture dependent upon groundwater constricts toward the coast.

At the valley mouths, disgorged sediment is sorted by constant north-northwest longshore currents and distributed along the shoreline. Coastal flats exposed by uplift provide abundant sand that is transported inland by constant north to north-northwest daily winds. Sand drifts inundate agricultural systems and force their abandonment. If they stabilize, the sands may be farmed over and subsequently experience flooding, erosion, or deflation, forcing renewed abandonment.

Locally, displacements along faults alter ground slope and change canal gradients, thereby curtailing water supply to the distal reaches of the channels. These tectonic events may lead to channel reconstruction, new course placement, or canal abandonment (Ortloff et al., 1983*b*).

This paper will focus on one of the above factors—river downcutting—and the effects it had on irrigation and human settlement in the Moche Valley.

PHYSICAL FACTORS

The Watershed

In concordance with adjacent drainages (Table 1), the Moche basin rises a short distance inland at a high elevation (3988 m) and descends the western slope of the Cordillera Negra at a very steep average gradient (2.2 degrees) over a very short (102 km) linear course perpendicular to the coast (Fig. 1). The steep river gradient and the often precipitous bedrock landscape through which the river descends suggests apparent ongoing uplift of the watershed, probably related to tectonic processes at the active Peruvian continental margin, where two lithospheric plates converge. The plate rotation model of Minster et al. (1974) predicts that the Nazca oceanic plate is converging with the South American continental plate at rates ranging from 8.9 cm per year near the equator to 11.1 cm per year in central Chile. Deep sea cores from the vicinity of the study area have been interpreted as compatible with convergence rates of ca. 10 cm per year; such a rate appears to have been the norm for the last 5 million years (Kulm et al., 1976:795, 800).

Table 1.—*Characteristics of rivers of western Peru.*

River	Basin size (km²)	Irrigated area (km²)	Length (km)	Flow volume ($m^3 \times 10^6$)	150 m elevation (km from mouth)	% Gradient 1000-Omasl
Chancay	3375	523.42	194	701	58	1.1
Zaña	1125	191.13	119	202	51	1.0
Jequetepeque	4050	295.78	154	945	30	1.1
Chicama	3004	403.71	164	783	27	1.1
Moche	1562	200.26	105	320	19	2.1
Virú	1308	164.05	89	105	24	2.2
Chao	600	NA	78	NA	22	2.4
Santa	11,250	86.43	332	4594	27	0.9

The Moche basin and adjacent drainages between 6° and 9° lie within the second of five longitudinal seismic provinces subdividing the Andean Cordillera (Barazangi and Isacks, 1976; Sillitoe, 1974). In recent decades, seismic activity has included, in 1970, the most devastating historic earthquake in the New World (Ericksen et al., 1970; Plafker et al., 1971), as well as prior gradual vertical oscillation of the coastline at an average rate of 1.8 cm per annum (Wyss, 1978).

Although the 1970 earthquake (which registered 7.7 on the Richter Scale) was not known to be associated with surface fault displacement, the watershed is cut by numerous geologic linears, many of which are presumably geological structures. A pronounced scarp parallels the Cordillera and subdivides the watershed into two longitudinal sections:

1. A coastal lowland consisting, not of marine sediments, but of Quaternary and recent alluvium and aeolian sands overlying igneous bedrock.
2. A broken highlands of highly dissected bedrock exposures with limited cover of Quaternary and recent alluvium.

The pronounced scarp intersects the coast at a low angle in the region between ca. 8° and 9° south latitude (Fig. 1), resulting in a wedge-shaped coastal lowland. The major scarp is, in turn, cut by transverse linears. Where these intersect the coast, inflections suggest offset and the occurrence of related fault displacement.

Like the adjacent rivers, the Rio Moche's valley coincides with a transverse linear. In the highlands the river channel is entrenched within a steep bedrock canyon. After crossing the scarp face, the flood plain widens as the valley is not restricted by bedrock. Below ca. 150 m, beyond the confines of the scarp, the gradient is lower and the river traverses alluvial fill to the coast. As in adjacent drainages, the northern side of the lower valley is characterized by mountain outliers which

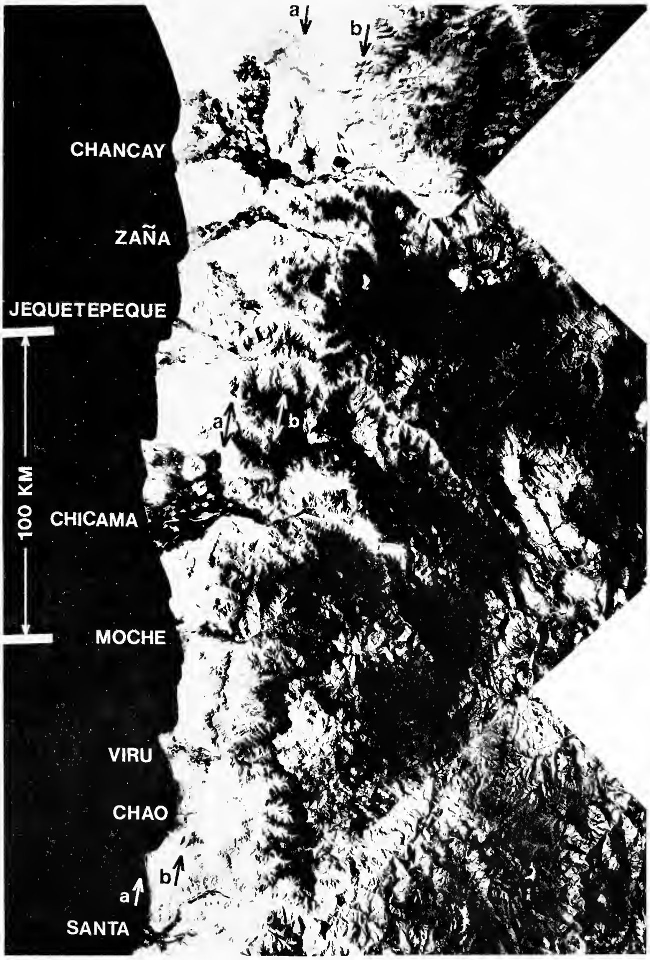


Fig. 1.—Uncorrected mosaic of LANDSAT images showing the Peruvian north coast from the Chancay drainage south to the mouth of the Santa River. Lines a-a and b-b mark the high-flexure scarp that divides the coastal plain from the mountains.

crop out from the ocean from within large expanses of relatively flat land, whereas south of the river the mountain fringe extends down to the coast and there is relatively little flat land.

The lower 48% of the Moche watershed lies in a hyperarid desert (Lettau and Lettau, 1978), where normally there is no annual precipitation below 1500 m. Infrequent desert rains occur only in association with strong El Niño perturbations of the normal ocean-atmosphere conditions, which have a statistical periodicity of about one per 15 or 16 years in the region of the Rio Moche (Nials et al., 1979). However, not all strong perturbations produce showers, so major rains—such as last occurred in 1925—may fall less than once per century or two. When a major deluge occurs, it is upon a steep, unvegetated landscape covered with accumulated debris. If, during the decades or centuries between major rains, the landscape experiences even minor ground slope alteration from seismic or gradual tectonic activity, then all of the normally dry desert drainages will be out of erosional equilibrium. When the destabilized hydrologic regime is supercharged by flooding, erosion and mass wasting can occur on a scale so vast that Holocene incidents, as last occurred ca. A.D. 1100, have been misidentified as products of earlier glacial epochs (Moseley et al., 1981).

Only the upper 52% of the Moche basin collects significant precipitation. Highland rainfall is markedly seasonal, with more than 75% falling in 25% of the calendar year. River flow peaks between February and March, then drops rapidly. For three-quarters of each year most river discharge is drawn off by irrigation agriculture in the lower valley, where there are ca. 19,950 ha of land under cultivation, most of which lies below 150 m.

The water table of the coastal lowlands, charged by river runoff, has a high-low cycle peaking between June and September, well after the river has crested. Groundwater provides ca. 16% of the present coastal agricultural water supply (ONERN, 1973). It is exploited via channelized springs or pukios, pumps, and sunken gardens. The latter are an indigenous technique where the land surface is excavated down to the level at which natural soil moisture can sustain plant growth. Sunken gardens are an efficient agricultural technique, although one restricted to areas with a high water table by the large labor expenditures needed for excavation.

The Moche basin and its agricultural area fit within a graded north-to-south sequence of large to small river valleys with agricultural areas of proportional size (Table 1; Fig. 2). This pattern begins with the Rio Chancay (6.5° south latitude) and, with one exception (Rio Zaña) continues south to the Rio Santa, where it is broken. The Santa is the largest river basin along the entire Andean desert coast, and while it carries 14 times the volume of the Rio Moche, it supports a significantly smaller agricultural area (43%).

The Hydrological Regime

If irrigation agriculture is to be analyzed as an artificial extension of the hydrological regime, then it must be recognized that this regime evolves in a mechanical manner in response to changes in land-to-sea level at the river mouth and along the littoral zone. Due to eustatic

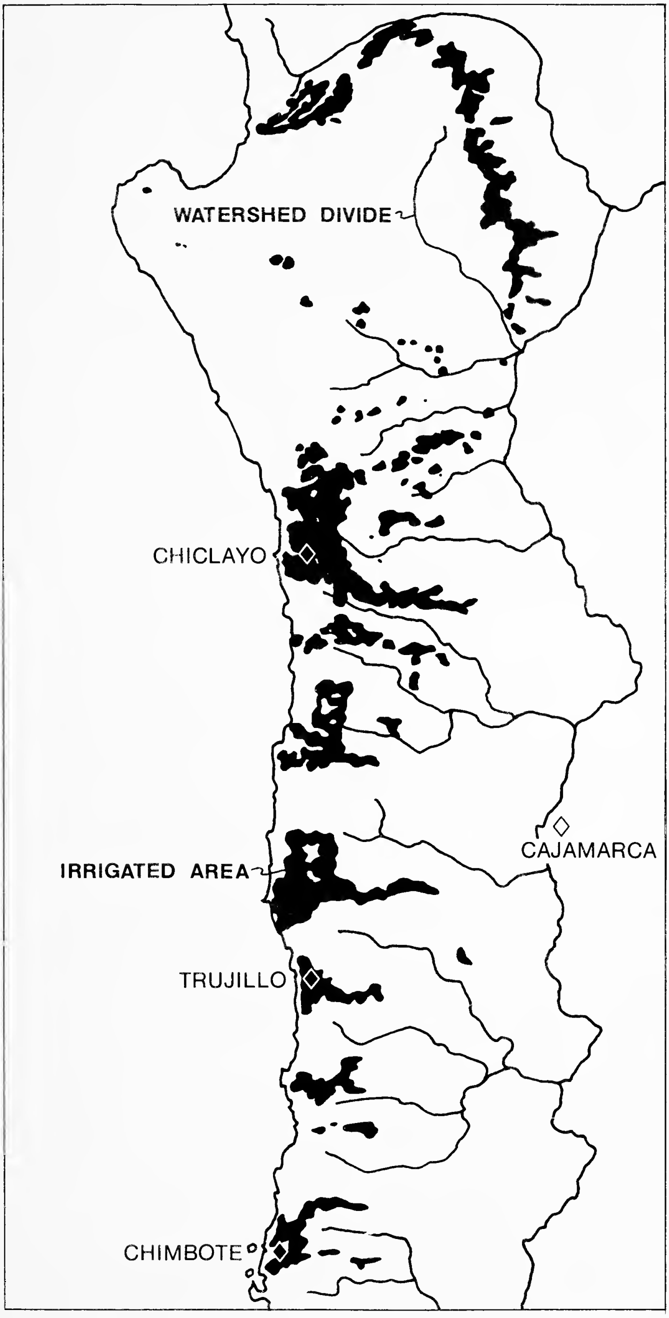


Fig. 2.—Cultivated areas of the Peruvian north coast.

and tectonic changes, the littoral zone, the river mouths, and the entire hydrological regime of the Cordillera Negra have never stabilized during the course of human occupation. With the onset of glacial meltback some 15,000 years ago, the level of the oceans rose an estimated 85 to 135 m and, in the course of 10,000 years, submerged the continental shelf, including more than 75 km of once-exposed coastal plain at the mouth of the Moche Valley (Richardson, 1981; Moseley, n.d.). Rising sea-to-land levels put river mouths into aggradational regimes and generated high groundwater conditions inland of the submergent coastline.

Although the ocean level began to stabilize approximately 5000 years ago, the watershed did not. Rather, there was a reversal of hydrological conditions because uplift of the watershed remained an ongoing proces. Whereas the sea rose faster than the land up to ca. 3000 B.C., the land has risen relative to the sea since then. Rising land-to-sea levels put rivers into a degrading regime and resulted in lowering of the groundwater table inland of the emergent coastline.

The change from a rising sea level to a rising land level is demarcated by a prominent wave-cut sea cliff that is largely continuous for the length of the coast between ca. 6.5° and 9°. The association of this cliff with the Holocene shift from submergent to emergent regimes is indicated by the absence, inland from it, of any Tertiary or Quaternary marine deposits or coastline features (Cossio and Jaen, 1967). Further, the earliest sedentary human communities to occupy the top of the cliff are radiocarbon dated to between 3200 and 2000 B.C. (Cardenas, 1977–78; Bird, 1951; Pozorski and Pozorski, 1979). The earliest mollusks, occurring both as stranded colonies on uplifted beach surfaces adjacent to the cliff base and in the cliff-top midden, date to ca. 3200 B.C. (Sandweiss et al., 1981). No human occupation prior to this date has been found below the sea cliff. The earliest human occupation tentatively associated with the highest (8 m) marine terraces at the mouth of the Moche Valley is dated, by ceramic style, to the latter half of the first millennium B.C. (Nials et al., 1979).

The contemporary littoral zone is seaward of the cliff, with intervening distances grading systematically from a maximum of 5 km near the mouth of the Rio Santa (9° south latitude) to a minimum of a few tens of meters at Puerto Eten, near the Rio Chancay (6° south latitude), indicating a north-to-south increase in shoreline width (Sandweiss et al., 1981). There also appears to be a north-to-south increase in uplift; no terracing is present near the mouth of the Rio Chancay (Shimada, 1981), whereas the highest terrace seaward of the cliff at the Rio Moche is 8 m. high (Cossio and Jaen, 1967), and uplifted terraces and beach ridges have their maximum reported height of 15 m near the Rio Santa (Sandweiss et al., 1981).

Although the sea cliff is largely continuous across the mouth of the Moche Valley, marine terracing and beach ridges are found in their most developed form on the northern, leeside of bays bracketing the valley mouth. The bays only have seaward projecting headlands on their south sides and they represent fault-bounded coastal deflections. The distribution of well developed raised beach surfaces in these settings may reflect consistent relative uplift of the south side of the faults.

The River Banks

In recent millennia the Rio Moche, below 150 m, has both downcut and cut laterally, principally southward. This movement has resulted in an asymmetrical erosional profile, with gentle slopes north and west of the river and a vertical bank formed by undercutting of valley-floor deposits on the south and east side of the river. Beginning ca. 6.5 km in from the river mouth and continuing upstream for more than 7 km to the valley neck, undercutting has exposed a largely continuous stratigraphic profile 10 m or more in height. Salient features of a 12+ m column (Fig. 3) near the profile's seaward end include:

A) Basal peat deposits that are radiocarbon dated to ca. 1000 B.C. (WSU No. 2190: 3010 ± 100 B.P.; WSU No. 2194: 3020 ± 60 B.P.) (Fig. 3h, i).
B) Ceramic inclusions in fluvial deposits overlying the peats that are dated on stylistic grounds to no later than ca. 500 B.C. (Fig. 3f).
C) Buried agricultural furrows and a small sherd-lined feeder canal at the top of the column, dating to the Early Chimu phase prior to ca. A.D. 1000.

The top of the column has been deflated, and behind the bank are yardangs, or butte-like erosional remnants of sandy loam, which stand several meters high and contain Early Chimu sherds. Early and Middle Chimu occupational debris are found on the deflated surfaces between the yardangs. Thus, the end of deposition and the onset of erosion can be dated to within the Early Chimu phase (Table 2).

The onset of erosion is the postulated product of river downcutting in response to tectonic activity. Unfortunately, the stratigraphy of the south bank sequence does not crop out downstream as far as the littoral and therefore cannot be tied to a specific uplifted beach surface.

The Water Table

Because river flow charges groundwater, uplift with consequently increased gradients and river downcutting would, expectably, alter water table conditions. Such a change in groundwater conditions can be seen

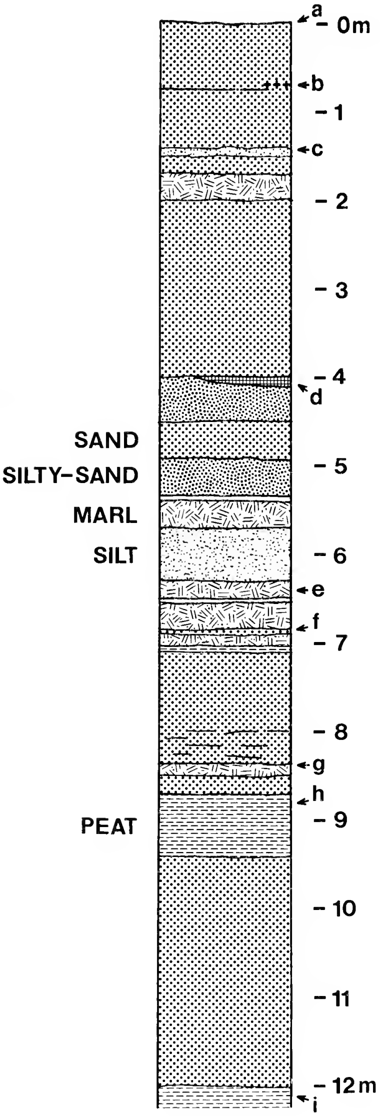
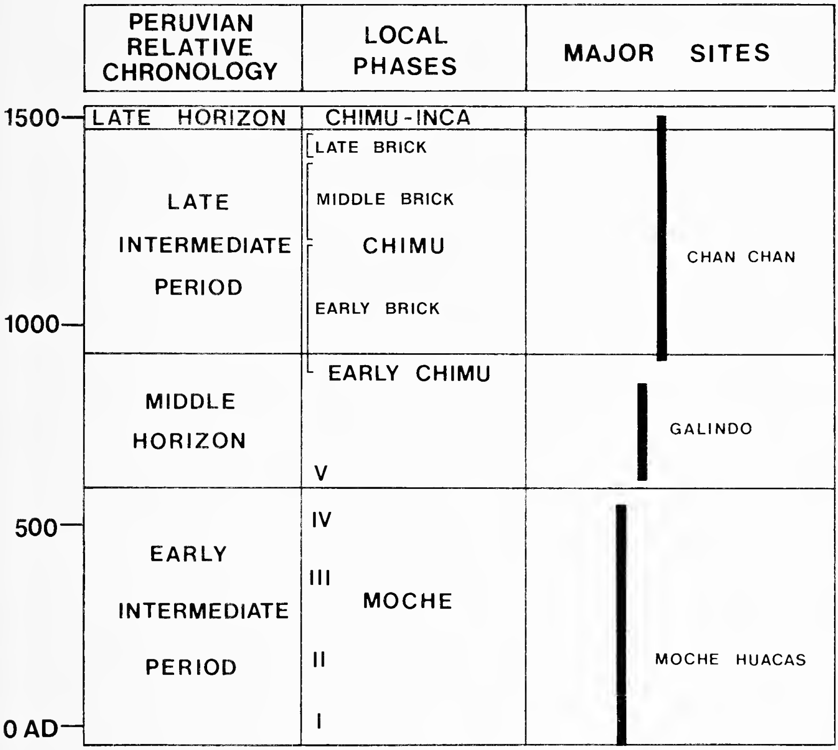


Fig. 3.—Rio Moche stratigraphic column at Pampa Casique. a) Chimu fields; b) Chimu feeder canal; c) buried fields; d) hearth; e) 2180 ± 170 B.P. (WSU-2192); f) pottery sherds; g) 2490 ± 90 B.P. (WSU-2193); h) 3020 ± 60 B.P. (WSU-2194); i) 3010 ± 100 B.P. (WSU-2190).

Table 2.



	PERUVIAN RELATIVE CHRONOLOGY	LOCAL PHASES	MAJOR SITES
1500	LATE HORIZON	CHIMU-INCA	
	LATE INTERMEDIATE PERIOD	LATE BRICK MIDDLE BRICK CHIMU EARLY BRICK	CHAN CHAN
1000			
	MIDDLE HORIZON	EARLY CHIMU V	GALINDO
500	EARLY INTERMEDIATE PERIOD	IV III MOCHE II I	MOCHE HUACAS
0 AD			

in the horizontal distribution of two agricultural techniques—spring fed canals and sunken gardens.

The earliest historical map of the valley's agricultural configuration, made in 1760, shows two spring fed canal systems north and west of the river (Kosok, 1965). The highest system was fed from a pond located about 75 m above sea level, 12 km inland, and 1.5 km north of the river. By 1942, when aerial photographs of the lower valley were made, this system was no longer operative, and the area it once irrigated was supplied by the major northside river fed canal (the N1). The lower canal system fed by groundwater was shown in the 1760 map as coming from a pond located about 42 m above sea level, 9 km inland, and 2 km north of the river. By 1942, this system (the Pukio system, Fig. 4) was no longer fed from a pond, but rather from two springs or seeps approximately 1 km apart. Today it is fed only by the lower spring.

Sunken gardens, which rely upon high groundwater conditions, extended inland at least 4.5 km at the beginning of the Chimu phase (Fig. 4). By 1942, this technique had dramatically contracted coastward and all sunken garden farming was limited to a region within 1 km or less of the shoreline, principally seaward of the wavecut cliff. Areas formerly cultivated by groundwater exploitation were irrigated from river and spring fed canals. Coastward encroachment of irrigation agriculture into these areas has continued in recent decades without the significant salinization problems that would be expected if the water table had not subsided, improving drainage. A measure of this subsidence is reflected by remnants of abandoned early Chimu gardens situated 4.5 km inland that now lie 10 to 12 m above the contemporary water table. Although this drop is a cumulative measure that includes the effects of mechanical pumping, the seaward contraction of groundwater agriculture which preceded pumping is most simply explained as a corollary of coastal uplift, river downcutting, and water table lowering.

CANAL STRATEGY

In a context of high aridity for unlined canals, less than 55% of the water that a canal receives from its river source reaches farmland, less than 45% is absorbed by the soil, and only about 16% is actually utilized by crops (USDA, 1955; West, 1981). Much of the loss occurs as seepage or evaporation during transport. Therefore, the highest system efficiency in open channel flow design entails moving the maximum amount of water the minimum possible distance to the largest possible planting area.

For the steep-gradient rivers of the Cordillera Negra, maximum design efficiency is represented by canals that transport and distribute water along a course perpendicular to the rivers. This configuration expresses a balanced relationship between separate functions of supply and distribution. Intake capability, slope, and channel hydraulic configuration set maximum limits on the volume of water that a canal can supply. However, the maximum limit on the size of the planting area over which this supply can be efficiently distributed is the downslope area included between the river and the canal. This "angle of reach" between river and canal thus establishes the distance of transport relative to area of planting surface (Fig. 5).

If a canal intake feeds from an entrenched river, then its initial lead-off channel must slope downstream at a low angle of reach before it can exit the confines of the downcut floodplain at an elevation suitable for perpendicular course placement. Given water loss in transport, the perpendicular course distance that the canal can supply is thus limited

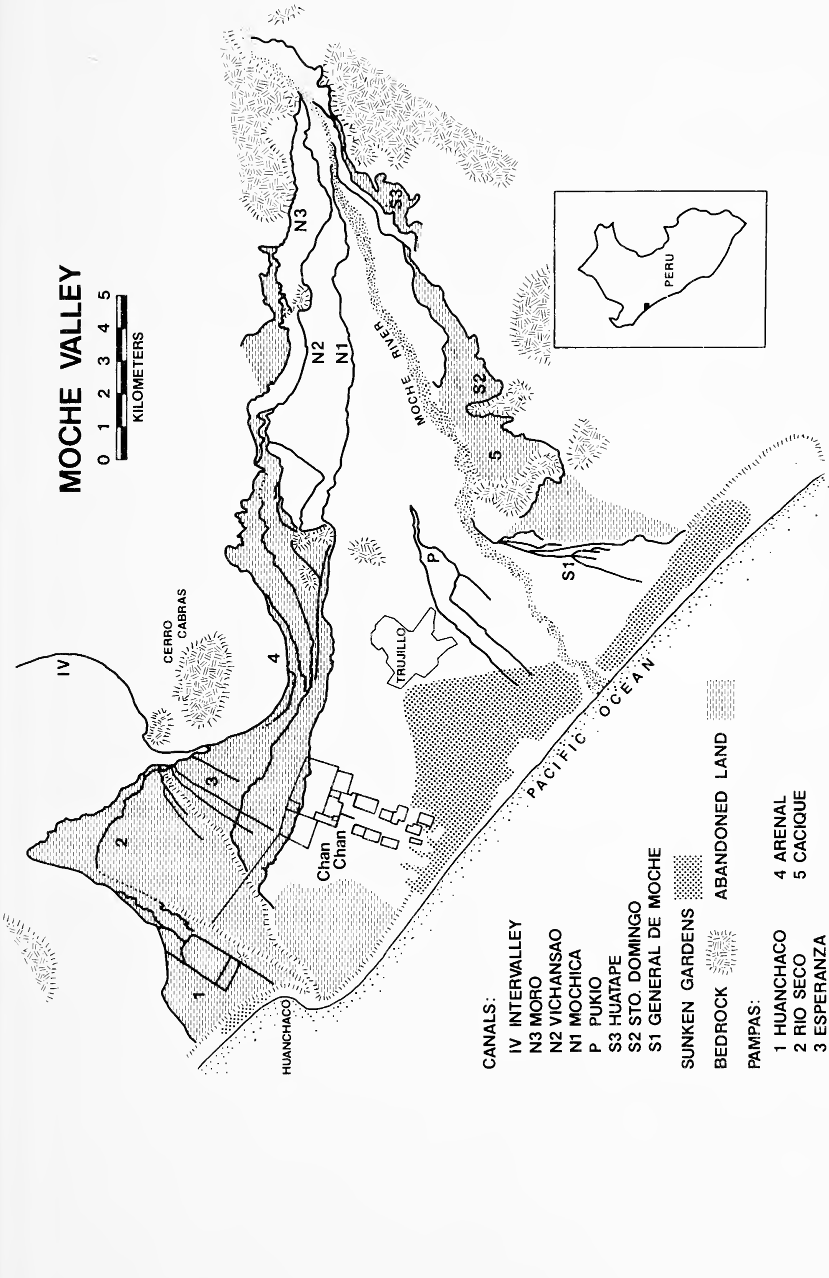
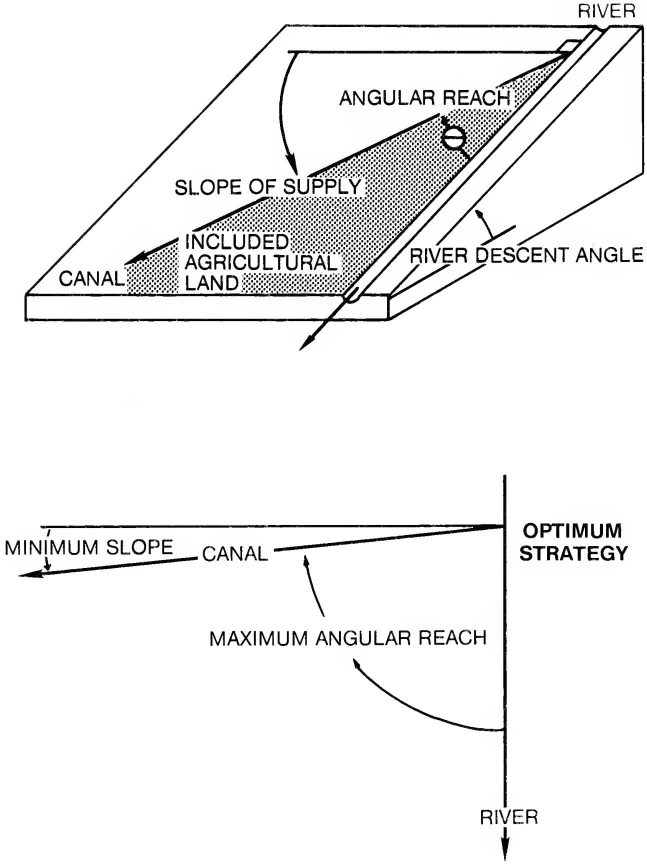


Fig. 4.—Map of the lower Moche Valley showing major canals, pampas, and areas of abandoned fields.



SLOPE, ANGLE, AND OPTIMUM STRATEGY

Fig. 5.—Irrigation parameters. The optimum strategy is to irrigate the maximum amount of land for a given canal length, thus minimizing water loss during transport to the fields.

by the length of the low-angle lead-off channel, and the lead-off distance is relative to the depth of river entrenchment.

Supply to the perpendicular course will decrease if the canal mouth and lead-off channel must be reworked in response to ongoing river downcutting, which strands the intake above the entrenching stream flow. By reworking and extending the stranded end of the lead-off channel upstream from its original position and having the prolonged lead-off channel intersect the river at a higher elevation, a new intake can be constructed which maintains the canal supply, but at the expense of increasing low-angle transport distance. In other words, as the lead-off channel is extended farther and farther upstream, it more nearly parallels the river, leading to a locally small angle of reach between the canal and river. As downcutting continues, upstream extension can be repeated, and the intake will "migrate" upriver until eventually a bedrock obstacle is encountered.

In the narrow bedrock valley neck, the task of trenching or tunneling through solid rock curtails lead-off extension, while aqueducting around the valley neck obstacles is inhibited by lateral river movement, which undercuts the canal. When bedrock abutment of the intake occurs, supply can be maintained only by lowering the intake to the river level by trenching the intake and lead-off channel to a lower slope. However, decreasing channel bed slope for a fixed canal cross-sectional area decreases the total supply flow rate.

When hydraulic efficiency of the lead-off channel is lost through upstream migration of the intake, or its lowering at bedrock abutments, there remains an option of constructing one or more new downstream intakes that connect into the original channel along its lower course, thereby augmenting the total supply. However, the point at which the canal swings out perpendicular to the river sets a limit on additional intakes. Beyond this point, recharge cannot occur, nor can downriver canals reach fields along the perpendicular course of the atrophying higher system.

In combination, bedrock abutment and elevational strictures on recharge from multiple intakes set finite limits on adjustment to ongoing river entrenchment, and thus on sustaining irrigation from perpendicular-reach canals at any given elevation. When these limits are reached, the supply capacity of the canal diminishes below the needs of the planting area encompassed within the angular reach of the canal. Due to water loss in transport, sustaining the farthest fields is uneconomical, so cultivation retreats upchannel, constricting back towards the river at a rate relative to the decreasing intake capacity.

Bedrock abutments at the valley neck inhibit building a new "replacement" canal system upstream from the old one, and thus promote new construction downstream, where there is sedimentary fill and room for intake adjustment in response to further river changes. In a context of continuing entrenchment, this fosters successive downstream construction and replacement of canal systems. Through time, irrigation agriculture retreats coastward at descending elevations in a step-like manner. Entrenchment eventually reaches the stage where the distance between the intake and the coast is insufficient for lead-off channels to pull out of the downcut landscape and swing laterally to a perpendicular course placement. Thus, in overview, the angle of reach and area of irrigation agriculture in any given valley are relative to its degree or depth of river entrenchment. The Rio Santa, which has an extraordinarily large discharge volume, supports an extraordinarily small agricultural area because it is the most deeply entrenched river on the north coast.

HISTORICAL PERSPECTIVE

The physical record of how irrigation systems behave through time is not unlike the record of glacial behavior. As ice or agriculture advance over a landscape, evidence of earlier advances or contractions is largely destroyed. However, as the ice melts or agriculture contracts, they leave behind moraines or abandoned fields and canals as evidence of their retreat. While there may have been more than one early agricultural advance in the Moche drainage, most abandoned agrarian structures of easily recognizable form date later than ca. A.D. 500 and pertain to two pre-Hispanic occupations—Moche and Chimu (Table 2). During the later occupation, the large metropolitan center of Chan Chan, north of the river, became the imperial capital of Chimor, a desert polity with political hegemony reaching over the coast from southern Ecuador to central Peru. Agricultural lands surrounding the city were worked and administered as a unified plantation system (Moseley and Deeds, 1982; Keatinge and Day, 1973; Keatinge, 1974). Pre-Hispanic agricultural works survive, in analyzable form, outside the area of contemporary farming, and therefore reflect agrarian collapse at the distal ends of the irrigation system. At the entrenching river, evidence of abandoned intakes and lead-off adjustment has been destroyed by river movement or masked by continuing cultivation.

The Canal Configuration

The river-fed irrigation system of the lower Moche drainage is based on three Primary Maximum Elevation Canals (PMECs) on each side of the river (Fig. 4). Maximum Elevation Canals are channels having the highest elevation in a particular section of the valley, and thus delimit the angular reach and irrigated area. These canals are numbered sequentially upstream and are lettered N or S, indicating whether they are north or south of the river. Although potential for angular reach increases in the upstream direction, the area currently served by each successively higher PMEC decreases (Table 3).

Local farmers indicate that within the span of living memory canal intakes have been a continuing source of problems. The S1 intake, which is bedrock abutted, has both an abandoned cement mouth and a higher, more recent, intake and flow diversion structure of rustic wood and cobble construction. The N2 intake has migrated upstream

Table 3.—*Characteristics of modern and ancient Moche Valley canals.*

Canal	Capacity (m^3)	Modern area served		Ancient maximum area	
		Ha	%	Ha	%
N3 Moro	2.5	700	6.7	1509	8.2
N2 Vichansao	3.0	1363	13.1	5821	31.6
N1 Mochica	10.0	4859	46.6	8992	48.8
Pukios	1.4	1504	14.4	—	—
S3 Huatape	0.6	258	2.5	309	1.7
S2 Santo Domingo	1.5	759	7.3	1793	9.7
S1 General de Moche	2.0	987	9.5	—	—
Totals	21.0	10,430	100.1	18,424	100.0

since the turn of the century and now has merged with the N3 intake at a valley neck bedrock abutment. Although both canals feed off the same intake and have only slightly different maximum capacities (2.5 versus 3.0 m^3/sec), the N3 is subject to silt clogging and irrigates only about half the area of its counterpart (ONERN, 1973). This condition would be expectable if the abutted N3 has experienced slope lowering and thus lost transport efficiency as a result of intake lowering prior to the N2's recent migration to the abutment.

Channel sections of operational PMECs intrude upon archaeological ruins of known antiquity, and therefore must date later than the structures they cut or the deposits they overlie. The S3 overrides Moche phase III deposits, whereas the N3 overlies phase IV materials but is, in part, functionally associated with the site of Galindo, a phase V settlement near the valley neck (Bawden, 1982). The operational N2 transects a ruin dating to the first millennium B.C., and an abandoned section of it cuts through a Moche phase IV mound (Pozorski, 1982). The S2 cuts Moche phase III–IV roads (Beck, 1979). Operational and abandoned sections of the N1 intrude upon Middle Chimu phase architecture at Chan Chan (Kolata, 1982; Lange, 1971), whereas the S1 lead-off channel crosses a surface created by 17th century mining of Huaca del Sol, a huge Moche pyramid, and therefore dates to the Colonial period or later (Topic, 1982; Hastings and Moseley, 1975).

All of the operational PMECs, except the S1, have abandoned courses extending out into what today is desert (Fig. 4). Abandoned extensions and field areas of the N3 and S3 are less well preserved than comparable aspects of the N2 and S2 systems, while abandoned N1 extensions and fields are in the best state of preservation.

Canal courses, such as those of the N3 and N2, converge and cross, and excavations demonstrate that abandoned courses are often occupied by multiple, superimposed channels. This situation may reflect both the resupplying of older courses and the intentional use of the sediments accumulated in beds of older channels as low-permeability linings to inhibit seepage. When such courses cross or merge, the series of superimposed channels may split and recombine in ways that defy surface detection. Much of the excavated information comes from channel transects downstream of unexplored course convergences and therefore does not securely monitor flow routing along potentially alternative paths. Thus, excavated transects must be approached as a series of isolated profiles that: a) establish maximum potential water supply vis-à-vis hydraulic limitations of channel design; and b) monitor realization of supply potentials vis-à-vis bedload sediments and soil oxidation, the presence of which establishes use, but the absence of which does not disprove use.

Canal Classes

Survey, excavation, and analysis of hydraulic design and engineering features allow recognition of three major classes of canal remnants (Ortloff et al., 1983*b*) (Tables 4–6).

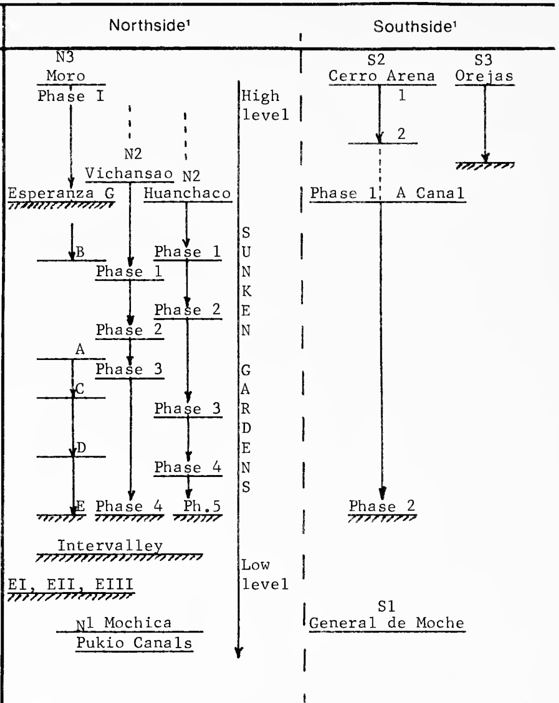
Class 1 canals have unlined parabolic channel cross-sections typical of the equilibrium shapes obtained after flow-induced sidewall erosion has occurred in channels dug into loosely consolidated soils. These channels supported subcritical flows and reflect hydraulic design mechanisms cognizant of that flow regime. Canal beds are oxidized from long or intensive use, generally exhibit extensive silt accumulations, and may underlie later canals built in or along the same course. This class includes last-use extensions of the N3 and the S3, and remnants of unconnected oxidized channels that originated higher up than the present N1 or S1 and that pertain either to early phases of the higher extant PMECs or to different, more ancient, systems.

Class 2 canals are generally trapezoidal in cross-section and are masonry lined with cobbles set in adobe mortar. These channels supported either subcritical or critical flows by design manipulations of bed slope, channel cross-section, and sidewall roughness. Oxidation is rare to absent, and while unused courses are present, silt accumulations indicate limited use occurred. This class includes last-use extensions of the N2, as well as the S2, which saw several sequential phases of masonry constructions that often overlie Class 1 channels.

Class 3 canals have unlined earth bank channels with profiles cut to trapezoidal form but eroded to a parabolic shape. Flow is subcritical, channel oxidation may occur, and bed sediment layers indicating use are present. This class includes the last and present phases of the N1 and the operational S1, as well as parts of the N2, N3, S2, and S3 canals.

Table 4.—*Characteristics of the three major classes of canal remnants in the Moche Valley, Peru.*

Canal Class	Description	Strategy	Association
1	Northside unlined parabolics with upvalley inlets Southside unlined N3 or N2; S3?	Maximize angular reach Maximize supply with subcritical hydraulics Inlet region rework as river downcuts	Moche/Chimu COASTAL UPLIFT RIVER DOWNCUTTING
2	Stone lined (Inter- and Intravalley) N2; S2	Maximize angular reach Maximize supply with critical/subcritical hydraulics & controls Reduce hydraulic resistance with canal cross-section shaping and canal straightening Inlet region rework as river downcuts	Chimu Major Flood
	Unlined parabolics with downvalley inlets N1; S1	Maximize angular reach Maximize supply with subcritical hydraulics Inlet region rework as river downcuts	Chimu



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[1] Underlined/slashes denote terminal phases.

Table 5.—*Characteristics of canals on Pampa Huanchaco, Moche Valley, Peru.*

Phase	Canal class	Supply canal	Maximum flow rate (m^3/sec)	Comments/use indications
1	1	N3 and/or	1.8	All branches used.
2	1	N2	4.8	All branches used.
3	2	N2	2.7	Not all constructed branches used.
4	2	N2	1.3	Length of used canals contracting.
5	2	N2	1.1	Far upstream segments used, abandonment of downstream segments.
Present	—	—	0	Total abandonment of Huanchaco system.

The pre-Hispanic water supply to the valley's northwestern plains can be studied in the N2 (Vichansao) profile from the excavation farthest upchannel and closest to the modern N2 (Table 6). Of four superimposed PMEC channels, the earliest is a Class 1 canal which had an estimated flow rate of 9.6 m^3/sec and which shows evidence of substantial use. The first superimposed channel had roughly half this capacity, a change that may reflect short-term alternative routing, as this second channel was replaced by a third, larger, Class 2 masonry channel that had an estimated capacity of 10.2 m^3/sec. After destruction by flash flooding around A.D. 1100 prompted reconstruction of the canal, the final channel was built. Its flow rate was 3.1 m^3/sec, which is essentially the same as the contemporary N2. The greatest present flow capacity is that of the contemporary N1, which can carry 10.0 m^3/sec. Therefore, if the N1 replaced the N2 after flooding and reconstruction, then the long-term PMEC sequence does not reflect, in design

Table 6.—*Characteristics of canals on north side of Rio Moche, Peru.*

Canal/phase	Canal class	Maximum flow rate (m^3/sec)	Comments/use indications
G Canal	1	1.1	Fed by N3; use indicated.
Moro/1	1	2.6	N3; all branches used.
Moro/2	1	5.8	N3; all branches used.
Vichansao/1	1	9.6	N2; Early Class 1 type.
Vichansao/2	2	5.0	N2; A-Complex; all later phases show use.
Vichansao/3	2	10.2(?)	N2; A-Complex; all later phases show use.
Vichansao/4	2	3.1	N2; A-Complex; all later phases show use.
Intervalley	2	4.7	Flow rate theoretical: no indications of use.
Mochica	3	10.0	N1; in use at present.

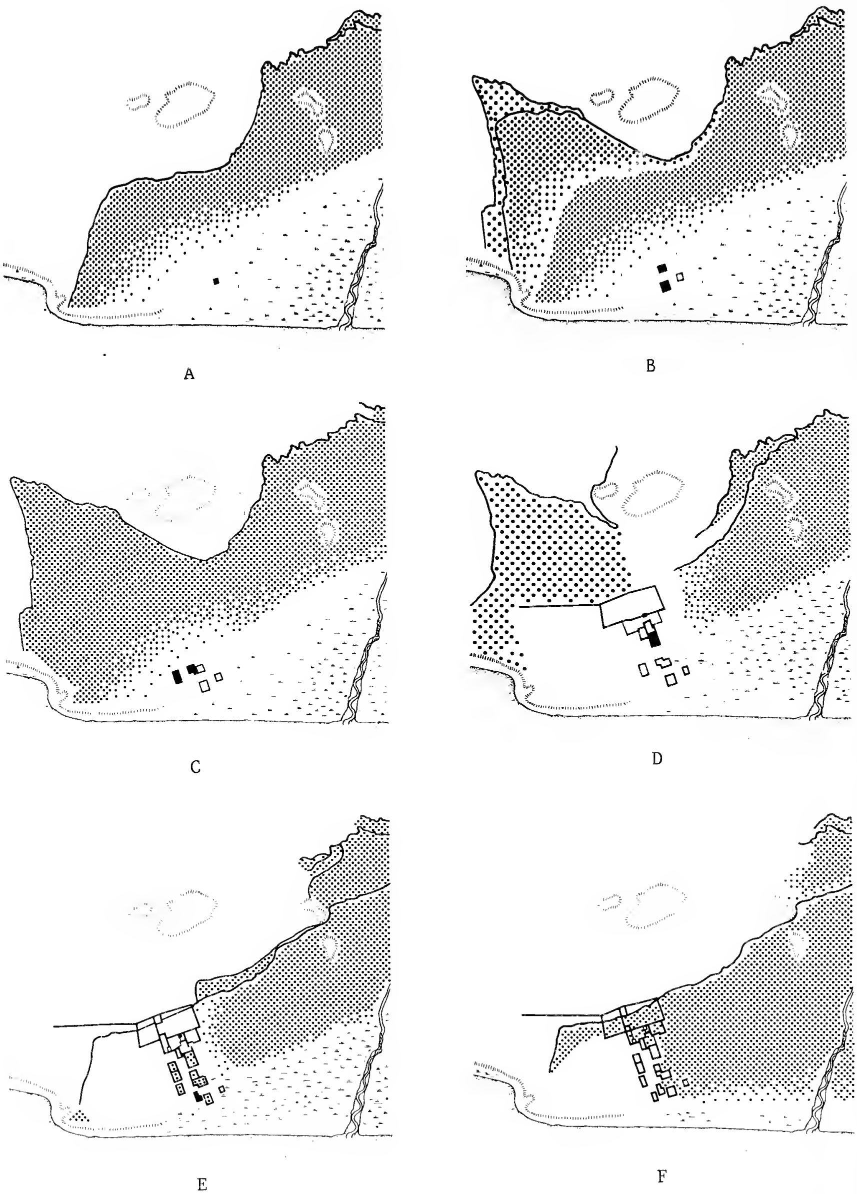
intent or flow capacity, a lack of water or decline in its availability. However, canal profiles at the distal end of the irrigation system do reflect decreased delivery of water. On Pampa Huanchaco, at the western terminus of irrigated land, the first three channels of a five-phase sequence reflect decreasing flow, whereas in two post-flood channels there was a marked decrease in flow rate (Table 5) (Ortloff et al., 1983*b*).

The Distal Canal Sequence

The largest area and longest reach achieved by well-preserved PMECs north of the river are on the western plains of Pampas Esperanza, Rio Seco, and Huanchaco, on the first of which Chan Chan was located. Past and present N1 courses cut into middle phase Chimu architecture at Chan Chan, including the city's north wall (which crosses and blocks feeders from the uphill Class 2 channels) and a walled road that was functionally compatible with a Class 2 extension of the N2 at the head of Pampa Esperanza. This Class 2 channel overlies a Class 1 canal, and both the wall and walled road override other Class 1 canal remnants (Beck, 1979). From these and other stratigraphic superpositions, it is evident that by Moche phase V times Pampa Esperanza was irrigated via a Class 1 extension of either the N3 or N2 and that the system had achieved an approximate perpendicular reach.

The Chimu inherited and reworked this system using Class 1 extensions of the Esperanza MEC in order to reclaim the two western-most pampas (Fig. 6a), which radiocarbon dates indicate was under irrigation by about A.D. 1050. The entire Class 1 canal system, which shows substantial use, was subsequently remodeled and the earlier earth-bank canals were replaced with Class 2 masonry-lined channels (Figs. 6b, 6c). In some cases, these new channels had a trapezoidal cross-section that minimized flow resistance and thus maximized the flow rate for the cross-sectional area. This Class 2 system, which can be traced intermittently back through the Vichansao's profile to the operational N2, saw little use and may still have been under construction at its distal end on Pampa Huanchaco when massive El Niño flooding—of a magnitude as yet unrepeated—occurred. This event, which transpired around A.D. 1100, eroded away more than a meter of valley floor along the river, washed out irrigation works in all parts of the valley, and adversely affected most of the north coast (Nials et al., 1979; Shimada, 1981).

The destroyed Class 2 system was reconstructed, but with significantly lower flow rates. Throughout the western plains the reconstructed system saw little, then ultimately no, use. When Chan Chan's 8 km-long north wall was built across Pampas Esperanza and Rio Seco, formerly farmed lands north and west of the city were left without



GROWTH OF CHAN CHAN AND ADJACENT AGRICULTURE

A

B

C

D

E

F

Fig. 6.—Growth of Chan Chan in relation to irrigation on Pampas Esperanza, Rio Seco, and Huanchaco. Dots represent field areas, marsh symbol represents areas of sunken gardens, and the rectangles represent the major compounds at Chan Chan (infilling shows the ones in use at each period). A) First compound was built between irrigated fields and

water. However, a major intervalley Class 2 canal, more than 70 km long, was cut to deliver Rio Chicama water to the head of Pampa Esperanza, and thereby resupply the dry N2 extension (Fig. 6d) (Kus, 1972; Day, 1974; Ortloff et al., 1982). A walled thoroughfare was ceremoniously built from Chan Chan out to the junction of the Intervalley and N2 canals and downstream Class 2 feeders were refurbished in order to distribute the intervalley water. However, masonry lining of the main intervalley course was completed only as far as an active fault north of the intervalley divide. Displacements along this fault, which coincide with a prominent geologic linear, are indicated by disrupted stream drainage patterns. Where the masonry-lined channel approaches the fault, it rests directly atop a bedrock block that has been upthrown at the fault. Today, this final segment of the finished Class 2 Intervalley Canal channel has experienced a 1 degree uphill slope change from its slope at the time of construction (Ortloff et al., 1982).

Radiocarbon dates indicate that significant agricultural activity on the western plains had ended by about A.D. 1350. The inland expansion of Chan Chan ended with the abortive intervalley project, and Late Chimu city construction moved sequentially coastward, back into the old urban core near the beach (Fig. 6e). This retreat is understandable, as the city depended on large, open wells for its potable water. When irrigation ceased to recharge the aquifer that these wells tapped and to mitigate seasonal water table fluctuations, urban growth was forced to reverse itself and follow the declining groundwater levels coastward to more accessible locations, in much the same manner as sunken garden farming retreated coastward (Moseley and Kolata, 1982; Moseley and Feldman, 1982).

The final step in the evolution of irrigation on Pampa Esperanza is represented by Chimu construction of the N1 PMEC and by westward extensions of Class 3 canals across the lower half of the plain. At one point, the N1 watered fields immediately northeast of the city wall, and an unsuccessful attempt was made to channel water along the upslope side of this wall. Next, a viable canal was cut through the wall

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←

sunken gardens. B) Expansion of irrigation upslope on Pampa Huanchaco. C) Unification of the irrigation system at its maximum extent. D) Expansion inland of Chan Chan, partial abandonment of the intravalley system, and construction of the Chicama-Moche Intervalley Canal. E) Abandonment of Pampa Huanchaco after failure of the Intervalley project, Moche Valley N1 canal built, and irrigation inside some of the older compounds at Chan Chan. F) Modern system, with areas of former sunken gardens now farmed by pump irrigation.

along a course that is today paralleled—at a lower elevation—by the contemporary N1. Fields and feeders were cut into middle and late phase architecture in the northern part of Chan Chan, but not into its densely occupied coastal sector. Today, some agriculture still goes on among the city's ruins (Fig. 6f).

Parallel events south of the river are understood in less detail. Early remnants of Class 1 systems are crossed by the last-use Class 2 channel of the S2, which apparently was a composite post-flood reconstruction of an earlier operational channel and which saw little use in its final form. There is a hiatus between abandonment of the S2 (by or during the Middle Chimu phase) and the Colonial period construction of the S1. However, this late canal required landscape alterations that would have obfuscated any prior S1 variants that might have been present during the Late Chimu phase.

LIMITATIONS ON THE DATA

Data from the Moche Valley support the hypothesis that agrarian collapse is an ongoing process principally related to uplift and ground slope change generated by high rates of tectonic activity along the continental margin, but punctuated by rare but recurrent El Niño flooding. It must be understood that the hypothesis of agrarian collapse has both geological components pertaining to the nature and rates of ground slope change, and hydrological components related to the mechanical consequences of river downcutting. At this stage of investigation, we stress that the latter are better documented and more fully understood than the former.

There is unequivocal evidence of river downcutting and course change in recent millennia. These changes correlate chronologically with both diminution of canal water supplies and contraction of ground water agriculture. Indeed, the latter are expectable hydrological and agro-engineering consequences of the former. River entrenchment can be triggered by a variety of independent processes ranging from deforestation, through minor shifts in precipitation patterns, to coastal uplift. Quaternary terraces and a downcut river profile can be traced through the neck of the Moche Valley downstream to within ca. 6.5 km of the river mouth. In this area the river crosses a pronounced linear (Fig. 1: a–a) associated with the major scarp running between ca. 9° and 6° south latitude. Below this crossing, the river profile has not been successfully traced to the coast. Therefore, river downcutting has yet to be stratigraphically tied to an uplifted beach surface, and alternative triggering mechanisms for entrenchment cannot be ruled out.

It is generally conceded that the present-day north coast marine and meteorological regime, which has communication with the broader tropical Pacific ocean-atmosphere circulation system, has been in place for the last five millennia (Richardson, 1981; Rollins et al., n.d.). El Niño perturbations are an integral feature of this climatic regime, and their occurrence in the archaeological record of recent millennia is well documented (Nials et al., 1979; Shimada, 1981). Thus, we think it questionable that the greater than 30% decrease in irrigated land during the last 1500 years is a product of climatic change or long term alteration of precipitation patterns triggering river entrenchment.

Agrarian abandonment in the rainfall zone of the highlands has yet to be quantified or investigated in detail. Our examination of relevant aerial photographic coverage suggests a disparity between past and present acreage of roughly comparable magnitude to that of the coast. Within the zone of annual precipitation, much—or perhaps most—of this abandoned land was farmed with the use of small canal systems. In theory, if such land supported a more erosion-resistant vegetation cover when under cultivation than when left abandoned, then a corollary of highland irrigation collapse could be "deforestation" and consequent erosion that could exacerbate river downcutting, leading to intake stranding of the coastal canal systems.

We believe that tectonic activity and ground slope alteration provide a much simpler and more unified explanation of coastal and highland agrarian collapse, as well as erosion and river downcutting. As discussed above, the northern watershed of the Cordillera Negra is crossed by a high flexure scarp (Fig. 1). Where this structure emerges from the sea, at 9° south latitude, cumulative coastline displacement securely dated to after ca. 3000 B.C. measures 5 km horizontally and more than 10 m vertically (Sandweiss et al., 1981). In the same area, recent gradual vertical oscillation has averaged 1.8 cm per annum (Wyss, 1978). We suggest that these data constitute a record of structurally unified movement transpiring over the length of the scarp northward to 6° south latitude. From south to north the scarp trends inland and progressively farther back from the sea. There is a corresponding decrease in horizontal separation between the modern littoral and the wave-cut sea cliff (which formed ca. 3000 B.C.), as well as a general vertical decrease in the height of uplifted sea floors and terraces (Cossio and Jaen, 1967). This could reflect a south to north decline in tectonic displacement. Alternatively, as the scarp pulls inland the coastal record of activity along its axis may simply become more indirect. In either case, there is evidence of past—as well as ongoing—tectonic activity in the study area. The same cannot presently be said of potential alternative causes of river downcutting.

In considering these limitations on the data, we should note the growing archaeological documentation of abandoned canal sections that presently run uphill or have gradients that would be inoperable today (Ortloff et al., 1982, 1983*a*; Kus, 1983; Pozorski and Pozorski, n.d.), as well as monumental architecture exhibiting progressive, cumulative slope and orientation alterations transpiring over long periods of occupation (Donnan and Ortloff, 1983). The obvious advantage of the tectonic hypothesis is that it readily accounts for these local phenomena, as well as for the regional contraction of all forms of agriculture.

CONCLUSIONS

Data from the Moche Valley support the hypothesis that agrarian collapse in the Cordillera Negra is closely tied to uplift and tilting of probable fault blocks along the Pacific watershed. The hydrological consequences of the uplift include water table subsidence and river entrenchment. The latter in turn is associated with the breakdown of large scale irrigation systems by loss of canal intake efficiency and eventual stranding of intakes above entrenching stream flow in bedrock canyons.

Within the Moche drainage, the collapse rate registers as roughly a 25% loss of arable land per millennium. The collapse pattern registers as both a "horizontal" contraction of farming toward the river and a "vertical" retreat downslope. As a result, progressively less land can be irrigated. In a like manner, coastal farming supported by groundwater has constricted riverward and seaward, and modern irrigation has moved into areas formerly farmed using groundwater. In the highlands terrace-agriculture has apparently also contracted inward and shifted downslope.

Collapse represents both an ongoing gradual process and one punctuated by radical environmental change. Episodic uplifts such as that suggested by raised coastal terraces and Holocene beach ridges must have extremely negative agricultural consequences. Episodic El Niño flash floods also have had demonstrably negative consequences. Flooding at ca. A.D. 1100 not only destroyed extant canal systems, but also radically changed river erosion and course patterns to such a point that the reconstructed irrigation system could not be effectively brought back into operation, leading to its replacement by new downstream canals that were not capable of supplying all of the land area that was formerly farmed. In turn, these replacement canals have developed chronic intake problems, leading to atrophy at their distal ends.

If agrarian collapse has been correctly analyzed, then future generations are not well served by the present practice of obliviously constructing major reclamation works within the uninvestigated ruins of larger past systems. These ruins both gauge and foreshadow ongoing environmental processes that modern technology is largely unaware of, but to which it is not immune.

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RESULTS OF THE ALCOA FOUNDATION-SURINAME EXPEDITIONS. VII. RECORDS OF MAMMALS FROM CENTRAL AND SOUTHERN SURINAME

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Abstract

The occurrence of three species of mammals previously unknown in Suriname is documented. The new taxa recorded include *Vampyrops aurarius, Vampyrops lineatus,* and *Natalus tumidirostris.* Additional information is provided on *Centronycteris maximiliana, Sigmomys alstoni, Zygodontomys brevicauda,* and *Cavia aperea* from Suriname.

Introduction

In October and November of 1981, the Section of Mammals of Carnegie Museum of Natural History conducted its fourth field season in Suriname. This trip included collecting at one locality in central Suriname and at two localities in the southern part of the country. Material acquired at these localities makes noteworthy contributions to knowledge of the mammals of Suriname.

Fieldwork was conducted at Tafelberg, the Sipaliwini airstrip, and Oelemarie. Tafelberg is a high plateau (500–1100 m) in central Suri-

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name, and is located within the Tafelberg Nature Reserve (Genoways et al., 1982; Schultz et al., 1977). The Sipaliwini airstrip is located in south-central Suriname on the Sipaliwini Nature Reserve, which ecologically is part of the Paru savannah of Brazil (Genoways et al., 1982; Schultz et al., 1977). Oelemarie is located in the southeastern corner of the country where dense lowland rainforest predominates.

At these localities, we obtained seven species of mammals either unknown previously from the country, known by a few specimens, or restricted geographically in Suriname. Three species represent new records of bats for the country, bringing the total number of bat species known in Suriname to 96 (Davis, 1966; Husson, 1978; Genoways and Williams, 1979, 1980; Genoways et al., 1981; Williams and Genoways, 1980*a*, 1980*b*). New distributional records also were documented for one other species of bat and three species of rodents that previously were known to be part of the mammal fauna of Suriname.

METHODS AND MATERIALS

All specimens collected were prepared as standard museum skins accompanied by skulls, or were preserved in 10% formalin. All specimens are deposited in the Section of Mammals of Carnegie Museum of Natural History.

Forearm and cranial dimensions were taken by means of dial calipers accurate to 0.1 mm. External measurements, recorded in millimeters, were taken in the field by the collector or preparator. Forearm and cranial measurements were taken as described by Genoways and Williams (1979).

Field weights in grams were taken with Pesola spring scales. The reproductive condition of standard museum specimens was determined by gross dissection in the field, whereas fluid-preserved specimens were dissected in the laboratory. Crown-rump length of fetuses and testes lengths of males were recorded in millimeters.

SPECIES ACCOUNTS

Centronycteris maximiliani maximiliani (Fischer)

Specimen examined (1).—MAROWIJNE: Oelemarie, 3°06′N, 54°31′W, 1.

Husson (1978) reported the only previously known specimen from Suriname from near the Tibiti River in Saramacca District. Our specimen was taken about 300 km southeast of that locality.

The specimen from Oelemarie was an adult male captured on 22 November. It weighed 5 g and had testes that measured 2 mm. The specimen was taken in dense rainforest with moderately developed understory. Other species of bats caught in the same area included *Pteronotus parnellii, Phyllostomus elongatus, Tonatia silvicola, Lonchophylla thomasi, Carollia perspicillata, Rhinophylla pumilio,* and two species of *Artibeus.*

Measurements of our specimen are as follows: length of forearm, 43.7; greatest length of skull, 15.1, condylobasal length, 14.0; zygomatic breadth, 9.1; mastoid breadth, 7.7; postorbital breadth, 3.0; length of maxillary toothrow, 5.9; breadth across upper molars, 6.7.

Vampyrops aurarius Handley and Ferris

Specimens examined (3).—SARAMACCA: SE side of Arrowhead Basin, Augustus Creek, Tafelberg, 600 m, 03°54′N, 56°10′W, 2; Geyskes Creek, Tafelberg, 700 m, 03°55′N, 56°10′W, 1.

These are the first localities of record for *Vampyrops aurarius* in Suriname. The nearest records of the species have been reported from Guiana Highlands of southeastern Venezuela (Handley and Ferris, 1972; Handley, 1976). Our specimens were collected in the largest highland area (600 and 700 m) of Suriname. All specimens were captured with mist nets placed over streams running through primary highland rainforest. Among the three females collected between 31 October and 3 November only one, from Arrowhead Basin, evinced any reproductive activity; this specimen was carrying a 45 mm (crown-rump) embryo on 31 October. The other two specimens are younger individuals in which the phalangeal epiphyses are just closing. The dorsal pelage of these two specimens is darker, shorter, and somewhat finer than that of the adult female.

We compared our specimens with Venezuelan material of this species in the National Museum of Natural History. Our specimens agree with these in details of external, cranial, and dental characters as described by Handley and Ferris (1972). The specimens from Suriname fall within the range of measurements of material from Venezuela as reported by Swanepoel and Genoways (1979). Measurements of our specimens are as follows: length of forearm, 52.3, 51.9, 52.7; greatest length of skull, 29.5, 29.1, 28.8; condylobasal length, 26.4, 25.9, 25.8; zygomatic breadth, 17.1, 17.1, 16.7; mastoid breadth, 14.2, 13.9, 13.9; postorbital breadth, 6.7, 6.6, 6.6; length of maxillary toothrow, 10.7, 10.8, 10.3; breadth across upper molars, 12.5, 12.7, 12.1.

Vampyrops lineatus E. Geoffroy

Specimens examined (1).—NICKERIE: Sipaliwini airstrip, 2°02′N, 56°07′W, 1.

This specimen documents the occurrence of *Vampyrops lineatus* in Suriname and on the Guyanan Shield. The nearest localities of record are in northeastern Brazil, Bolivia, Peru, and Colombia (González and Vallejo, 1980; Koopman, 1982; Mares et al., 1981; Sanborn, 1955).

The specimen is a female that was carrying a nearly full-term embryo (crown-rump length, 36 mm) when it was captured on 14 November. The bat was caught in a net placed on the bank of the Sipaliwini River. Vegetation in the area varied from dense secondary-growth to gallery forest. Other species of bats collected at the locality included *Lonchophylla thomasi, Carollia perspicillata,* three species of *Artibeus, Sturnira tildae, Uroderma bilobatum, Lasiurus ega, Molossops planirostris,* and *Molossus molossus.*

This specimen was compared with specimens of *V. lineatus* housed in the National Museum of Natural History and Carnegie Museum of Natural History. It compares favorably with material from Brazil and Bolivia, and its measurements match closely the published measurements of specimens from Brazil, Paraguay, and Uruguay (González and Vallejo, 1980; Swanepoel and Genoways, 1979). Measurements of our specimen are as follows: length of forearm, 47.2; greatest length of skull, 25.7; condylobasal length, 22.5; zygomatic breadth, 15.1; mastoid breadth, 12.5; postorbital breadth, 6.4; length of maxillary toothrow, 8.7; breadth across upper molars, 10.2.

Natalus tumidirostris haymani Goodwin

*Specimen examined (1).—*NICKERIE: *Sipaliwini airstrip, 2°02′N, 56°07′W, 1.*

This specimen represents the first known record of the family Natalidae in Suriname. The species has been reported from Curaçao (as the subspecies *N. t. tumidirostris*), Colombia and Venezuela (*N. t. continentis*), and Trinidad (*N. t. haymania*).

The specimen is a male that weighed 6.2 g and had testes measuring 2 mm when it was captured on 16 November. It was netted along a trail that passed through mature tropical rainforest. Other species of bats collected with this specimen included *Pteronotus parnellii, Micronycteris minuta, Phylloderma stenops, Phyllostomus elongatus, P. hastatus, Tonatia brasiliense, T. carrikeri, Carollia brevicauda, C. perspicillata, Rhinophylla pumilio,* three species of *Artibeus, Sturnira lilium, S. tildae, Uroderma bilobatum, Vampyrops helleri, Thyroptera tricolor,* and *Myotis nigricans.*

The specimen has a rostrum that is noticeably swollen so it hides the molar teeth when viewed from above. Also, the posterior margin of the palate is deeply emarginate to the level of the middle of the second molar. These characteristics clearly identify the specimen as *N. tumidirostris* and distinguish it from *N. stramineus* (Goodwin, 1959). We tentatively assigned our specimen to the subspecies *haymani* from Trinidad rather than to *continentis,* which has been used for all mainland specimens in the past. The specimen is larger cranially than any reported specimen of *N. t. continentis* and agrees more closely with known material of *N. t. haymani* (Goodwin, 1959). The specimen also has a second upper premolar with a longitudinal axis that is not in a parallel plane with those of the first and third premolars. Goodwin (1959) regarded this dental feature as characteristic of *N. t. haymani.*

Clearly, a more detailed analysis will be necessary to thoroughly understand geographic variation in this species. Measurements of our specimen are as follows: length of forearm, 40.7; greatest length of skull, 17.4; condylobasal length, 15.7; zygomatic breadth, 8.6; mastoid breadth, 8.0; postorbital breadth, 3.3; length of maxillary toothrow, 7.1; breadth across upper molars, 5.5.

Sigmomys alstoni savannarum Thomas

Specimen examined (1).—NICKERIE: Sipaliwini airstrip, 2°02′N, 56°07′W, 1.

Husson (1978) reported two specimens of *Sigmomys alstoni* from the savannah habitat at the Sipaliwini airstrip and two damaged skulls that were removed from the stomach of a white-tailed kite (*Elanus leucurus*) taken at Zanderij, Para District. Although *Sigmomys* apparently occurs in the coastal savannah and in the savannah at Sipaliwini, these few earlier records together with our extensive trapppng efforts during four different field seasons indicate that either this species is uncommon in Suriname or, for some reason, difficult to obtain.

Our specimen is a near adult female that was trapped during the day on 12 November. The habitat was a small clearing in the grass bordering the airstrip. The specimen weighed 74 g and was lactating. Examination of reproductive organs revealed two placental scars. Other species of rodents taken in the same grassy habitat bordering the airstrip included *Holochilus braziliensis, Oryzomys delicatus, Zygodontomys brevicauda,* and *Cavia aperea.*

External and cranial measurements of our specimen are as follows: total length, 252; length of tail, 107; length of hind foot, 30; length of ear, 21; greatest length of skull, 32.8; condylobasal length, 30.6; zygomatic breadth, 19.6; interorbital constriction, 5.4; mastoid breadth, 4.0; length of nasals, 12.4; length of maxillary toothrow, 6.4; length of diastema, 8.5.

Husson (1978) discussed the use of the generic name *Sigmodon* instead of *Sigmomys* for this species. He applied the name *Sigmodon* because of the work of Hershkovitz (1955, 1966) and Cabrera (1961), but thought *Sigmomys* should be recognized as a valid subgenus. We elected to use the generic name *Sigmomys* because in our opinion the grooved upper incisors of this species are sufficiently important to warrant separation of this taxon at the generic level.

Zygodontomys brevicauda microtinus (Thomas)

Specimens examined (8).—NICKERIE: Sipaliwini airstrip, 2°02′N, 56°07′W.

Husson (1978) examined a large series of *Z. brevicauda* from Suriname, but all of the specimens were obtained in the coastal savannah region. The southernmost locality of his material was 90 km inland. Our specimens indicate the geographical distribution is considerably more extensive in Suriname than previously was assumed. The specimens from the Sipaliwini airstrip were taken approximately 320 km south of the southernmost locality reported by Husson (1978).

Between 13 November and 18 November, eight individuals were collected in grassy savannah habitat bordering the airstrip. Other rodent species collected in the same habitat are listed in the account for *Sigmomys alstoni.* One male and one female were immature as indicated by the lack of toothwear and by weights of only 20 and 30 g, respectively; the male had testes measuring 5, whereas the female evinced no gross reproductive activity. Three adult males had testes measuring 8, 9, and 10, and weights of 48, 55, and 62 g, respectively. Two adult females contained two and three embryoes which had crown-rump measurements of 3 and 4 mm. A third female was lactating, but evinced no other gross reproductive activity. Weights of the three adult females were 37, 45, and 52 g.

External and cranial measurements of three adult males and three adult females, respectively, are as follows: total length, 215, 230, 245, 234, 219, 226; length of tail, 86, 95, 100, 99, 88, 92; length of hind foot, 25, 26, 28, 26, 26, 25; length of ear, 20, 19, 20, 21, 20, 19; greatest length of skull, 29.5, 31.6, 32.4, 30.4, 30.5, 29.7; condylobasal length, 27.6, 29.6, 30.3, 28.4, 28.3, 27.9; zygomatic breadth, 15.6, 16.6, 16.6, 16.1, 16.1, 15.9; interorbital constriction, 5.0, 5.1, 5.0, 4.9, 4.9, 4.9; mastoid breadth, 12.5, 13.0, 13.2, 13.2, 12.4, 12.8; length of nasals, 12.2, 13.3, 12.9, 12.5, 12.3, 12.1; length of maxillary toothrow, 4.3, 4.5, 4.6, 4.4, 4.7, 4.5; length of diastema, 8.0, 8.7, 8.9, 8.3, 8.0, 8.0.

The systematic relationship between the *Zygodontomys* from Sipaliwini and the northern coast currently is not understood because these savannah habitats are separated by approximately 300 km of continuous tropical rainforest. The name *Z. brevicauda microtinus* is used for these specimens primarily because this is the name applied by Husson (1978) to populations in Suriname. Investigations currently are being conducted on *Zygodontomys* in Suriname to determine their taxonomic relationship.

Cavia aperea guianae Thomas

Specimens examined (3).—NICKERIE: Sipaliwini airstrip, 2°02′N, 56°07′W, 3.

The existence of *Cavia aperea* in Suriname previously was based on one specimen obtained by Husson (1978) near the Sipaliwini airstrip. We obtained three additional specimens at the same locality. Clearly, the species is rare in Suriname and probably is restricted to savannah areas in the extreme southern portion of the country.

The three specimens are females, one of which is an adult and the other two are juveniles. The adult was shot early in the morning of 14 November as it traveled with another adult and three young. The group of *Cavia* had just left a tall grassy area and easily were seen on the mowed grass surrounding the airport buildings. The adult female weighed 380 g and was lactating. Examination of the uterus revealed one placental scar. One juvenile was trapped on the same date; another juvenile was trapped on 16 November. Both juveniles were trapped during day time in tall grass bordering the airstrip. Weights for these specimens were 83 and 110 g. They evinced no reproductive activity.

Observations from our collecting and information acquired from local hunters indicate *Cavia* is relatively abundant at Sipaliwini. They apparently are crepuscular to diurnal and may travel in small groups. Distinct paths and cuttings were observed in many areas where the grass was about 1 m in height. Local hunters commented that *Cavia* are seen less frequently during dry periods. Other rodent species collected in the same habitat are listed in the account for *Sigmomys alstoni*.

External and cranial measurements of the adult female are as follows: total length, 265; length of tail, 7; length of hind foot, 45; length of ear, 22; greatest length of skull, 59.3; condylobasal length, 54.6; zygomatic breadth, 31.6; interorbital constriction, 11.7; mastoid breadth, 20.8; length of nasals, 19.4; length of maxillary toothrow, 13.6; length of diastema, 16.0.

We follow Husson (1978) in applying the name *aperea* to *Cavia* from Sipaliwini. Husson (1978) briefly discussed the taxonomy of the species in Suriname and gives his reasons for the use of this name.

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TAXONOMIC REVIEW OF TEMMINCK'S TRIDENT BAT, *ASELLISCUS TRICUSPIDATUS* (TEMMINCK, 1834) (MAMMALIA: HIPPOSIDERIDAE)

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Abstract

Specimens of Temminck's trident bat (*Aselliscus tricuspidatus*) from Australasia were analyzed for morphological variation. Univariate and multivariate analyses were used to determine individual, secondary sexual, and geographic variation within the species. Individual variation was greater in females than in males although this variation generally was minor in all cases. Females were found to be significantly larger than males in four of seven measurements tested. The analysis of geographic variation revealed that four subspecies can be recognized within the species; two of these are described as new.

Introduction

Two species of trident bats are currently recognized in the genus *Aselliscus* (Corbet and Hill, 1980:52). Temminck's trident bat, *Aselliscus tricuspidatus* (Temminck, 1834), is known from Buru and Batjan islands in the Moluccas eastward through New Guinea and the Solomons as far as Espiritu Santo Island in the New Hebrides (Laurie and Hill, 1954:62). The second species in the genus, *Aselliscus stoliczkanus* (Dobson, 1871), occurs from Burma and southern China southward

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through southeastern Asia as far as Penang Island in peninsular Malaysia.

Aselliscus tricuspidatus (Temminck, 1834) was proposed for a female specimen collected by Muller and Macklot from Ambon Island, Moluccas. A subspecies, *A. t. novehebridensis,* was described by Sanborn and Nicholson (1950:331) based on specimens from Espiritu Santo Island, New Hebrides, at the eastern limits of the range of the species.

Although few specimens are available from some areas within the known range of the species, enough specimens are available at this time to review the taxonomy of the species. The objectives of the study were to analyze nongeographic and geographic variation within the species, and then to assess the taxonomic significance of the variation.

MATERIALS AND METHODS

A total of 211 specimens of *Aselliscus tricuspidatus* were examined. Only adults were used for statistical comparisons; these were so judged by the complete fusion of the epiphyseal phalanges and of the sutures in the basioccipital-basisphenoidal region of the skull. Conventional standard external measurements, when given, were recorded from the specimen label. Forearm and cranial measurements were taken with dial calipers.

One external and six cranial measurements were selected for comparison and are given in millimeters. Measurements are defined below.

Length of forearm.—Greatest distance from posterior extremity of the olecranon process of the ulna to the distal extremity of the carpals.

Condylocanine length.—Greatest distance from posterior portion of occipital condyles to anteriormost edge of canines.

Zygomatic breadth.—Greatest width across zygomatic arches, measured at right angle to longitudinal axis of cranium.

Postorbital constriction.—Least width across constriction posterior to orbits, measured at right angle to longitudinal axis of cranium.

Mastoidal breadth.—Greatest width across mastoidal processes, measured at right angle to longitudinal axis of cranium.

Length of maxillary toothrow.—Least distance from anterior lip of alveolus of C^1 to posterior lip of alveolus of M^3.

Breadth across upper molars.—Least distance, measured at right angle to longitudinal axis of cranium, from labial side of respective crowns of M^3 of each toothrow.

Localities from which specimens were examined were grouped into 13 geographical samples for analyses of data. These samples (identified by number, see Fig. 1), with the localities included in each group, are as follows: 1) Indonesia: Buru; 2) Indonesia: Ambon, Seram, and Gorong Islands; 3) Indonesia: Kai Islands; 4) Indonesia: Misor Islands and Yapen Island; 5) Indonesia: Irian Jaya: Hollandia and south side Humboldt Bay; 6) Papua New Guinea: Kaiseren Augusta River; Ama; 7) Papua New Guinea: Madang; 8) Papua New Guinea: Woodlark Island; Misima Island; and Kiriwina Island; 9) Solomon Islands: Russell Islands; New Georgia Island; San Jorge Island; and Guadalcanal; 10) Solomon Islands: Rennell Island; 11) Solomon Islands: San Cristobal Island and Uki Ni Masi; 12) Santa Cruz Island; 13) New Hebrides: Espiritu Santo Island.

Univariate analyses of secondary sexual variation and individual variation were performed using the UNIVAR program developed and introduced by Power (1970). Standard statistics (mean, range, standard deviation, standard error, variance, and coefficient of variation) are generated by this program. A single classification analysis of variance (ANOVA; F-test, significance level 0.05) was employed to test for significant differences

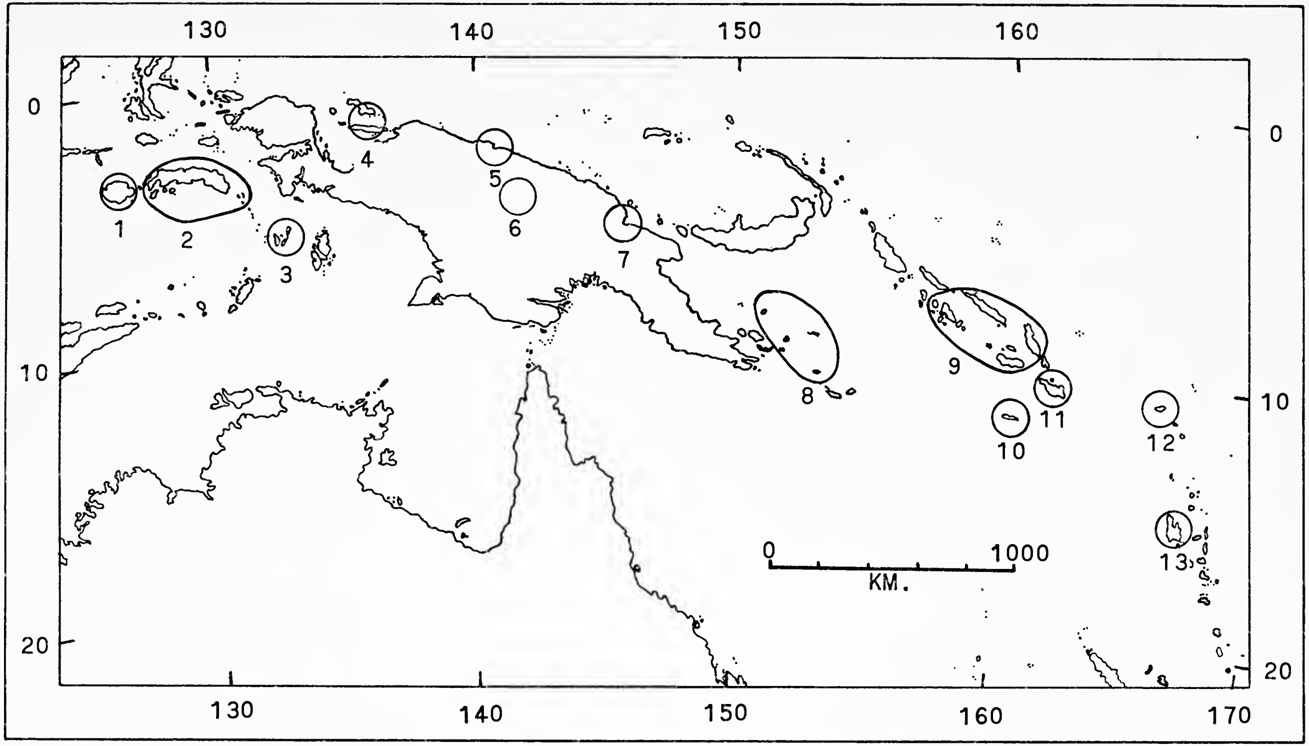

Fig. 1.—Geographic areas included in the 13 geographic samples of *Aselliscus tricuspidatus.* See Materials and Methods section of text for list of localities included in each sample.

between or among means (Sokal and Rohlf, 1969). When means were found to be significantly different, the Sums of Squares Simultaneous Test Procedure (SS-STP) determined the maximally nonsignificant subsets.

Stepwise discriminant analysis and canonical analysis (BMDP7M, Dixon and Brown, 1977) perform a multiple discriminant analysis in a stepwise fashion, selecting the variable entered by finding the variable with the greatest F value. The F value for inclusion was set at 0.01, and the F value for deletion was set at 0.05. Canonical coefficients were derived by multiplying the coefficient of each discriminant function by the mean of each corresponding variable. The program also classifies individuals by placing them with the group that they are nearest to on the discriminant functions.

Results

Nongeographic Variation

Using a single classification analysis of variance, individual and secondary sexual variations were examined in a single sample of *Aselliscus tricuspidatus* from the vicinity of Hollandia, Dutch New Guinea [=Jayapura, Irian Jaya, Indonesia] (Table 1). Age variation was not considered because only adults were available for study.

Individual variation.—Coefficients of variation (CV) of one external and six cranial measurements are represented in Table 1. CVs ranged from 1.05 (mastoidal breadth of females) to 5.45 (postorbital constriction of females). Both CVs for postorbital constriction were above 5 (5.19 in males) whereas the next highest CV was 2.47 for length of maxillary toothrow of females.

Coefficients of variation are listed in Table 2 for additional geographic samples of males and females. These values generally match the low values listed in Table 1. Among the geographic samples of males, only postorbital constriction shows a high CV value. In the geographic samples of females, again the postorbital constriction exhibits high CV values. In addition, OTU 2 has high CV values for length of forearm and breadth across upper molars while OTU 4 has a high CV value for mastoidal breadth and OTU 9 has a high value for length of maxillary toothrow. Other than postorbital constriction, which was the smallest measurement taken, coefficients of variation for all of the measurements in this study were generally low and in accordance with similar measurements of previous studies of bats (Long, 1968; Hayward, 1970; Smith, 1972; Davis, 1973; Swanepoel and Genoways, 1979; Martin and Schmidly, 1982).

Secondary sexual variation.—Based upon the results of a single classification analysis of variance between males and females from Hollandia, Irian Jaya, females were found to be significantly larger than males in four of the seven measurements tested for secondary sexual variation (Table 1). The length of maxillary toothrow showed the highest value for significant differences between the two sexes. In two of the remaining three measurements, females averaged larger than males.

Table 1.—*Nongeographic variation in selected external and cranial measurements of 15 females and 12 males of* Aselliscus tricuspidatus *from the vicinity of Jayapura, Irian Jaya, Indonesia [=Hollandia, Dutch New Guinea]. Statistics given are mean, two standard errors of the mean, range, coefficient of variation, F-value, and critical F-value (lower value). Means that were found to be not significantly different at the 5 per cent level are marked* ns.

Sex	Mean ± 2 SE	Range	CV	Fs/F
		Length of forearm		
Female	42.19 ± 0.42	41.0–43.3	1.93	6.85
Male	41.29 ± 0.56	39.2–42.6	2.33	4.24
		Condylocanine length		
Female	13.19 ± 0.08	13.0–13.4	1.11	4.57
Male	13.04 ± 0.12	12.8–13.5	1.58	4.24
		Zygomatic breadth		
Female	7.63 ± 0.07	7.3–7.8	1.68	*ns*
Male	7.56 ± 0.08	7.3–7.8	1.74	
		Postorbital constriction		
Female	1.95 ± 0.05	1.7–2.1	5.45	*ns*
Male	1.98 ± 0.06	1.8–2.2	5.19	
		Mastoidal breadth		
Female	7.04 ± 0.04	6.9–7.2	1.05	*ns*
Male	6.98 ± 0.07	6.8–7.2	1.63	
		Length of maxillary toothrow		
Female	5.05 ± 0.06	4.8–5.2	2.47	15.20
Male	4.89 ± 0.05	4.8–5.1	1.62	4.24
		Breadth across upper molars		
Female	5.30 ± 0.06	5.0–5.4	2.26	6.76
Male	5.19 ± 0.05	5.0–5.3	1.73	4.24

In no instance were males significantly larger than females. Thus because females are significantly larger than males in some measurements, samples of males and females were kept separate for the purpose of analyzing geographic variation.

Geographic Variation

Univariate and multivariate analyses were performed to compare the geographic samples in order to establish the relationships among the populations studied. Specimens of *Aselliscus tricuspidatus* were grouped into 13 geographic samples (OTUs) separated by sexes, for the analysis of geographic variation (for localities included in each geographic sample, see Materials and Methods section and Fig. 1). No females were available for geographic samples 12 and 13.

Univariate analyses.—Geographic samples of three or more individuals were entered in the Sum of Squares Simultaneous Test Procedure (SS-STP) to determine the maximally nonsignificant subsets between and among means of each variable for the geographic samples. Table 2 gives standard statistics for the seven variables from the 13 geographic samples. Table 3 lists a series of means with maximally nonsignificant subsets of the seven variables in order to demonstrate trends in geographic variation.

Results of the univariate analyses of geographic variation indicate that the New Hebrides sample (OTU 13) is characterized by individuals of large size for the species. Individuals from mainland New Guinea (OTUs 4–7) are slightly smaller in most variables than those from New Hebrides. Two geographical groups of OTUs are characterized by small individuals, namely the samples from the Moluccas (OTUs 1–3) and the East Papuan islands and the Solomons (OTUs 8–11). Individuals from Santa Cruz (OTU 12) are small but tend in some measurements to be as large as individuals from New Hebrides.

Patterns of geographic variation indicate that the New Hebrides sample (OTU 13) is large for measurements of length of forearm, condylocanine length, zygomatic breadth and breadth across upper molars. The New Guinea mainland group (OTUs 4–7) is large for the measurements of length of forearm, condylocanine length (especially in females), zygomatic breadth, and breadth across upper molars. The western group (OTUs 1–3 from the Moluccas) show small size for the measurements of condylocanine length, postorbital constriction, mastoidal breadth, and breadth across molars. This group exhibits relatively large size for length of maxillary toothrow in males. Except for postorbital constriction, the samples from the East Papuan islands and the Solomons (OTUs 8–11) exhibit small size in all measurements, especially in condylocanine length, zygomatic breadth, mastoidal breadth, and breadth across upper molars in both sexes.

Multivariate analyses.—Canonical analyses provide a procedure for graphically representing phenetic relationship among samples with the morphometric characters weighted by variance-covariance analysis. The two-dimensional plots of the male and female samples of *Aselliscus tricuspidatus* are presented in Fig. 2. In the males, small individuals are separated to the right on the first variate as two groups. The Moluccan samples (OTUs 1–3) and the East Papuan island sample (OTU 8) and the Solomon Islands samples (OTUs 9 and 11) are grouped together. In the center, the Santa Cruz Island sample (OTU 12) is grouped with the samples from Misor and Yapen islands of northeast New Guinea (OTU 4) and the mainland New Guinea individuals (OTUs 5 and 7). On the left are the large individuals from New Hebrides (OTU 13). The Sepik River sample (OTU 6) is separated on Variate II on

Table 2.—*Geographic variation in selected external and cranial measurements of samples of males followed by females of* Aselliscus tricuspidatus. *Statistics given are sample size, mean, two standard errors of the mean, range, and coefficient of variation. Means only are listed for samples of less than four individuals. See Fig. 1 and text for key to locality numbers and definition of measurements. No data for zygomatic breadth of males are available for locality 10.*

Locality	N	Mean ± 2 SE	Range	CV
		MALES		
		Length of forearm		
1	2	39.8, 38.6		
2	6	39.7 ± 0.78	38.8–41.2	2.40
3	2	38.1, 37.8		
4	1	41.4		
5	12	41.3 ± 0.56	39.2–42.6	2.33
6	1	40.4		
7	4	41.3 ± 1.33	39.6–42.6	3.23
8	15	39.2 ± 0.34	37.4–40.1	1.66
9	2	39.3, 37.5		
10	2	39.3, 37.6		
11	11	39.4 ± 0.50	37.7–40.5	2.11
12	3	39.0, 39.1, 37.4		
13	2	41.5, 40.3		
		Condylocanine length		
1	3	12.3, 12.3, 12.7		
2	6	12.6 ± 0.96	12.4–12.7	0.96
3	2	12.2, 12.1		
4	1	13.3		
5	12	13.0 ± 0.12	12.8–13.5	1.58
6	1	13.0		
7	4	13.1 ± 0.17	12.9–13.3	1.31
8	16	12.4 ± 0.08	12.1–12.7	1.34
9	2	12.4, 12.3		
10	2	12.4, 12.1		
11	10	12.5 ± 0.12	12.2–12.7	1.46
12	2	13.2, 12.3		
13	2	13.5, 13.2		
		Zygomatic breadth		
1	2	7.0, 6.9		
2	5	6.8 ± 0.14	6.6–7.0	2.22
3	2	7.1, 7.0		
4	1	7.9		
5	12	7.6 ± 0.08	7.3–7.8	1.74
6	1	7.7		
7	4	7.6 ± 0.17	7.4–7.8	2.24
8	6	7.1 ± 0.10	6.9–7.2	1.71
9	2	7.0, 6.8		
11	10	7.1 ± 0.09	6.8–7.3	2.08
12	2	6.7, 7.6		
13	2	8.0, 7.8		

Table 2.—*Continued.*

Locality	N	Mean ± 2 SE	Range	CV
		Postorbital constriction		
1	3	1.7, 1.7, 1.7		
2	6	1.6 ± 0.10	1.5–1.8	7.41
3	2	1.9, 2.0		
4	1	2.2		
5	12	2.0 ± 0.06	1.8–2.2	5.19
6	1	1.8		
7	4	1.9 ± 0.10	1.8–2.0	4.97
8	17	1.9 ± 0.04	1.8–2.1	3.92
9	2	1.9, 1.7		
10	2	2.0, 2.0		
11	10	2.0 ± 0.03	1.9–2.0	2.70
12	3	1.5, 1.9, 1.8		
13	2	1.7, 1.8		
		Mastoidal breadth		
1	3	6.4, 6.4, 6.6		
2	5	6.7 ± 0.19	6.4–6.9	3.11
3	2	6.6, 6.5		
4	1	7.2		
5	12	7.0 ± 0.07	6.8–7.2	1.63
6	1	6.9		
7	4	7.0 ± 0.13	6.8–7.1	1.80
8	16	6.6 ± 0.09	6.1–6.8	2.75
9	2	6.7, 6.6		
10	2	6.8, 6.3		
11	10	6.6 ± 0.07	6.4–6.7	1.56
12	3	6.6, 7.0, 6.8		
13	2	7.0, 6.9		
		Length of maxillary toothrow		
1	3	4.9, 4.9, 5.0		
2	6	5.0 ± 0.08	4.8–5.1	2.08
3	2	4.8, 4.8		
4	1	5.2		
5	12	4.9 ± 0.05	4.8–5.1	1.62
6	1	5.5		
7	4	5.1 ± 0.00	5.1	0.00
8	17	4.8 ± 0.04	4.7–5.0	1.69
9	2	4.8, 4.8		
10	2	4.9, 4.8		
11	11	4.9 ± 0.06	4.7–5.0	1.92
12	2	5.0, 5.2		
13	2	5.2, 5.2		
		Breadth across upper molars		
1	2	4.9, 4.9		
2	6	4.9 ± 0.10	4.7–5.0	2.38
3	2	4.9, 4.9		
4	1	5.4		

Table 2.—*Continued.*

Locality	N	Mean ± 2 SE	Range	CV
5	12	5.2 ± 0.05	5.0–5.3	1.73
6	1	5.3		
7	4	5.3 ± 0.10	5.2–5.4	1.82
8	17	4.9 ± 0.05	4.7–5.1	2.10
9	2	5.0, 4.8		
10	2	5.0, 4.8		
11	11	4.9 ± 0.08	4.7–5.1	2.58
12	3	4.6, 5.4, 4.8		
13	2	5.5, 5.5		
		FEMALES		
		Length of forearm		
1	1	40.5		
2	3	39.8 ± 2.26	38.2–42.0	4.91
3	1	39.2		
4	3	41.6 ± 1.22	40.4–42.4	2.54
5	15	42.2 ± 0.42	41.0–43.3	1.93
6	2	42.6, 41.3		
7	2	42.1, 42.3		
8	7	39.8 ± 0.40	38.9–40.4	1.33
9	4	39.2 ± 0.80	38.5–40.1	2.03
10	2	38.4, 38.4		
11	9	39.4 ± 0.54	38.7–40.9	2.05
		Condylocanine length		
1	1	12.8		
2	3	12.5 ± 0.23	12.3–12.7	1.60
3	1	12.7		
4	3	13.3 ± 0.40	12.9–13.5	2.60
5	15	13.2 ± 0.08	13.0–13.4	1.11
6	2	13.5, 13.5		
7	2	13.0, 13.1		
8	8	12.5 ± 0.08	12.4–12.7	0.85
9	4	12.5 ± 0.25	12.2–12.8	2.00
10	2	12.4, 12.1		
11	9	12.4 ± 0.07	12.2–12.5	0.88
		Zygomatic breadth		
1	1	7.0		
2	3	7.0 ± 0.13	6.9–7.1	1.66
3	1	7.1		
4	3	7.5 ± 0.24	7.3–7.7	2.76
5	15	7.6 ± 0.07	7.3–7.8	1.68
6	2	7.5, 8.0		
7	2	7.6, 7.6		
8	2	7.0, 7.1		
9	4	7.0 ± 0.13	6.8–7.1	1.80
10	1	7.0		
11	9	7.0 ± 0.07	6.9–7.2	1.50

Table 2.—*Continued.*

Locality	N	Mean ± 2 SE	Range	CV
		Postorbital constriction		
1	1	1.9		
2	3	1.7 ± 0.18	1.5–1.8	9.17
3	1	2.1		
4	3	1.8 ± 0.13	1.7–1.9	6.30
5	15	2.0 ± 0.05	1.7–2.1	5.45
6	2	2.0, 2.2		
7	2	2.0, 1.9		
8	8	1.9 ± 0.05	1.8–2.0	3.35
9	4	1.8 ± 0.14	1.7–2.0	7.86
10	2	2.0, 1.8		
11	9	1.9 ± 0.06	1.8–2.1	4.34
		Mastoidal breadth		
1	1	6.5		
2	3	6.7 ± 0.07	6.6–6.7	0.87
3	1	6.7		
4	3	7.3 ± 0.48	6.8–7.6	5.73
5	15	7.0 ± 0.04	6.9–7.2	1.05
6	2	7.1, 7.3		
7	2	6.9, 7.1		
8	8	6.7 ± 0.06	6.5–6.8	1.38
9	4	6.6 ± 0.15	6.5–6.8	2.28
10	2	6.6, 6.5		
11	9	6.5 ± 0.07	6.5–6.8	1.55
		Length of maxillary toothrow		
1	1	5.0		
2	3	4.8 ± 0.07	4.8–4.9	1.19
3	1	5.0		
4	3	5.2 ± 0.07	5.1–5.2	1.12
5	15	5.1 ± 0.06	4.8–5.2	2.47
6	2	5.1, 5.0		
7	2	5.1, 5.1		
8	8	4.8 ± 0.05	4.7–4.9	1.54
9	4	4.9 ± 0.22	4.6–5.1	4.55
10	2	4.9, 4.7		
11	9	4.8 ± 0.06	4.6–4.9	1.93
		Breadth across upper molars		
1	1	4.9		
2	3	5.0 ± 0.23	4.8–5.2	4.00
3	1	4.8		
4	3	5.3 ± 0.12	5.2–5.4	1.89
5	15	5.3 ± 0.06	5.0–5.4	2.26
6	2	5.3, 5.4		
7	2	5.4, 5.3		
8	8	4.9 ± 0.05	4.8–5.0	1.54
9	4	4.9 ± 0.05	4.8–4.9	1.03
10	2	4.8, 4.7		
11	8	4.8 ± 0.11	4.6–5.0	3.34

Table 3.—*Results of seven SS-STP analyses of geographic variation in samples of males followed by females of* Aselliscus tricuspidatus. *Vertical lines to the right of each series of means connect maximally nonsignificant subsets at the 0.05 level of significance. See Fig. 1 and text for key to geographic samples included in each locality number and definitions of measurements.*

Males					Females				
Locality	Mean	Results SS-STP			Locality	Mean	Results SS-STP		
					Length of forearm				
5	41.3	│			5	42.2	│		
7	41.3	│	│		4	41.6	│	│	
2	39.7		│	│	8	39.8		│	│
11	39.4			│	2	39.8		│	│
8	39.2			│	11	39.4			│
					9	39.2			│
					Condylocanine length				
7	13.1	│			4	13.3	│		
5	13.0	│			5	13.2	│		
2	12.6		│		8	12.5		│	
11	12.5		│		9	12.5		│	
8	12.4		│		2	12.5		│	
					11	12.4		│	
					Zygomatic breadth				
7	7.6	│			5	7.6	│		
5	7.6	│			4	7.5	│		
11	7.1		│		11	7.0		│	
8	7.1		│	│	9	7.0		│	
2	6.8			│	2	7.0		│	
					Postorbital constriction				
5	2.0	│			5	2.0	│		
11	2.0	│			11	1.9	│		
7	1.9	│			8	1.9	│		
8	1.9	│			4	1.8	│	│	
2	1.6		│		9	1.8	│	│	
					2	1.7		│	
					Mastoidal breadth				
7	7.0	│			4	7.3	│		
5	7.0	│			5	7.0	│		
2	6.7		│		2	6.7		│	
11	6.6		│		8	6.7		│	
8	6.6		│		9	6.6		│	
					11	6.5		│	
					Length of maxillary toothrow				
7	5.1	│			4	5.2	│		
2	5.0	│	│		5	5.1	│		
11	4.9		│		9	4.9	│	│	
5	4.9		│		8	4.8		│	
8	4.8			│	2	4.8		│	
					11	4.8		│	

Table 3.—*Continued.*

Males				Females			
Locality	Mean	Results SS-STP		Locality	Mean	Results SS-STP	
			Breadth across upper molars				
7	5.3	│		4	5.3	│	
5	5.2	│		5	5.3	│	
11	4.9		│	2	5.0		│
2	4.9		│	8	4.9		│
8	4.9		│	9	4.9		│
				11	4.8		│

the upper left from the rest of the mainland New Guinea samples in the center of the plot. In the females, most of the separation can be accounted for on the first variate. Two groups are present in the plot of females. The mainland New Guinea samples, including the Misor and Yapen islands sample, are represented by OTUs 4–7 on the left of the plot. The right of the plot includes two geographic groups. The Moluccan samples are represented by OTUs 1–3 although the three geographic samples are separated somewhat by Variate II. The samples from the East Papuan islands and the Solomon Islands are grouped on the left on Variate I. OTU 9 is separated from the other samples on Variate II.

The amount of total dispersion accounted for in the male and female samples, respectively, was 50.8 and 79.3% for Variate I, and 36.7 and 11.5% for Variate II. The total dispersion accounted for on the first two axes for male and female samples, respectively, was 87.5 and 90.8%.

Morphometric characters used in this analysis are listed in Table 4, from the most useful to the least useful in discriminating groups. For males, zygomatic breadth, mastoidal breadth, and breadth across upper molars have the strongest influence in separating those samples on the first variate of the discriminant projection plot of Fig. 2. The length of maxillary toothrow separates OTU 6 from the remaining groups while the length of postorbital constriction predominantly separates the groups in the lower right of the projection plot. Condylocanine length separates those groups in the lower left of the projection plot. In females, all seven variables equally separate the two major groups on the first variate while zygomatic breadth and postorbital constriction have a positive effort on Variate II.

The classification matrix for males and females of *Aselliscus tri-*

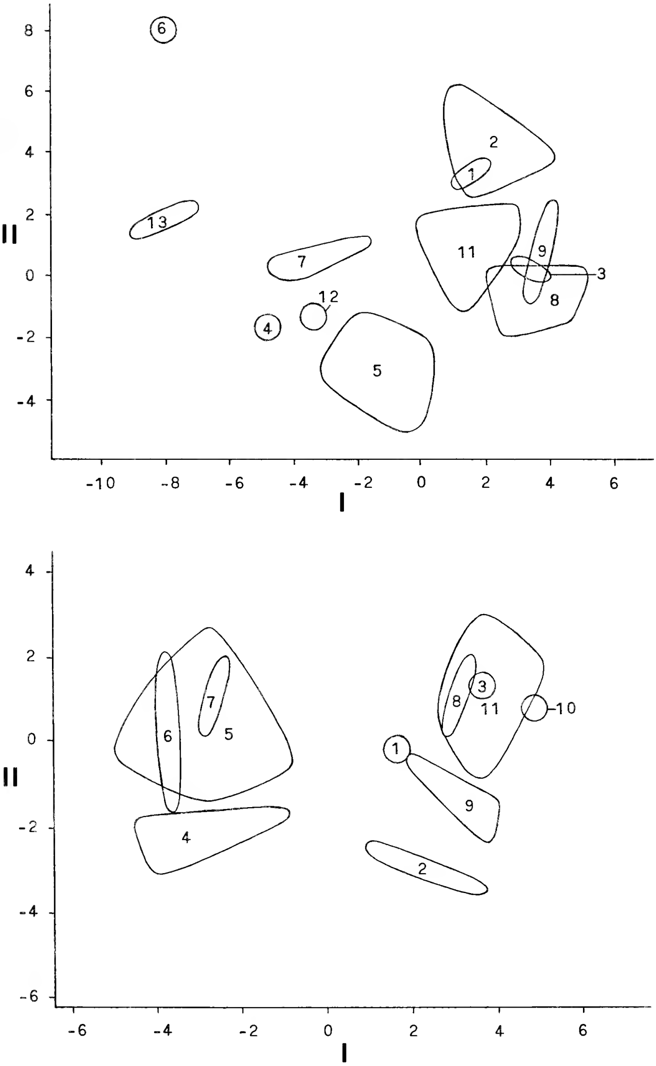

Fig. 2.—Two-dimensional projection of the first two canonical variates of male (upper) and female (lower) geographic samples of *Asellíscus tricuspidatus,* based on a classification of variance-covariance among one external and six cranial measurements.

Table 4.—*Variables used in discriminant function analyses of males and females of* Aselliscus tricuspidatus. *Characters are listed in order of their usefulness in distinguishing groups, with the character with the greatest between-groups variance and the least within-groups variance being selected first. The statistics are recalculated at each step.*

Step	Character	F-value	U-statistic
	Males		
1	Zygomatic breadth	25.47	0.1054
2	Length of maxillary toothrow	13.06	0.0192
3	Postorbital constriction	6.76	0.0056
4	Mastoidal breadth	3.63	0.0024
5	Condylocanine length	2.13	0.0013
6	Length of forearm	1.41	0.0009
7	Breadth across upper molars	0.47	0.0007
	Females		
1	Condylocanine length	21.70	0.1250
2	Postorbital constriction	3.68	0.0562
3	Zygomatic breadth	2.70	0.0291
4	Length of forearm	1.86	0.0175
5	Mastoidal breadth	1.67	0.0108
6	Breadth across upper molars	0.87	0.0081
7	Length of maxillary toothrow	0.95	0.0059

cuspidatus analysed in the canonical analysis is given in Table 5. All females were correctly classified for each geographical sample. For males, two individuals from the vicinity of Hollandia and Humboldt Bay were placed with the Sepik River sample while five were classified with the Madang sample. A single male from the Solomon Islands sample was placed with the Kai Island sample, both groups being generally small in size. A single male from San Cristobal Island was classified with the Rennell Island sample.

The geographic variation found in *A. tricuspidatus* is almost exclusively metrical in nature, with variation occurring between different islands and island groups. There exists overlap in dimensional features between populations from widely separated islands or between islands that differ sharply in size, in the latter case probably directly reflecting the size of the population that the island can support. Although color of pelage was checked in the various geographic samples studied, no discernable geographic variation in pelage color was noted even though individual variation from yellowish brown to orange and even reddish color was recorded.

Taxonomic Conclusions

Based upon our interpretations of the univariate and multivariate analyses, we found that *Aselliscus tricuspidatus* can be divided into four

Table 5.—*Classification matrix for male and female samples of* Aselliscus tricuspidatus, *based upon the discriminant functions of seven morphometric characters. Values indicate the number of individuals classified into each group. Sample 10 and samples 12 and 13 are unrepresented in the male and female classification matrices, respectively.*

	Classification groups												
Sample	1	2	3	4	5	6	7	8	9	10	11	12	13
Males													
1) Buru	2	0	0	0	0	0	0	0	0		0	0	0
2) Anbon and Seram	0	5	0	0	0	0	0	0	0		0	0	0
3) Kai I.	0	0	2	0	0	0	0	0	0		0	0	0
4) Misor and Yapen	0	0	0	1	0	0	0	0	0		0	0	0
5) Humboldt Bay	0	0	0	0	12	0	0	0	0		0	0	0
6) Sepic River	0	0	0	0	0	1	0	0	0		0	0	0
7) Madang	0	0	0	0	0	0	4	0	0		0	0	0
8) East Papuan Is.	0	0	0	0	0	0	0	5	0		0	0	0
9) Solomon Is.	0	0	0	0	0	0	0	0	2		0	0	0
11) San Cristobal I.	0	0	0	0	0	0	0	0	0		8	0	0
12) Santa Cruz	0	0	0	0	0	0	0	0	0		0	1	0
13) New Hebrides	0	0	0	0	0	0	0	0	0		0	0	2
Females													
1) Buru	1	0	0	0	0	0	0	0	0	0	0		
2) Ambon and Seram	0	3	0	0	0	0	0	0	0	0	0		
3) Kai I.	0	0	1	0	0	0	0	0	0	0	0		
4) Misor and Yapen	0	0	0	3	0	0	0	0	0	0	0		
5) Humboldt Bay	0	0	0	0	8	2	5	0	0	0	0		
6) Sepic River	0	0	0	0	0	2	0	0	0	0	0		
7) Madang	0	0	0	0	0	0	2	0	0	0	0		
8) East Papuan Is.	0	0	0	0	0	0	0	2	0	0	0		
9) Solomon Is.	0	1	0	0	0	0	0	0	3	0	0		
10) Rennell I.	0	0	0	0	0	0	0	0	0	1	0		
11) San Cristobal I.	0	0	0	0	0	0	0	0	0	1	7		

distinct geographic groups based upon size. The largest size for the species is found in individuals from New Hebrides. Slightly smaller in size are individuals from the New Guinea mainland and Misor and Yapen islands. Individuals from the Moluccas and from the islands east of the mainland of New Guinea as far east as Santa Cruz Island are among the smallest in size. Although the individuals from Santa Cruz Island approach the New Hebrides sample in size in certain measurements, they are nonetheless nearer to the populations immediately to the west.

The samples from the Moluccas are referrable to *A. t. tricuspidatus*; those from New Hebrides to *Aselliscus tricuspidatus novehebridensis* Sanborn and Nicholson, 1950. The remaining two geographic groups are described as new subspecies in the following accounts.

ACCOUNTS OF SUBSPECIES

Aselliscus tricuspidatus tricuspidatus (Temminck, 1834)

1834. *Rhinolophus tricuspidatus* Temminck, Tijdschr. Natuurk. Gesch., 1(1):20, pl. 1, fig. 4.
1871. *Phyllorhina tricuspidata,* Peters, Monats. K. Preuss. Akad. Wissensch., Berlin, p. 314.
1904. *Hipposiderus tricuspidata,* Trouessart, Cat. Mamm., Suppl., p. 70.
1941. *Aselliscus tricuspidatus,* Tate, Amer. Mus. Nov., 1140:2.

Holotype.—RMNH "cat. a, v. sp. a," female; from Ambon Island, Moluccas, Indonesia.

Measurements of holotype.—Length of forearm, 39.3; condylocanine length, 12.5; zygomatic breadth, 7.1; width of postorbital constriction, 1.7; mastoidal breadth, 6.7; alveolar length of maxillary toothrow, 4.9; and breadth of palate at M^3–M^3, 5.2.

Distribution.—Known from the Moluccan islands of Morotai, Batjan, Buru, Ambon, Seram, Gorong, and Kai.

Diagnosis.—Externally and cranially small-sized for the species (Tables 2, 3); forearm averaging small; cranially small, interorbital and mastoidal region narrow, breadth of palate narrow, and skull short; maxillary toothrow long relative to skull length in males.

Specimens examined (29).—Indonesia: Moluccas, Buru Island, Leksoela, 4 (4 BMNH); Batjan Island, 6 (6 BMNH); Ambon, 1 (1 RMNH, holotype); Seram, 14 (7 BMNH, 7 ZMA); Gorong Islands, 1 (1 BMNH); Kai Islands, 3 (3 BMNH).

Additional records.—Indonesia: Moluccas, Buru Island, Mefa; Leksula (Dammerman, 1929:161). Indonesia: Moluccas, Kai Islands (Peters and Doria, 1880:692).

Remarks.—Dobson (1878*c*:132) reports *Aselliscus tricuspidatus* from Morty Island [=Morotai Island] from the Halmahera group in the northern Molucca Islands. Dobson's specimen is a spirit-preserved, unregistered specimen in a poor state of preservation in the collection of the British Museum (Natural History). Such measurements as could be taken are as follows: length of forearm, 38.5; zygomatic width, 6.8; postorbital constriction, 1.7; length of the maxillary toothrow, 5.1; and breadth of palate at M^3–M^3, 4.9. The sex of the specimen could not be established. It is referred to the nominate subspecies.

Aselliscus tricuspidatus novehebridensis Sanborn and Nicholson, 1950

1950. *Aselliscus tricuspidatus novehebridensis* Sanborn and Nicholson, Fieldiana Zool., 31:331.

Holotype.—FMNH 55219, male; from cave on Segond Channel, Espiritu Santo Island, New Hebrides.

Measurements of holotype.—Total length, 60; length of tail, 20; length of hindfoot, 7; length of ear, 12; length of forearm, 41.5; condylocanine length, 13.5; zygomatic breadth, 8.0; width of postorbital constriction, 1.7; mastoidal breadth, 7.0; alveolar length of maxillary toothrow, 5.2; and breadth of palate at M^3–M^3, 5.5.

Distribution.—Known from the islands of Espiritu Santo, Aore, and Malekula.

Diagnosis.—Externally and cranially large-sized for species; length of forearm long; condylocanine length of skull long; palate and zygoma broad.

Specimens examined (2).—Espiritu Santo Island, New Hebrides, 2 (2 FMNH, including holotype).

Additional records.—New Hebrides: Aore Island, Aouta; Aore Island, Aouta Plantation; Espiritu Santo Island, Hog Harbor; and Malekula Island, Senwar Cave, Tenmial, northwest coast of island (Hill, 1983:151).

Remarks.—Hill (1983:151–152) reports 34 additional specimens of this subspecies from three islands in the New Hebrides and also gives measurements. Based upon this new material, it is evident that *A. t. novehebridensis* is larger than was indicated by the description, with forearm length reaching 43.5 in females and 42.2 in males in this new material.

Aselliscus tricuspidatus koopmani, new subspecies

Holotype.—Adult female, skin and skull, AMNH 159400; Liluta, 10 m, Kiriwina Island, Papua New Guinea, obtained on 15 December 1956 by R. F. Peterson, original number 14,977, on the Fifth Archbold Expedition to New Guinea.

Measurements of holotype.—Total length, 58; length of tail, 19; length of hindfoot, 7; length of forearm, 40.4; condylocanine length, 12.4; zygomatic breadth, 7.1; width of postorbital constriction, 2.0; mastoidal breadth, 6.7; alveolar length of maxillary toothrow, 4.9; and breadth of palate at M^3–M^3, 4.9.

Distribution.—Known from New Ireland and New Britain islands in the Bismarck Archipelago, Louisiade Archipelago, Trobriand Islands, Woodlark Island, and Solomon Islands to Santa Cruz Island.

Diagnosis.—Externally and cranially small for species; length of forearm short; skull short and narrow, with relatively broad interorbital region relative to skull size.

Comparisons.—*Aselliscus tricuspidatus koopmani* can be distinguished from the adjacent subspecies of the species (see Fig. 3) by its smaller size, both externally and cranially.

Etymology.—This new subspecies is named for Karl F. Koopman, Curator of Mammals, American Museum of Natural History, New York, in recognition of his keen interest in Australasian bats and for first mentioning (Koopman, 1982:17) the small size of specimens included in this new subspecies.

Specimens examined (138).—Papua New Guinea: New Ireland, no specific locality, 1 (1 BMNH); Papua New Guinea: Woodlark Island, Kulumadau, 200 m, 52 (52 AMNH);

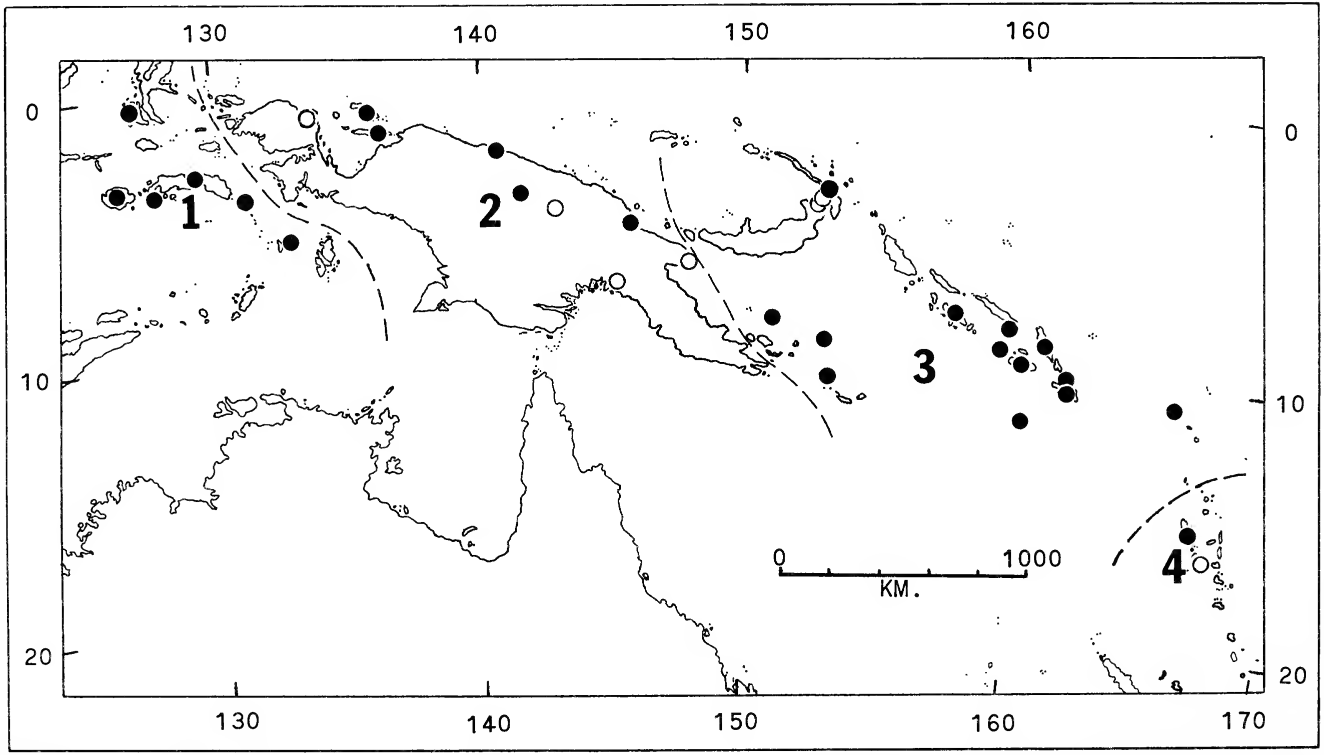

Fig. 3.—Geographic distribution of subspecies of *Aselliscus tricuspidatus*: 1) *A. t. tricuspidatus*; 2) *A. t. novaeguineae*; 3) *A. t. koopmani*; and 4) *A. t. novehebridensis*. Closed circles represent localities of specimens examined and open circles represent localities of additional records from the literature. The record from Morotai Island (Dobson, 1878*c*:132) is just off of the map at 2°10′N, 128°30′E in the northern Molucca Islands.

Papua New Guinea: Woodlark Island, no specific locality, 1 (1 BMNH); Papua New Guinea: Louisiade Archipelago, Misima Island, Kulumalia Mine, 150 m, 32 (32 AMNH); Papua New Guinea; Trobriand Islands, Kiriwina Island, Liluta, 3 (3 AMNH, including holotype); Solomon Islands: New Georgia Island, Munda Point, 8 (8 FMNH); Solomon Islands: New Georgia Island, no specific locality, 1 (1 BMNH); Solomon Islands: San Jorge Island, Talise, 1 (1 BMNH); Solomon Islands: Russell Islands, Banika Island, 1 (1 FMNH); Solomon Islands: Malaita Island, Riba Caves, near King George V School, Auki, 1 (1 BMNH); Solomon Islands: Guadalcanal, Aola, 2 (2 BMNH); Solomon Islands: Rennell Island, Tigoa, 4 (4 BMNH); Solomon Islands: San Cristobal, Warihito River—Goge River confluence, about 6 mi inland from Wainoni Bay, 27 (27 BMNH); Solomon Islands: Uki Ni Masi, 1 (1 FMNH); Santa Cruz Islands: Santa Cruz Island, 3 (3 AMNH).

Additional records.—Solomon Islands: Rennell Island, Kogoata Cave, Tigoa; Niupani (Hill, 1968:56). Papua New Guinea: New Ireland Province, near Sohun (Smith and Hood, 1981:108). Papua New Guinea: East New Britain Province, near Gunanur Plantation (Smith and Hood, 1981:108). Papua New Guinea: East New Britain Province, Duke of York Island (Dobson, 1877:121; 1878*a*:317).

Remarks.—The specimens from Santa Cruz Island and Uki Ni Masi [=Ugi Island] were originally reported by Sanborn (1931:24) as *Hipposiderus tricuspidatus.*

Specimens from New Ireland and New Britain islands are assigned to this new subspecies based upon the individual examined from New Ireland and the measurements reported by Smith and Hood (1981: 107). Variation in larger samples from these two major islands should be checked further to verify the subspecies to which they actually belong.

Aselliscus tricuspidatus novaeguineae, new subspecies

Holotype.—Adult female, skin and skull, CM 63498; Ama, 140 m, East Sepik Province, Papua New Guinea (04°09′S, 141°41′E), obtained on 9 March 1980 by Stephen L. Williams, original number 5089, Bernice P. Bishop—New Guinea field series BBM-NG 107652.

Measurements of holotype.—Total length, 71; length of tail, 25; length of hindfoot, 8; length of ear, 15; length of forearm, 41.3; condylocanine length, 13.5; zygomatic breadth, 8.0; width of postorbital constriction, 2.2; mastoidal breadth, 7.3; alveolar length of maxillary toothrow, 5.0; and breadth of palate at M^3–M^3, 5.4.

Distribution.—New Guinea and adjacent islands of Misor and Yapen in Irian Jaya.

Diagnosis.—Externally and cranially medium- to large-sized for species; length of forearm long; skull long and broad, condylocanine length long, and palate and zygoma broad.

Etymology.—This new subspecies is named for the island of New Guinea.

Specimens examined (42).—Irian Jaya, Schouten Islands, Misor Island, Korido, 1 (1 BMNH); Irian Jaya, Geelvink Bay District, Yapen Island, 1 mi NW Sumberbaba, 1000 ft, 2 (2 AMNH); Irian Jaya, Yapen Island, Dawai River, 1 (1 AMNH); Irian Jaya, Jayapura, 25 (20 AMNH, 3 USNM, 1 MVZ, 1 FMNH); Irian Jaya, South side Humboldt Bay, 4 (4 RMNH); Papua New Guinea: West Sepik Province, Kaiseren Augusta River

(4°4′18″S, 141°7′15″E), 1 (1 RMNH); Papua New Guinea: East Sepik Province, Ama, 140 m, 2 (1 CM, 1 PNGM, including holotype and BBM-NG 105921 to be deposited in PNGM); Papua New Guinea: Madang Province, Sempi, 13 mi N Madang, 4 (4 MVZ); Papua New Guinea: Madang Province, Sempi Cave, 13.5 mi N, 1.5 mi W Madang, 1 (1 MVZ); Papua New Guinea: Madang Province, South Banup Cave, 6.5 mi S, 4.5 mi W Madang, 1 (1 MVZ).

Additional records.—New Guinea: no specific locality (Dobson, 1878*b*:876). Papua New Guinea: Madang Province, 8 km E Baku, Gogol Valley, (Hill, 1983:152). Papua New Guinea: Morobe Province, Huon Peninsula, no specific locality (Koopman, 1982: 16, [=Finschhafen, Koopman, *in lit.*]). Papua New Guinea: Gulf Province, Putei (McKean, 1972:27). Papua New Guinea: East Sepik Province, Wagu (McKean, 1972:27). Indonesia: Irian Jaya, Andai (Peters and Doria, 1880:692).

Remarks.—The two females from Ama were mist-netted in forest on 9 March 1980. Neither contained embryos although the holotype was lactating. Each weighed 4 g. A male (MVZ 138607) from Sempi Cave, Papua New Guinea, had testes measuring 3.5 mm in length and 1.5 mm in width when captured on 1 August 1969. A female (MVZ 138605) from Sempi had no embryos when checked on 24 July 1969. A male (MVZ 138603) from South Banup Cave, 6.5 mi S, 4.5 mi W Madang, Papua New Guinea, had testes measuring 3 by 2 mm when captured on 25 August 1969. The record from Putei reported by McKean (1972: 27) is the only report of this species from the southern portion of New Guinea. Additional collecting by mist-netting as well as visiting caves should result in specimens from elsewhere in the region, especially in Irian Jaya.

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SOUTH ASIAN MIDDLE EOCENE MOERITHERES (MAMMALIA: TETHYTHERIA)

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Abstract

Anthracobune and *Lammidhania* from the middle Eocene of South Asia (Pakistan and India) are confirmed as belonging to the Moeritheriidae. Newly collected material permits more complete description of *A. pinfoldi*, additional comparisons with late Eocene northern African *Moeritherium*, and some minor systematic adjustments. It is now clear that there are two distinct species of *Anthracobune*. The Moeritheriidae remain of uncertain position within the Tethytheria.

Introduction

The moeritheres, distinctive subungulate mammals, have long been considered an exclusively African late Eocene to early Oligocene radiation with possible relationships to the Proboscidea. Discovery of new middle Eocene specimens from Pakistan and reinterpretation of previously-described materials from Pakistan and India now confirm their presence also in the middle Eocene of South Asia (India and Pakistan). This paper reviews and illustrates the South Asian moeritheres, describes the new material, and amplifies the reasons for the assignment to the Moeritheriidae.

Abbreviations:

AMNH —American Museum of Natural History, New York.
H-GSP —Howard University-Geological Survey of Pakistan project.
BM(NH)—British Museum (Natural History), London.
YPM —Yale Peabody Museum, New Haven, Connecticut.

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Submitted 21 March 1983.

LUVP	—Lucknow University Vertebrate Paleontology Collection, Lucknow, India.
Munich	—Institut für Paläontologie und historische Geologie, Munich, Federal Republic of Germany.
L	—maximum length.
W	—maximum width.
Wa	—maximum anterior width.
Wp	—maximum posterior width.

PREVIOUS STUDIES

African moeritheres were first found along the margin of the Fayum depression in northern Egypt (Andrews, 1901, 1906). Subsequent discoveries in Libya, Mali, and Senegal have given late Eocene and early Oligocene *Moeritherium* (the only African genus) a substantial northern African distribution (Coppens and Beden, 1978; Tassy, 1981).

Eocene vertebrates have been known from northern South Asia (Fig. 1) since 1877, but detailed work began only in 1940 when Pilgrim described two of the three taxa here regarded as Asian moeritheres. In the small collection made by Attock Oil Company geologists from north of the village of Basal in what is now known as the Punjab Province of Pakistan, Pilgrim recognized the new genus *Anthracobune* with two species (*A. pinfoldi* and *A. daviesi*) and a third ("*A.*" *wardi*) of possible affinities. The holotype of *A. pinfoldi* is two dentary fragments (BM(NH) M 15792) (Fig. 2a), and Pilgrim also placed three other lower jaw fragments in that species. *A. daviesi* was defined from a single maxillary fragment (BM(NH) M 15795) (Fig. 2b) containing what Pilgrim regarded as P^3 and P^4. The holotype of "*A.*" *wardi* is the posterior half of a lower molar (BM(NH) M 15799) (Fig. 2c).

In 1958, Dehm and Oettingen-Spielberg added a further species, *Pilgrimella pilgrimi,* based on an isolated upper molar (Munich 1956 II 20) (Fig. 4a) to this group of what were then regarded as anthracotheres. Sahni and Khare (1973), working in rocks of equivalent age and similar facies in Jammu and Kashmir, India, recovered a maxilla with P^2–M^2 (LUVP 15006) (Fig. 4b) which they assigned to *P. pilgrimi.*

Gingerich (1977) restudied Pilgrim's materials in the British Museum (Natural History), located several specimens that had not been discussed by Pilgrim, and determined that the holotype of "*A.*" *wardi* should be placed in a new genus, *Lammidhania*; he left this genus as well as *Anthracobune* and *Pilgrimella* in the Anthracotheriidae. Gingerich also synonymized *A. pinfoldi* and *A. daviesi* on the basis of size and occurrence, as none of the specimens in Pilgrim's sample preserved the same teeth. Thus *A. pinfoldi* became the first of this group to be known from both upper and lower dental materials. Gingerich et al. (1979) also retained all three genera in the Artiodactyla, but removed BM(NH) 32168 from *Lammidhania* to cf. *Anthracokeryx.*

Coombs and Coombs (1979) analyzed the ordinal affinities of *Pil-*

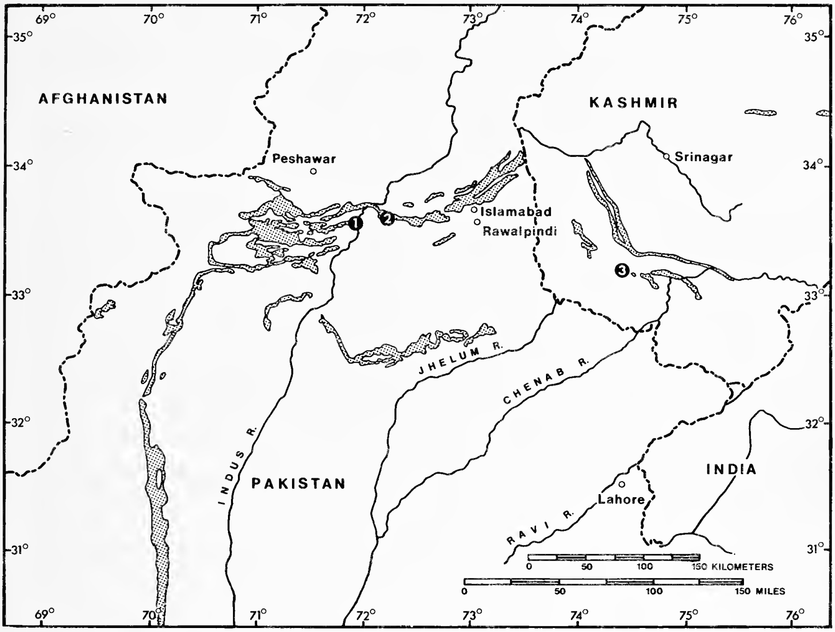

Fig. 1.—Distribution of Eocene sedimentary rocks of western India and northern Pakistan. 1. Chorlakki and Kohat area, Northwest Frontier Province. 2. Basal and Ganda Kas area, Kala Chitta Hills, Punjab Province. 3. Subathu Formation, Jammu and Kashmir State.

grimella based on a detailed study of a cast of LUVP 15006; they then removed *Pilgrimella* from the Artiodactyla and concluded that it is a perissodactyl not assignable to any known family.

West (1980), working with several newly-collected specimens from north of Basal (the product of field work by the H-GSP project in area 2 of Fig. 1), described a lower dentition (H-GSP 1981) (Figs. 5 and 6) readily referable to the same species as LUVP 15006. That lower dentition obviously belongs to *Anthracobune,* and West assigned the new material, plus *P. pilgrimi,* to *A. pinfoldi,* which was placed in the Moeritheriidae. *A. daviesi* was not considered, and it and *Lammidhania* were left in the Artiodactyla.

Gingerich and Russell (1981) retained both *Anthracobune* and *Pilgrimella* as valid genera and put them, as well as *Lammidhania,* in the Moeritheriidae. In the same paper, the material used as the holotype of the presumed sirenian *Ishatherium subathuensis,* described by Sahni and Kumar (1980) from the early or middle Eocene of Jammu and

Kashmir, was regarded as a partial upper molar of *Pilgrimella.* Gingerich and Russell then speculated on possible relationships between these South Asian species and the eastern Asian Phenacolophidae.

Field work by the Howard University—Geological Survey of Pakistan project in March 1982 produced a second maxilla and an associated scapula fragment (H-GSP 82-31P) (Fig. 3) here placed in *Anthracobune.* Study of these and all related specimens confirms the synonymy of *A. pinfoldi* and *A. daviesi* as suggested by Gingerich et al. (1979) as well as the synonymy of *Anthracobune* and *Pilgrimella* proposed by West (1980). LUVP 15006 and several other specimens (Table 1) are the same size as Dehm and Oettingen-Spielberg's holotype of *Pilgrimella pilgrimi*; that species, now regarded as valid (*contra* West 1980), is placed in *Anthracobune.*

SYSTEMATIC PALEONTOLOGY

Order Uncertain or Proboscidea
Family Moeritheriidae Andrews 1906
Genus ***Anthracobune*** Pilgrim 1940

Synonymy.—*Pilgrimella* Dehm and Oettingen-Spielberg, 1958.

Emended diagnosis.—Approximately two-thirds the size of *Moeritherium*; P_3 and P_4 have distinct trigonids and two talonid cusps; lower molars increase in size posteriorly, are transversely lophodont with deep median valleys, have distinct posterior cingular cusps (doubled on M_3), and have a paraconid connate with the metaconid; third and fourth upper premolars have both labial and lingual cusps; upper molars, increasing in size posteriorly, are lophodont with well-developed conules anterior to the major cusps and have no obvious ectoloph. The lower jaws are pronouncedly shallow anteriorly, with a short symphysis which extends posteriorly only to the level of P_1.

Included species.—*A. pinfoldi* Pilgrim, 1940; *A. pilgrimi* (Dehm and Oettingen-Spielberg, 1958).

Distribution.—Late early and/or early middle Eocene, northern South Asia.

Anthracobune pinfoldi Pilgrim 1940
Figs. 2a, b; 3a, b

Synonymy.—*Anthracobune daviesi* Pilgrim 1940.

Holotype.—BM(NH) M 15792 plus M 15794 (added by Gingerich in 1977).

Referred specimens.—BM(NH) M 15795 (holotype of *A. daviesi*), M 15793, 32169, and H-GSP 82-31P.

Table 1.—*Measurements, in millimeters, of selected specimens of* Anthracobune.

A. pinfoldi, BM(NH) M 15795, holotype of "*A. daviesi*"		
P^2	L	approx. 15.5
	W	18.7
P^3	L	19.0
	W	23.1
A. pinfoldi, H-GSP 82-31P		
P^3	L	19.1
	W	23+
P^4	L	20.3
	W	26+
M^1	L	25.0
	W_{ant}	26+
	W_{post}	22.5
M^2	L	26.3
	W_{ant}	30+
	W_{post}	25+
M^3	L	27+
	W_{ant}	27.6
	W_{post}	18+
A. pilgrimi, Munich 1956 II 20, holotype		
M^1	L	18.2
	W_{ant}	18.4
	W_{post}	19.6
A. pilgrimi, Munich 1956 II 21		
M^2	L	21.0
	W_{ant}	19.4
	W_{post}	14.5
A. pilgrimi, H-GSP 538		
M^2	L	21.0
	W_{ant}	22.0
	W_{post}	17.5
A. pilgrimi, LUVP 15006 (cast)		
P^2	L	17.6
	W	12.2
P^3	L	17.3
	W	17.7
P^4	L	15.7
	W	18.6
M^1	L	18.1
	W_{ant}	16.8
	W_{post}	14.0
M^2	L	19.0
	W_{ant}	20.0
	W_{post}	17.0

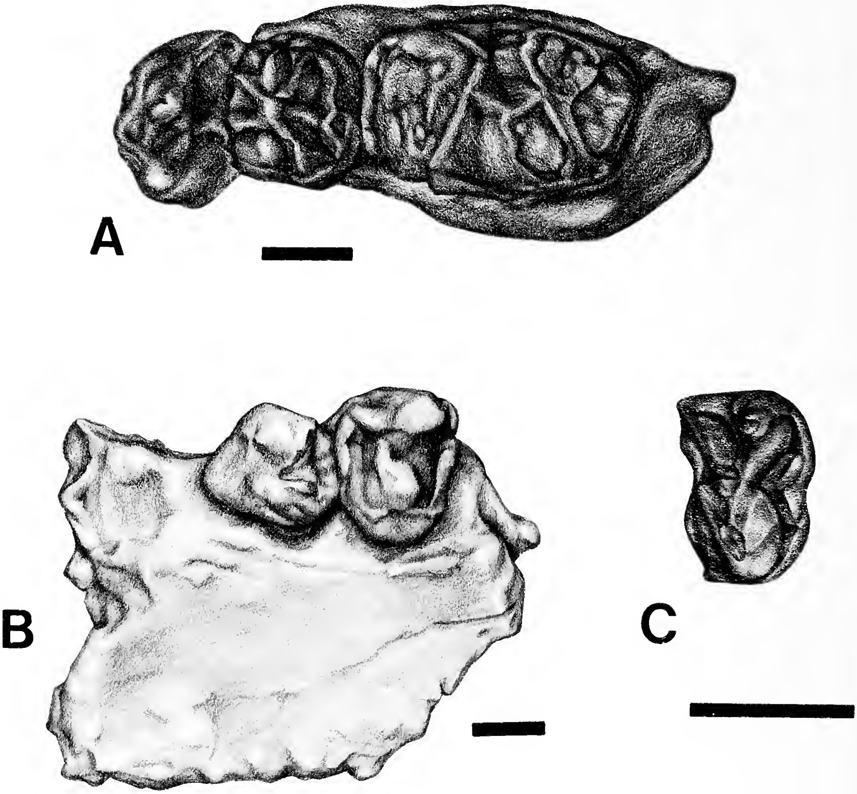

Fig. 2.—*Anthracobune* holotypes; all scale units equal 1 cm. a) *A. pinfoldi,* BM(NH) M 15792; b) *A. daviesi,* BM(NH) M 15795; c) "*A.*" *wardi,* BM(NH) M 15799.

Type locality.—North of Basal, Attock District, Punjab Province, Pakistan (West and Lukacs, 1979).

Diagnosis.—Large species of *Anthracobune* (P^3 length 19 mm; M^2 length 26+ mm; M_3 length 17–19.5 mm); upper premolars with single labial cusps.

Remarks.—The recovery of H-GSP 82-31P from H-GSP locality 146 (West and Lukacs, 1979) finally allows proper identification of the teeth preserved in BM(NH) M 15795, the holotype of *A. daviesi,* as P^2 and P^3. Both BM(NH) M 15795 and H-GSP 82-31P have only a single labial cusp on P^3, in contrast with the incipiently paired cusps in material regarded below as *A. pilgrimi.* Although the sample size now numbers only five specimens, the size differences between this suite

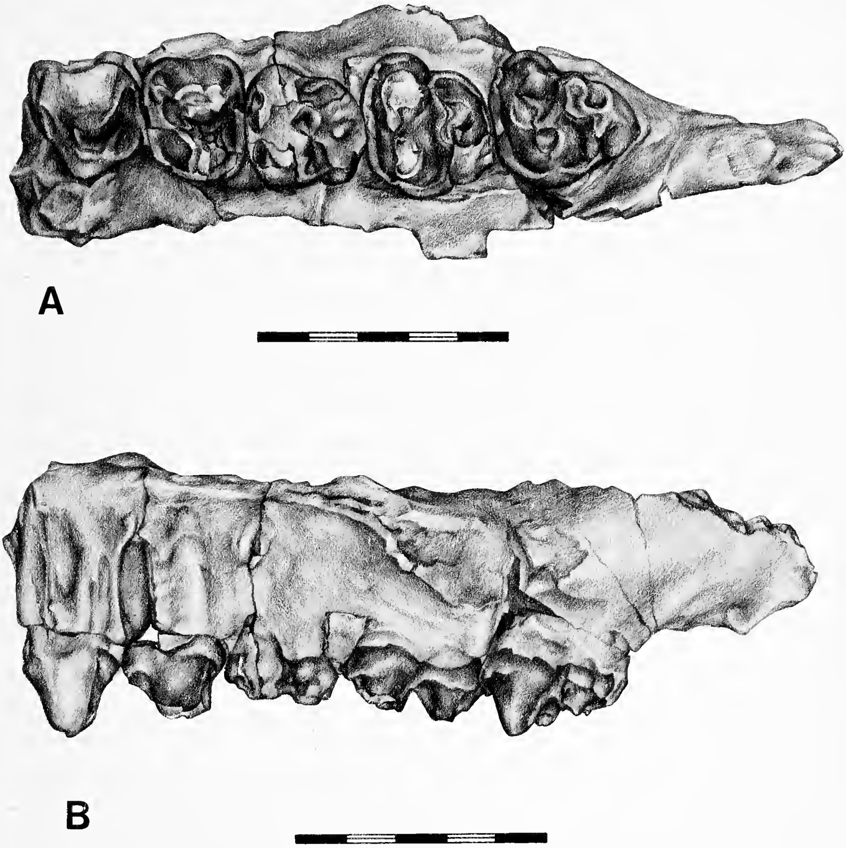

Fig. 3.—*Anthracobune pinfoldi,* H-GSP 82-31P; all scale units equal 1 cm. a) Occlusal view; b) lateral view.

and *A. pilgrimi* is substantial enough (15% to 30% in various dental measurements) to assure the reality of these two species of *Anthracobune.* Because of the difficulties of working with such small samples, West (1980) inappropriately extended *A. pinfoldi* to include physically small specimens which here are excluded.

The dentition of H-GSP 82-31P, the first known upper cheek teeth of *A. pinfoldi,* is similar to that of *A. pilgrimi* which has previously been described (Sahni and Khare, 1973; Coombs and Coombs, 1979). The third premolar is three-rooted and high-crowned. There is a single high labial cusp and a lower lingual cusp which are joined by a low anterior crest. The degree of enamel spalling allows recognition of a low cingulum only posteriorly.

P^4 also is three rooted and, although preservation is poor, probably was not as high crowned as P^3. The single external cusp gives off low anterior and posterior crests to the vicinity of the external ends of the flat anterior and posterior cingula. There apparently is no external cingulum.

The first upper molar is four rooted and noticeably wider anteriorly than posteriorly. The bulbous paracone contributes to this. The external cingulum, discontinuous along the posterior part of the paracone, extends anteriorly into a small parastyle. The "ectoloph" between the paracone and metacone is very low, at essentially the same level as a medial elevation that extends from the posterior corner of the protocone to the anterior side of the metaconule. The metaconule is anteriorly situated. The internal and posterior cingula are discontinuous around the hypocone, unlike the condition in *A. pilgrimi.*

M^2 is much less worn than M^1, but is structurally very similar. Its cingulum, prominent except around the posterior part of the paracone, extends anteriorly into a small parastyle. Narrow crests from the posterior flank of the paracone and the anterior flank of the metacone converge on a tiny mesostyle. As with M^1, the posterior part of the tooth is substantially narrower than the anterior part. Both conules are large; the metaconule is situated well anterior of a metacone-hypocone line and is strongly connected to each. The paraconule is forward of a paracone-protocone line and is similarly well joined to both conules. The major cusps are conical.

The upper third molar shows the same degree of wear as M^2. The anterior cusps, paracone, paraconule and protocone, are all approximately equal in size. There is a strong anterior cingulum and the external cingulum is slightly expanded in the position of a parastyle. The valley between the paracone and metacone is deeper than that between the protocone and metaconule. Most of the hypocone is broken away, but it seems to have been a low cingular cusp immediately posterior to the metacone. The internal cingulum, discontinuous around the protocone, also is broken away in the hypocone area.

A fragment of the proximal end of the right scapula was found in direct association with the maxilla. The glenoid cavity is oval and shallow with rounded margins. Anteriorly it extends into a bulbous notched coracoid process. The coracoid edge is concave, approximately parallel to the spine. The postero-internal corner of the glenoid cavity is broken away, but it appears from the small unbroken area that the coracoid border also is concave. This indicates that the distal part of the scapula, the blade, is broadly flaring. The spine rises abruptly about 3.5 cm from the margin of the glenoid cavity. Although it is broken,

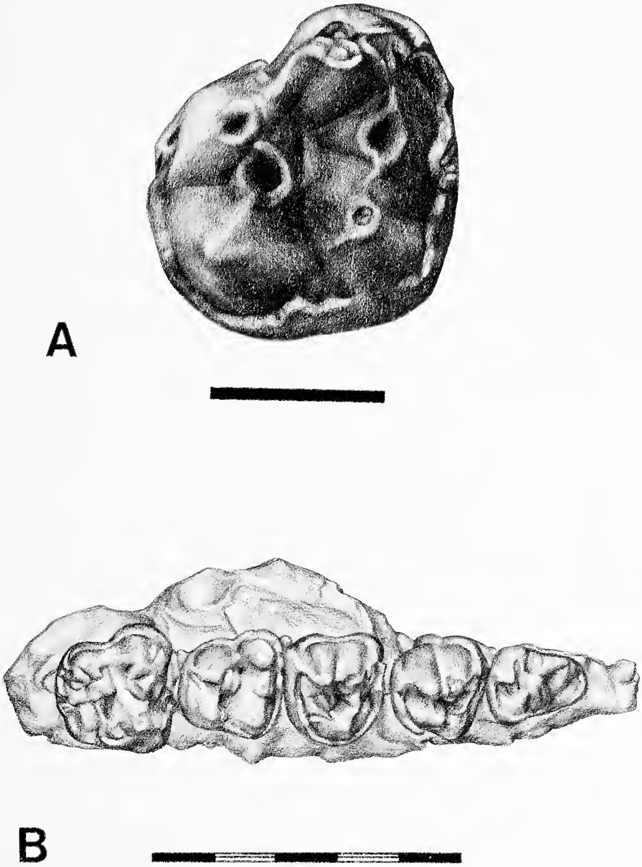

Fig. 4.—*Pilgrimella pilgrimi* (=*Anthracobune pilgrimi*); all scale units equal 1 cm. a) Munich 1956 II 20, holotype; b) LUVP 15006.

the spine is slanted slightly toward the glenoid border, producing a deeper and sharper fossa than on the coracoid side.

Anthracobune pilgrimi (Dehm and Oettingen-Spielberg 1958)
Figs. 4a, b; 5; 6

Synonymy.—*Pilgrimella pilgrimi* Dehm and Oettingen-Spielberg 1958.
Pilgrimella pilgrimi Sahni and Khare 1973.
Pilgrimella pilgrimi Coombs and Coombs 1979.
Anthracobune pinfoldi (part) West 1980.

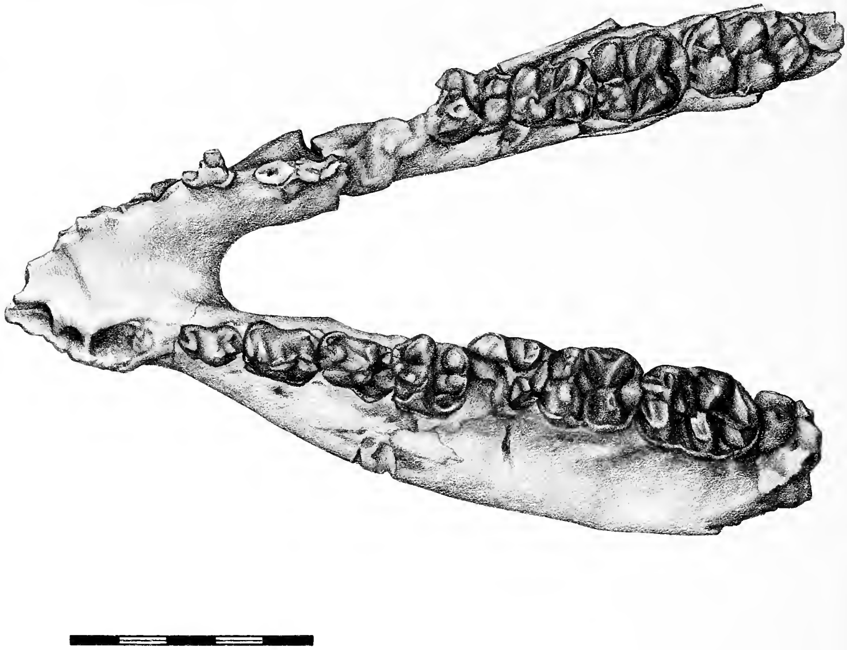

Fig. 5.—*Anthracobune pilgrimi,* H-GSP 1981, occlusal view; scale units equal 1 cm.

Holotype.—Munich 1956 II 20.

Referred specimens.—LUVP 15006; H-GSP 538, 568, 1981, 1975; Munich 1956 II 21.

Type locality.—Dehm loc. 24 (=H-GSP loc. 67 of West and Lukacs 1979), north of Basal, Attock District, Punjab Province, Pakistan.

Diagnosis.—Small species of *Anthracobune* (P^3 length 16–17 mm; M^2 length 16–21 mm; M_3 length 25–26 mm); upper premolars with two labial cusps.

Remarks.—This is the better known of the two species of *Anthracobune.* The entire postcanine lower dentition is included in a pair of well-preserved dentaries (H-GSP 1981), and the upper teeth (P^2–M^2) are preserved in LUVP 15006. That maxilla was described by Sahni and Khare (1973) and reviewed by Coombs and Coombs (1979). The dentition of H-GSP 1981 was fully described previously (West, 1980), but when that paper was written the preparation of the dentary bones was incomplete. Subsequently, they have been fully cleaned and freed of matrix and are illustrated in Figs. 5 and 6. Some of the features

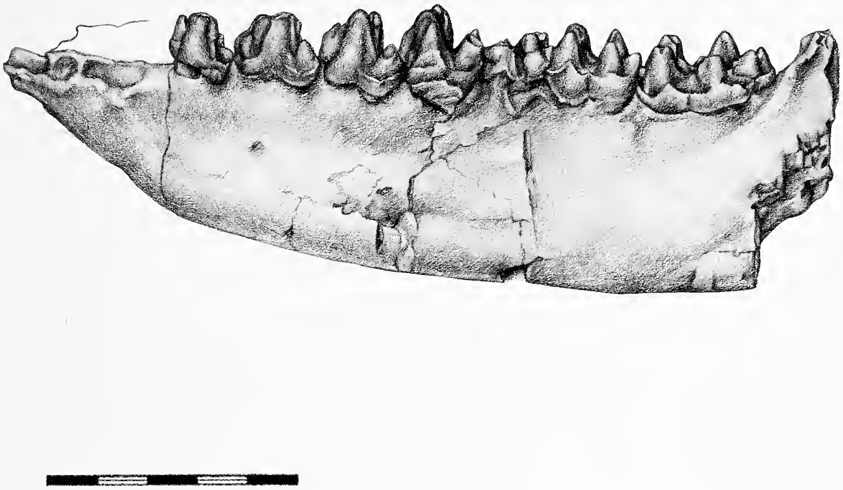

Fig. 6—*Anthracobune pilgrim,* H-GSP 1981, lateral view; scale units equal 1 cm.

described earlier, including the shallow symphyseal region and alveoli for the anterior teeth are now much clearer. In addition, a prominent bulge extends along the lingual side of the dentary bones from the posterior premolars anteriorly almost to the symphysis on both sides. The bone in the symphysis is approximately as thick as that of the bulge. The lingual surface of the symphysis parallels the flattened labial surface, emphasizing the rapid anterior shallowing of the jaw. Detailed preparation of the incisor region now indicates the probable presence of three procumbent incisors, all smaller than the canine.

Lammidhania Gingerich 1977

Synonymy.—"*Anthracobune*" *wardi* Pilgrim 1940.

Diagnosis.—Size (M_3 length 24 mm) and general morphology similar to *Anthracobune*; lower molars relatively narrower than in *Anthracobune*; three lower premolars.

Included species—*L. wardi* (Pilgrim 1940).

Lammidhania wardi (Pilgrim 1940)

Fig. 2c

Synonymy.—"*Anthracobune*" *wardi* Pilgrim 1940.

Holotype.—BM(NH) M 15799.

Referred specimens.—H-GSP 1000, 982, 1633.

Diagnosis.—As for the genus.

Remarks.—The differences between *Lammidhania wardi* and *Anthracobune pilgrimi* are primarily in the area of premolar number and morphology and relative robustness of the cheek teeth. These characters are minimally adequate for generic distinction (*Lammidhania* is more derived than *Anthracobune* in the loss of a premolar, probably P_1) but the close higher-level relationship between these genera is clear. West (1980) erred when he suggested that the premolar condition of *Lammidhania* was indicative of an artiodactyl relationship and the molar structure was a convergence with *Anthracobune.* My current preference is to regard *Lammidhania* as a moerithere, closely related to and doubtfully separate from *Anthracobune.*

MOERITHERE AFFINITIES OF *ANTHRACOBUNE* AND *LAMMIDHANIA*

The initial placement of *Anthracobune* in the Moeritheriidae (West, 1980) relied to a significant extent on mandibular and dental characters readily seen in H-GSP 1981 and LUVP 15006. These included relatively wide lower cheek teeth, prominent lophodonty and hypoconulids, a procumbent symphyseal area, complex premolars, and an abruptly rising ascending ramus. The absence of an ectoloph in the upper molars, enlarged conules on both the paraloph and metaloph, and strong cingula ally the upper teeth with moeritheres. The new data available from H-GSP 82-31P further support moerithere affinities—the nature of the anterior root of the zygoma with its opening for the anterior orbital foramen and the distinct enlargement dorsal to M^2–M^3 and the flaring scapula with a prominent coracoid process.

Anthracobune is more primitive than *Moeritherium* in the forward placement of the symphysis, retention of all the incisors, only moderately enlarged canines, posterior position (adjacent to posterior end of M_3) of the ascending ramus, more molariform P_4, smaller M_3 heel, and interruption in the lophs on the lower molars. In the maxilla, primitive features of *Anthracobune* are the lack or incomplete separation of the paracone and metacone on P^3 and P^4, the degree of independence of the molar conules, the relatively great anterior breadth of the molars, and the posterior position of the downturned and enlarged maxillary root of the zygomatic arch.

In all these characters, *Anthracobune* is less derived than is *Moeritherium,* and more similar to the presumed ancestral tethythere stock. It has fewer similarities with the most primitive known sirenians, as it possesses a short and shallow mandibular symphysis, only four premolars, and small mental foramina, and lacks any indication of pachyostosis. Similarly, the South Asian creatures are more primitive than the northern African late Eocene–early Oligocene barytheres which have lost the canines, one incisor and P_1, have a very deep and massive symphysis, and a prominent anteriorly-situated ascending ramus.

ENVIRONMENTS

Both the middle Eocene Asian and late Eocene-early Oligocene African moeritheres have been collected from rocks deposited in similar coastal environments. The *Anthracobune* and *Lammidhania* materials for which adequate data are available (those collected near Basal by the Munich and H-GSP projects) have come from throughout the Kuldana Formation. That rock unit is composed primarily of freshwater calcareous mudstone, fine-grained sandstone, and granular calclithite. Foraminifera-bearing limestone lenses are present, indicative of the proximity of the fluctuating Tethys shoreline (West and Luckacs, 1979). To the west, in the Chorlakki area of the Kohat Basin (No. 1 on Fig. 1), Eocene rocks produce a similar fauna; Gingerich et al. (1983) and Wells (1983) regarded these as indicative of coastal environments surrounding a saline epicontinental sea remnant of the contracting Tethys.

The faunas accompanying *Anthracobune* and *Lammidhania* (West, 1980; Gingerich and Russell, 1981 Gingerich et al., 1983; and references cited therein) include numerous primitive whales as well as typical terrestrial organisms. Thus both lithological and paleontological data are compatible with an amphibious habit for the middle Eocene Asian moeritheres.

The moerithere-bearing beds in the Fayum of Egypt indicate a nearshore environment (Bown *et al.,* 1982). The late Eocene fossiliferous unit, the Qasr el-Sagha Formation, ranges from "interdeltaic shallow marine and littoral" to "deltaic . . . with distributory channel sands" (Simons, 1968). Overlying it, the Jebel el Qatrani Formation is more terrestrial, representative of a channel floodplain complex. The Qasr el-Sagha Formation contains numerous moeritheres in association with archaeocete whales (Andrews, 1906), a situation parallel to that of the Kuldana Formation in Pakistan.

CONCLUSIONS

Three species of primitive moeritheres are now recognized in late early to early middle Eocene rocks in South Asia. They are representative of a slightly earlier stage in the evolution of this group than is African *Moeritherium,* but existed under ecologic conditions quite similar to those of the North African localities.

While these new interpretations expand the moeritheres both geologically and geographically, they still are distinct from the other tethytheres (*fide* McKenna, 1975). Middle Eocene moeritheres do not, at this time, contribute toward more precisely relating moeritheres to the remaining tethytheres; at the very least, the moerithere-sirenian dichotomy occurred earlier in the Eocene (Domning et al., 1982; Sereno, 1982), and the moeritheres may be best regarded as a close sister group of the Sirenia and of the Proboscidea if they are not properly placed in that order.

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This contribution is part of the ongoing work of the Howard University—Geological Survey of Pakistan "Fossil Mammals of Pakistan" project directed by Drs. S. Taseer Hussain (Howard University) and S. M. Ibrahim Shah (Geological Society of Pakistan). The field work benefitted from the able services of Mr. Muhammed Arif, Assistant Director, Geological Survey of Pakistan.

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REVISION OF THE WIND RIVER FAUNAS, EARLY EOCENE OF CENTRAL WYOMING. PART 4. THE TILLODONTIA

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Abstract

Two species of *Esthonyx*—*E. bisulcatus* and *E. acutidens*—are recorded from the Lysite Member, and the Red Creek Facies and Lost Cabin Member, respectively, of the Wind River Formation. *Trogosus,* hitherto unknown from this formation, has been recovered from two localities in the upper part of the Lost Cabin Member. The first occurrence of *Trogosus,* along with that of other typical Bridgerian mammals, marks the Wasatchian-Bridgerian boundary and, in part, defines the Gardnerbuttean (earliest Bridgerian) subage. A reconstruction of the phylogenetic relationships of North American and Asian tillodonts suggests that the North American genera *Esthonyx, Megalesthonyx,* and *Trogosus* may have had independent origins from among Asian tillodonts.

Introduction

Tillodonts were among the first fossil mammals reported from the Wind River Basin. Of the two species Cope (1880, 1881) named from the Wind River Formation—*Esthonyx acutidens* and *E. spatularius*—the type of the latter appears to have come from the Bighorn Basin (Gazin, 1953). Subsequently, excellent material of *E. acutidens* from the Boysen Reservoir area, Wind River Basin (White, 1952), was studied by Gazin (1953) in his major review of the Tillodontia. He formally recognized *E. bisulcatus* Cope, 1874 and *E. acutidens* from the "Lysite" and "Lost Cabin" beds, respectively, of the Wind River Formation—

Submitted 13 May 1983.

a conclusion corroborated in subsequent reviews (Kelley and Wood, 1954; Guthrie, 1967, 1971)—and suggested that *E. acutidens* may also occur in the Lysite Member. Gingerich and Gunnell (1979), in the last major treatment of tillodont systematics and evolution, did not specify the biostratigraphic occurrences of either species in particular basins. They reported *E. bisulcatus* from Lysitean and Lostcabinian aged horizons, and *E. acutidens* from "Lost Cabin beds and equivalents" (p. 146) and early Bridgerian horizons in western North America. Importantly, *Trogosus* has never been reported from the Wind River Formation.

Since Guthrie's (1967, 1971) work, 20 specimens from the Lysite Member (nine localities), 34 from the Lost Cabin Member (12 localities), and two from the Red Creek Facies (two localities; Stucky, 1983) have been added to the sample of tillodonts from the Wind River Formation. Two of the specimens—from the Lost Cabin Member—represent *Trogosus,* and the remainder, *Esthonyx.* Four of the localities (CM loc. 34; UCM locs. 80101, 81028, 79040), all in the upper part of the Lost Cabin Member, are earliest Bridgerian (=Gardnerbuttean, Robinson, 1966) rather than latest Wasatchian, according to biostratigraphic evidence presented here and elsewhere (Stucky, 1982, 1983; Krishtalka and Stucky, 1983). This conclusion is reflected in the "known occurrence" data in the systematic section below.

Abbreviations in text and tables are as follows: AMNH, American Museum of Natural History; CM, Carnegie Museum of Natural History; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, People's Republic of China; UCM, University of Colorado Museum; Loc., locality.

SYSTEMATICS

Order Tillodontia Marsh, 1875
Family Esthonychidae Cope, 1883

Gazin (1953) and Gingerich and Gunnell (1979) have reviewed the taxonomic history of tillodonts. Five North American genera are generally recognized—*Esthonyx* Cope, 1874; *Trogosus* Leidy, 1871; *Anchippodus* Leidy, 1868; *Tillodon* Gazin, 1953; *Megalesthonyx* Rose, 1972. *Esthonyx* has been reported from the Clarkforkian, Wasatchian, and earliest Bridgerian, *Trogosus* and *Tillodon* only from the Bridgerian, and *Megalesthonyx* from the late Wasatchian. The age of *Anchippodus,* although suggested to be Bridgerian (Gazin, 1953), cannot be determined from present evidence.

One esthonychid, *E. munieri* (Lemoine, 1889) is known from the Sparnacian or Cuisian of the Paris Basin, and four have been reported from the early Tertiary of China. Two of these, *Lofochaius* Chow et al., 1973, and *Meiostylodon* Wang, 1975, are early or middle Paleocene in age, (Li and Ting, 1983), whereas *Kuanchuanius* Chow, 1963, and *Adapidium* Young, 1937, come from middle and late Eocene horizons, respectively. *Basalina* Dehm and Oettingen-Spielberg, 1958, from the middle Eocene of Pakistan, may be an esthonychid (Gingerich and Gunnell, 1979; Lucas and Schoch, 1981).

Esthonyx Cope, 1874

Gazin (1953) recognized five North American species of *Esthonyx,* which from stratigraphically oldest to youngest are: *E. grangeri* Simpson, 1937; *E. latidens* Simpson, 1937; *E. spatularius* Cope, 1880 (all Clarkforkian and Graybullian, Bighorn Basin); *E. bisulcatus* Cope, 1874 (Graybullian and Lysitean, Bighorn, Wind River, San Juan and Piceance basins); *E. acutidens* Cope, 1881 (?Lysitean and Lostcabinian, Bighorn, Wind River, Washakie and Piceance basins). He also identified *Esthonyx* sp. from the Lostcabinian part of the Huerfano Formation, the Cathedral Bluffs Tongue of the Wasatch Formation and the Lysitean of the Knight (=Wasatch) Formation.

Gingerich and Gunnell (1979) added two new species of *Esthonyx*—*E. xenicus* and *E. ancylion*—from the Clarkforkian of the Bighorn Basin, synonymized *E. latidens* with *E. grangeri,* and redefined the hypodigms of the other North American species. Part of the hypodigm of *E. xenicus* includes specimens previously referred to *E. spatularius* and *E. bisulcatus.* They posited two lineages of *Esthonyx* in Clarkforkian and Wasatchian strata of western North America. Species in the first lineage—*E. xenicus-E. ancylion-E. grangeri*—lack symphysial fusion, retain a double-rooted P_2, have non-overlapping stratigraphic ranges, and increase in size anagenetically. Species composing the second lineage—*E. spatularius-E. bisulcatus-E. acutidens*—have a fused mandibular symphysis, a single-rooted P_2, and show an anagenetic increase in size and hypsodonty. According to Gingerich and Gunnell (1979)—*E. spatularius* and *E. bisulcatus* do not overlap in range; specimens that are intermediate in age are also morphologically intermediate and tentatively referred to the former, with the provision that they may represent a new, intermediate species; and finally, the relationship between *E. bisulcatus* and *E. acutidens* is less clear, because they are contemporaneous in the middle and upper part of the *Heptodon* Range-Zone of the Bighorn Basin (Schankler, 1980).

The *E. xenicus* lineage begins in the early Clarkforkian, and the *E. spatularius* one at the onset of the Wasatchian. When the two lineages are compared, there is significant overlap in size between *E. spatularius* and *E. xenicus-E. ancylion,* and between *E. bisulcatus* and *E. ancylion.* Thus, it is difficult to identify specimens of similar size, unless they preserve the mandibular symphysis and/or anterior premolars. Accordingly, we suggest additional diagnostic features, given that the figures and descriptions in Gingerich and Gunnell (1979) accurately reflect the range of intraspecific morphologic variation. The *E. xenicus-ancylion-grangeri* group may be characterized by inflated metaconids, appressed paraconids and metaconids and low paracristids on M_{1-3}, and very narrow stylar shelves and salients on P^4–M^3. In contrast, the *E. spatularius-bisulcatus-acutidens* group has well-separated paraconids and metaconids, an unexpanded metaconid, and a high paracristid on M_{1-3}, and an expanded stylar shelf and salients on P^4–M^3. These characters may aid in identifying specimens that lack the diagnostic anterior portions of the lower dentition.

The *E. xenicus-ancylion-grangeri* lineage, known only from the northern part of the Bighorn Basin (including the Clark's Fork Basin), appears to be a chronospecies that increases in size. The divisions between the species are stratigraphic and necessarily arbitrary.

On the other hand, the *E. spatularius-bisulcatus-acutidens* clade is not necessarily one chronospecies. The first two species compose a morphocline of increasing size and hypsodonty through time, and individual specimens are indistinguishable except stratigraphically. In agreement with Bown (1979), they are here considered conspecific. *E. bisulcatus-E. acutidens* show similar anagenetic change, but their apparent co-occurrence at a number of horizons in the Bighorn Basin (Schankler, 1980) as well as non-overlapping ranges in size in the Wind River Basin (see below) imply that, for the present, they should be retained as separate species. Continued analyses of the Bighorn Basin material and denser samples from the Wind River Basin should clarify this issue.

Gingerich and Gunnell (1979) have attempted to define statistically the Clarkforkian and Wasatchian species of *Esthonyx.* They (1979:128) derive a 0.095 standard deviation value (for Ln [L × W] of M_1) from the "largest sample" of *Esthonyx* and use it to compute a diagnostic difference of 3.3 standard deviation units between the type specimens of *E. xenicus* and *E. ancylion,* and 5.1 standard deviation units between the types of the latter and *E. grangeri.* The three type specimens are compared to one another rather than to the descriptive statistics of any sample. In this light, these comparisons, although interesting, appear to violate principles of statistical analysis. The standard deviation of a sample is not applicable as a model to any other sample, population, or individual. Also, there are no statistical procedures that test for the significance of the difference between individual specimens, measurements of which can only be compared to the mean of a population or statistical sample (by means of a Z-test) (Simpson et al., 1960: 173; Sokal and Rohlf, 1969).

The assignment in Gingerich and Gunnell (1979) of a Lostcabinian age to the San Jose tillodont, *E. bisulcatus,* has been revised. Recent analyses of the AMNH (Lucas et al., 1981) and CM (unpublished data) collections from the Regina and Tapicitos members of the San Jose Formation found evidence that the San Jose faunas are late Graybullian to Lysitean—the absence of the index fossil *Lambdotherium,* as well as *Shoshonius,* and the presence of a host of typical early to middle Wasatchian mammals (*Ambloctonus, Didymictis protenus, Ectoganus, Apheliscus, Pelycodus jarrovii, Navajovius, Chriacus, Anacodon, Homogalax*).

Esthonyx bisulcatus Cope, 1874
(Fig. 1; Tables 1, 3)

Referred specimens.—Partial dentary with P_4–M_2—CM 39205; P_3, dP_4—CM 37053; M_1—CM 39941, 39645, 39902, 37052; M_2—CM 39160, 37054, 22660 (2 teeth); M_3—CM 36117, 37056, 28722, 53785; lower molar fragments—CM 37055, 35929, 19902; partial maxilla with M^{1-3}—CM 39644; M^3—CM 54155; upper molar fragments—CM 35978, 35979, 35980.

Localities.—CM locs. 797, 799, 802, 806, 807, 927, 929, 931, 1091 (Lysitean, Lysite Member).

Known distribution.—early Wasatchian—Hoback and Powder River basins (Wasatch Fm.), Wyoming; early to late Wasatchian—Bighorn Basin (Willwood Fm.), Wyoming; middle Wasatchian—Wind River Basin (Wind River Fm.), Wyoming, San Juan Basin (San Jose Fm.), New Mexico.

Description and discussion.—The known morphology of *E. bisulcatus* is described in Gazin (1953) and Gingerich and Gunnell (1979). In the Wind River Basin this species is restricted to, but occurs through-

Table 1.—*Dimensions of lower teeth of* Esthonyx bisulcatus *from the Lysite Member, Wind River Formation, Wyoming.*

Specimen no.	Locality	P_3		P_4		M_1		M_2		M_3	
		L	W	L	W	L	W	L	W	L	W
CM 37053	807	6.1	3.8	8.7	5.3						
CM 39205	931			7.8	5.7	7.8	6.5	8.6	6.8		
CM 39941	797					7.5	6.1				
CM 39645	802					7.8	6.2				
CM 39902	797					7.8	6.2				
CM 37052	927					8.0	6.0				
CM 39160	806							8.5	6.5		
CM 22660	799							8.5	6.5		
CM 22660	799							8.5	6.5		
CM 53785	1091							8.4	6.1		
CM 37054	807								6.4		
CM 36117	929									10.0	5.2
CM 37056	929									10.0	
CM 28722	807										5.4

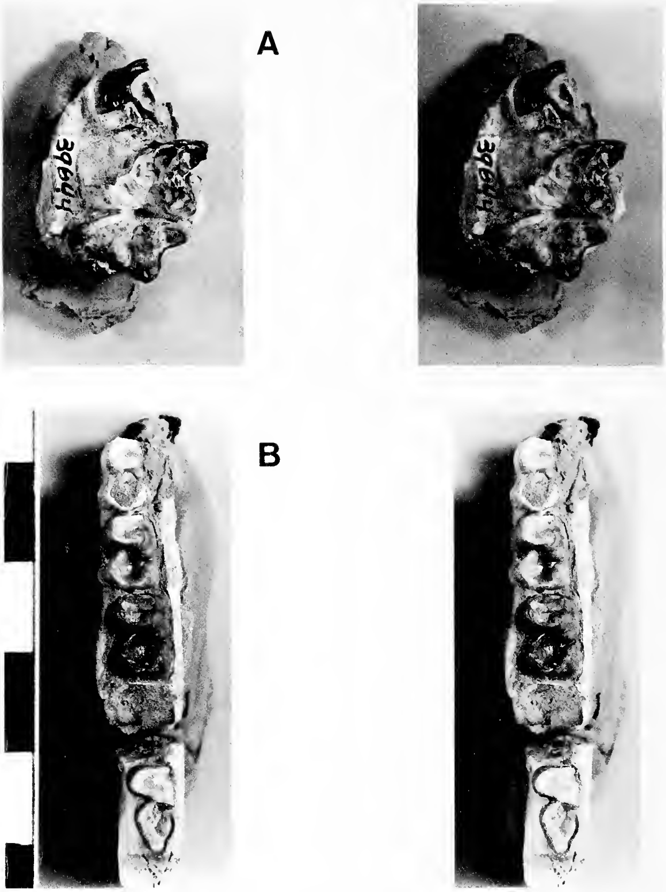

Fig. 1.—*Esthonyx bisulcatus.* A) CM 39644, LM^{1-3}; B) CM 39205, LP_4–M_2, and CM 36117, LM_3; all to same scale (1 cm).

out, the Lysite Member of the Wind River Formation. The absence of *E. bisulcatus* from localities in the Red Creek Facies (Stucky, 1983; Stucky and Krishtalka, 1982) of the Wind River Formation in the Red Creek-Deadman Butte area is coincident with the Lostcabinian age assigned to these sediments.

In *E. bisulcatus,* compared to Wind River *E. acutidens,* the teeth are significantly smaller (no overlap in range), P_4–M_3 are less hypsodont and bear a less robust metaconid, P_4 has a metastylid, M_{1-3} have a stronger metastylid, and P^4–M^3 have narrower stylar shelves with less expanded parastylar and metastylar salients.

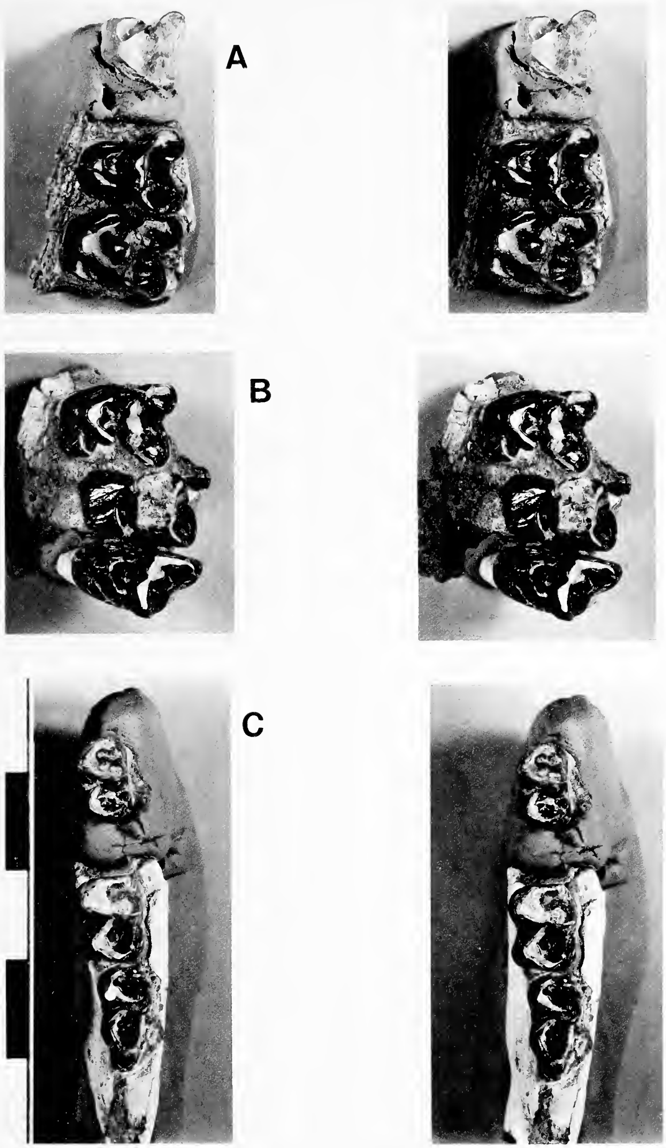

Fig. 2.—*Esthonyx acutidens.* A) CM 22311, RDP^4, and CM 42127, LP^4–M^1; B) CM 30943, LM$^{1-2}$, and CM 22310, LM^3; C) CM 35869, LP$_4$, and CM 22308, LM$_{2-3}$; all to same scale (1 cm).

Table 2.—*Dimensions of lower teeth of* Esthonyx acutidens *from the Lost Cabin Member, Wind River Formation, Wyoming.*

Specimen no.	Locality	P_4		M_1		M_2		M_3	
		L	W	L	W	L	W	L	W
CM 35869	34	8.8	6.1						
CM 35870	34	9.0	6.2						
CM 42131	34	8.1	5.2	8.8	6.6				
CM 22309	34			8.9	7.0				
CM 37236	34			8.6	7.0				
CM 30941	34			8.8	6.6				
CM 30942	34			8.7	6.5				
UCM 45384	80089			8.7	6.6	9.3	6.0		
CM 22312	90					10.3	7.2		
CM 22312	90					9.1	7.1		
CM 22312	90					9.8	7.5		
CM 30940	34					9.4	6.8		
CM 37235	34					10.0	7.0		
CM 36457	91					10.0	7.9		
CM 37238	34					9.5	8.0		
CM 42130	1077					10.9	7.5		
CM 22308	34					9.0	7.8	10.8	5.9
CM 55193	34							11.5	5.7
CM 37239	34								7.6

None of the specimens referred here preserves the mandibular symphysis or the anterior dentition—features used by Gingerich and Gunnell (1979) to distinguish between the two lineages of tillodonts. However, the teeth exhibit the stylar shelf development and lower molar hypsodonty that is typical of *E. bisulcatus* and *E. acutidens.* They lack the anteriorly expanded metaconid that appears to be characteristic of the *E. xenicus-ancylion-grangeri* chronospecies.

Esthonyx acutidens Cope, 1881
(Fig. 2; Tables 2–3)

Referred specimens.—Partial dentary with M_{1-2}—CM 21232; M_{2-3}—CM 22308; P_4–M_1—UCM 45384; P_4, M_1—CM 42131; P_4—CM 35869, 35870; M_1—CM 22309, 37236, 30941, 30942; M_2—CM 22312, 30940, 37235, 37238, 36457, 42130; M_3—CM 37239, 55193; lower molar fragments—CM 21131, UCM 46397; partial maxilla with P^4–M^1—CM 42127; M^{1-2}—CM 30943; M^{2-3}—CM 36477; ?associated dP^4, M^1—CM 22311; I/, M/—UCM 45528; P^4—CM 30939, 55192; M^1—CM 22312, 42128, 42133; M^2—CM 22312, 37237, 21113, 35841, 55191; M^3—CM 22310 (2 teeth), 30938, 22313, 55190, 55491; fragmentary upper molars—CM 42129, UCM 46368, 44321 (M/, /M).

Localities.—CM locs. 91, 98, 1048, UCM loc. 80063 (Lostcabinian, Lost Cabin Member); UCM locs. 80089, 81009 (Lostcabinian, Red Creek Facies); CM loc. 34, UCM loc. 80101 (Gardnerbuttean, Lost

Table 3.—*Dimensions of upper teeth of* Esthonyx *and* Trogosus *from the Wind River Formation, Wyoming.*

Specimen no.	Locality	P^4		M^1		M^2		M^3	
		L	W	L	W	L	W	L	W
Esthonyx acutidens									
CM 55192	34	9.0	12.7						
CM 30939	34	9.0	11.3						
CM 42127	34	8.8	12.0						
CM 22311	34	8.4	8.6						
CM 42128	34			8.2	12.6				
CM 30943	34			8.5	12.3	8.9	13.4		
CM 22312	90			9.5	13.9	9.7	15.7		
CM 35841	34					9.7	14.2		
CM 55191	34					8.8	14.2		
CM 22313	91							8.0	15.6
CM 36477	34							7.6	12.9
CM 30938	34							7.5	13.4
CM 22310	34							7.3	13.5
CM 42131	34							7.2	13.0
Esthonyx bisulcatus									
CM 39644	802					8.1	13.0	7.0	12.4
CM 54155	1091							7.2	12.7
Trogosus sp.									
UCM 46536	81028					22.7	36.1		

Cabin Member); CM 90, 857, 1077 (Lostcabinian or Gardnerbuttean, Lost Cabin Member).

Known distribution.—Late Wasatchian—Bighorn Basin (Willwood Fm.), Green River Basin (Wasatch Fm.), Wyoming; late Wasatchian to early Bridgerian—Wind River Basin (Wind River Fm.), Wyoming, Huerfano Basin (Huerfano Fm.), Colorado.

Description and Discussion.—In the Wind River Basin this species is recovered only from the Lost Cabin Member and Red Creek Facies of the Wind River Formation, which, in combination with the restriction of *E. bisulcatus* to the Lysite Member, may be important biostratigraphically.

As was the case with *E. bisulcatus,* none of the material of *E. acutidens* referred here preserves the mandibular symphysis or teeth anterior to P_4. Referral of the material to *E. acutidens* is based on diagnostic criteria on $P^4/_4$–$M^1/_1$ outlined earlier. Compared to *E. bisulcatus,* the teeth of *E. acutidens* from the Wind River Formation are significantly larger, P_4 lacks a metastylid, M_{1-3} have weaker metastylids, and P_4–M_3 are more hypsodont with lingually robust metaconids; the stylar shelves on P^4–M^3, although variable in degree of development, are more expanded, especially in the parastylar area on M^{2-3}.

E. acutidens, the youngest recorded species of the genus, has not been recovered from post-Gardnerbuttean horizons, and apparently became extinct sometime during the earliest Bridgerian (Stucky, 1983). It last appears at one locality (two horizons) in the upper part of the Lost Cabin Member, where it overlaps in range with *Trogosus,* and at Huerfano locality II (McKenna, 1976), where it co-occurs with *Trogosus.*

Trogosus Leidy, 1871

In his review of *Trogosus,* Gazin (1953) named two new species (*T. hillsi, T. grangeri*) from the Huerfano Basin, and cited five species that had previously been described from Bridger B horizons in the Bridger Basin. He recognized two of the latter as valid (*T. castoridens, T. hyracoides*), two as invalid (*T. minor, T. ? vetulus*), and one as questionable (*T. ? latidens*), but later (Gazin, 1976) included *T. latidens* in his comprehensive faunal list for the Bridger Formation.

Robinson (1966), impressed with the degree of variation in the *Trogosus* material from Huerfano, suggested that the differences between *T. hillsi* and *T. grangeri* were probably due to sexual dimorphism, and synonymized the two as *T. grangeri.*

This is the first record of *Trogosus* from the Wind River Basin.

***Trogosus* sp.**
(Table 3)

Referred specimens.—Partial M_1 or M_2, UCM 47717; M^2, UCM 46536.

Localities.—UCM locs. 79040, 81028 (Gardnerbuttean, Lost Cabin Member).

Known distribution.—Earliest Bridgerian—Wind River Basin (Wind River Fm.), Wyoming; see text for occurrences of *Trogosus.*

Discussion.—These two teeth closely resemble comparable parts of the dentition of *Trogosus.* They are much larger than *Esthonyx* and *Megalesthonyx,* and M^2 (Stucky, 1982, Fig. 34) lacks the mesostyle that is characteristic of the latter. The two teeth are closest in size to *T. castoridens* and *T. hyracoides,* but, in the absence of diagnostic features of the skull and dentition (Gazin, 1953), the material cannot be referred to a species of *Trogosus.* Both of the localities at which *Trogosus* occurs are in the upper part of the Lost Cabin Member and are Gardnerbuttean (=early Bridgerian) in age (see below).

BIOSTRATIGRAPHIC IMPLICATIONS

Esthonyx and *Trogosus,* together with certain other taxa, have proven to be reliable indicators of biostratigraphic age. *Esthonyx* is common in most Clarkforkian through Lostcabinian faunas. Its first appearance, along with that of other taxa, marks the onset of the Clarkforkian (Rose, 1981). The *E. xenicus-ancylion-grangeri* lineage is characteristic of the Clarkforkian in the Bighorn Basin (Gingerich and Gunnell, 1979) and becomes extinct in the early Wasatchian. The *E. spatularius-bisulcatus* chronospecies is characteristic of Graybullian and Lysitean horizons, and apparently extends into the Lostcabinian in the Bighorn Basin (Schankler, 1980). The first appearance of *E. acutidens* may mark the beginning of the Lostcabinian; this species is an index fossil of that subage, but it is also known from post-Lostcabinian (Gardnerbuttean) faunas at two localities—one in the Huerfano Formation (Huerfano II), and one in the Wind River Formation (CM. loc. 34, upper part of Lost Cabin Member). Its last appearance (contra McKenna, 1976) is not necessarily indicative of a late Wasatchian age.

Before the Bridgerian Land-Mammal Age was formally named, horizons in the Huerfano Formation (Huerfano B) that yielded *Trogosus,* as well as certain other taxa, were correlated with part of the Bridger Formation (Osborn, 1897, 1909, 1919, 1929; Matthew, 1899, 1909; Simpson, 1933). Subsequently, the Wood Committee (Wood et al., 1941) listed *Tillotherium* (=*Trogosus*) as an index fossil of the Bridgerian, and assigned this age to the fauna from Huerfano B. Robinson (1966), however, concluded that the Huerfano B fauna was representative of a new, latest Wasatchian subage, the Gardnerbuttean, which was younger than the Lostcabinian but older than the Bridgerian. Later, a new record of *E. acutidens* from Huerfano locality II (Huerfano B) led McKenna (1976) to question the utility of the Gardnerbuttean. Huerfano locality II is the only fossiliferous horizon that preserves the co-occurrence of *Esthonyx* and *Trogosus.*

Trogosus has also been recorded from the Aycross Formation (McKenna, 1980; Bown, 1982; CM collections), the Cathedral Bluffs Tongue of the Wasatch Formation (Morris, 1954; Gazin, 1962), Bridger A and B horizons in the Bridger Basin (McGrew and Sullivan, 1971; Gazin, 1976), the Green River Formation (CM collections, Powder Wash, Utah), and possibly from the Arkosic facies of the New Fork Tongue of the Wasatch Formation (Stucky, 1983). The record of *Trogosus* from the Wind River Basin comes from two localities in the upper part of the Lost Cabin Member, UCM locs. 79040 and 81028. The former also preserves *Palaeosyops* (=*Eotitanops,* see Wallace, 1980) *borealis, Hyrachyus* sp. cf. *H. eximius, Antiacodon pygmaeus,* and *Pantolestes* sp. cf. *P. longicaudus.* The M^2 of *Trogosus* is the only known specimen from UCM loc. 81028.

These taxa—*Trogosus, Palaeosyops, Hyrachyus, Antiacodon, Pantolestes*—and others, such as *Helohyus* and *Helaletes,* are restricted in the Wind River Formation to localities in the upper part of the Lost

Cabin Member. All of these taxa appear to be reliable index fossils of the Bridgerian. Most of them occur in faunas of unequivocal Bridgerian age (Gazin, 1976; Bown, 1982; McKenna, 1980; McGrew and Sullivan, 1971) and their first appearance can be used to mark the onset of the Bridgerian (Stucky, 1983). Some faunas—from Huerfano B, Cathedral Bluffs, upper part of the Lost Cabin Member—in which many of these Bridgerian taxa co-occur with typical late Wasatchian mammals, such as *Esthonyx, Shoshonius, Coryphodon, Bunophorus, Diacodexis, Hyracotherium,* and *Phenacodus,* have been assigned alternatively to either the latest Wasatchian (Robinson, 1966; Gazin, 1962; McKenna, 1976) or the earliest Bridgerian (Morris, 1954; West and Dawson, 1973; Gingerich, 1979; Bown, 1982; Stucky, 1982). We opt for the latter conclusion on the basis that the first appearances of the Bridgerian taxa, which apparently occur penecontemporaneously, are more reliable criteria of the Wasatchian-Bridgerian boundary than are the last appearances of the Wasatchian taxa, which are asynchronous and geographically disjunct. In short, the principle advocated here is that the first appearance of taxa through immigration or cladogenesis is a finer correlative tool and biostratigraphic measure than is the extinction and last appearance of taxa, or stage of evolution of taxa within an anagenetic lineage (Repenning, 1967; Savage, 1977; Woodburne, 1977; Rose, 1981).

Accordingly, the faunas from localities in the upper part of the Lost Cabin Member, as well as those from Huerfano B, Cathedral Bluffs, and the Arkosic facies of the New Fork Tongue of the Wasatch Formation (in part) are here considered Bridgerian. They preserve the first appearance of the Bridgerian taxa *Trogosus, Antiacodon, Palaeosyops,* and *Hyrachyus,* and the unique, earliest Bridgerian faunal assemblages that define the Gardnerbuttean (Stucky, 1983).

PHYLOGENETIC RELATIONSHIPS

All North American tillodonts appear to be united in having enlarged $I^2/_2$, strong, broad postcingula and stylar shelves on the upper molars, a talonid basin on P_{3-4}, high arcuate crests and metastylids on the lower molars, and in the loss of $P^1/_1$ and I^1 (Fig. 3, node 1). Two lineages of *Esthonyx,* the most primitive North American tillodont, appear to have diverged in the early Tertiary. One, the *E. xenicus-ancylion-grangeri* chronospecies, retains an unfused mandibular symphysis and a two-rooted P_2, but seems to be derived in having the paraconid on the lower molars close to an anteriorly inflated metaconid (Fig. 3, node 2). The second lineage of *Esthonyx* and all other North American tillodonts (Fig. 3, node 3) are advanced in having a fused mandibular symphysis (to at least below P_3), greatly reduced conules on M^{1-3}, and more hypsodont and deeply basined P_4–M_3, with higher, more arcuate

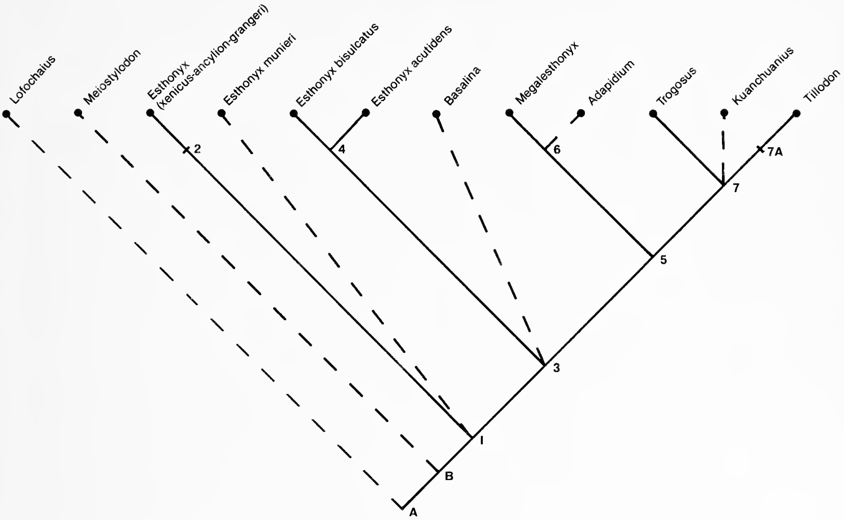

Fig. 3.—Proposed phylogenetic relationships among Tillodontia. *Node A*—P^4–M^3 with wing-like stylar salients, and postcingulum. *Node B*—I_2 enlarged; M^{1-2} with more expanded stylar shelf and postcingulum. *Node 1*—$I^2/_2$ more enlarged; M_{1-2} more hypsodont, with strong metastylid, arcuate paracristid and posthypocristid, reduced hypoconulid; M^{1-3} less transverse; I^1, $P^1/_1$ lost; P_{3-4} with talonid basin (?primitive). *Node 2*—M_{1-3} paraconid closer to anteriorly inflated metaconid; chronocline of increasing size from *E. xenicus-E. ancylion-E. grangeri. Node 3*—Mandibular symphysis fused to below P_3 or P_4; P_4–M_3 more hypsodont, with higher cristids, deeper basins and more U-shaped paracristid; M^{1-3} with reduced conules. *Node 4*—M^{1-3} with expanded stylar salients and deeper ectoflexi; P_2 single-rooted. *Node 5*—$I^2/_2$ enlarged, with restricted band of enamel; P_4–M_3 more hypsodont; M_{1-3} cristid obliqua more lingual, originating from below the metaconid; increase in size; reduction of C_1, P_2, P_4 talonid. *Node 6*—M^{1-2} with mesostyle. *Node 7*—Mandibular symphysis fused to below M_1; $I^2/_2$ greatly enlarged; increase in size; longer I^3-C-P^2 diastemata; P_2 single-rooted; $I^1/_1$, C, P_3 talonid reduced. *Node 7A*—I_3 lost; longer C–P_2 diastema.

cristids and stronger metastylids. *E. bisulcatus* (=*E. spatularius*) and *E. acutidens* (Fig. 3, node 4) have, in addition to these features, expanded stylar salients and deeper ectoflexi on M^{1-3}, and a single-rooted P_2. *E. bisulcatus* appears to be one Graybullian through Lysitean chronospecies; the lack of overlap in size between the latter and *E. acutidens,* and their apparent co-occurrence in Lostcabinian beds in the Bighorn Basin may imply specific distinction and a cladogenetic event.

Remaining tillodonts—*Megalesthonyx, Trogosus, Tillodon* (Fig. 3, node 5)—are much larger and more derived in having a restricted band of enamel on $I^2/_2$ (I^2 not known in *Megalesthonyx*), a cristid obliqua on the lower molars that originates lingually from the metaconid, more hypsodont cheek teeth, and reduced C_1, P_2, and P_4 talonid. In *Mega-*

lesthonyx (Fig. 3, node 6) a mesostyle is developed on the only known upper molar. *Trogosus* and *Tillodon* (Fig. 3, node 7) are still larger, with the mandibular symphysis extending to below M_1, a greatly enlarged $I^2/_2$, single-rooted P_2, longer diastemata between I^3-C-P^2, and reduced $I^1/_1$, C, and P_3 talonid. *Tillodon* (Fig. 3, node 7A) appears to be most advanced in the loss of $I^3/_3$ and in the enlarged C_1–P_2 diastema.

Most non-North American tillodonts are known from relatively poor material. *E. munieri,* based on three isolated teeth from the early Eocene of France, cannot at present be allied with either lineage of *Esthonyx* in North America. *Basalina,* known from a fragmentary dentary with a broken P_4 from the Eocene of Pakistan, has a fused mandibular symphysis (to below P_4), and unreduced C_1, P_2 (double rooted), and P_4 talonid (Lucas and Schoch, 1981). As such, it appears to be less derived than *Megalesthonyx, Trogosus,* and *Tillodon,* and more closely related to *E. bisulcatus* and *E. acutidens* (Fig. 3, node 3). Given the absence of $P^1/_1$ in all known tillodonts (Gazin, 1953), the reconstruction of the dental formula of *Basalina* by Lucas and Schoch (1981) in the diagnosis (p. 90) and their figure (Plate 15, Fig. 2) is questionable. More reasonable is the alternative interpretation (p. 91) of a two-rooted P_2 and the absence of P_1.

Lofochaius and *Meiostylodon,* from the early or middle Paleocene of China (Li and Ting, 1983), are known from P^4–M^3 and from M^{1-2} and I_2, respectively. They are tillodont-like in the enlargment of I_2 and in the wing-like stylar salients and expanded postcingula on the cheek teeth. In comparison to *Esthonyx, Lofochaius,* with transverse upper molars and narrower stylar shelves and postcingula, is the most primitive known tillodont (Fig. 3, node A). *Meiostylodon* retains transverse M^{1-2} and unreduced conules, but approaches *Esthonyx* in the development of the postcingula and stylar shelves, and appears to be intermediate morphologically between *Lofochaius* and *Esthonyx* (Fig. 3, node B). *Esthonyx* and all other tillodonts (Fig. 3, node 1) are more derived, in comparison, in having less transverse P^4–M^3. The other characters listed for this node are not preserved in *Lofochaius* and *Meiostylodon*; some or all may or may not have been present in these taxa.

Adapidium, from the late Eocene of China, has hypsodont lower molars with a lingual cristid obliqua that originates from below the metaconid (Fig. 3, node 5). It appears to be most closely related to *Megalesthonyx* (Fig. 3, node 6) in sharing the development of a mesostyle on at least M^1 (unpublished, unnumbered IVPP specimen), although this may have evolved independently.

Kuanchuanius (see Chow, 1963), from the middle Eocene of China, shares with *Trogosus* (Fig. 3, node 7) the derived features of very large size, a mandibular symphysis that extends to below M_1, a greatly enlarged I_2 with a restricted band of enamel, reduced I_1 and C_1, a single-rooted P_2, and hypsodont lower molars.

The inferred phylogenetic relationships of the four Chinese Paleogene tillodonts may suggest that the origin of tillodonts occurred in Asia during the early Paleocene, and was followed by at least two periods of origin and immigration of North American taxa. *Meiostylodon* and *Kuanchuanius* are suitable morphologically and temporally to be near the ancestry of the larger *Esthonyx* and *Trogosus,* respectively. *Megalesthonyx* appears abruptly in the Lostcabinian of North America and may have shared a common ancestry with *Adapidium.* The presence of a mesostyle on M^2 seems to remove *Megalesthonyx* from the ancestry of *Trogosus* or *Tillodon.* Less plausible is the alternative hypothesis (Rose, 1972), which involves the appearance and subsequent loss of the mesostyle in an *Esthonyx-Megalesthonyx-Trogosus* lineage.

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CAPTORHINOMORPH "STEM" REPTILES FROM THE PENNSYLVANIAN COAL-SWAMP DEPOSIT OF LINTON, OHIO

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ABSTRACT

Two new specimens, plus one previously misidentified as an adelospondylous amphibian bring to four the known captorhinomorph reptile remains in the classic Linton fauna. The skull and jaw specimens are clearly assignable to the Mazon Creek genus *Cephalerpeton,* although specifically distinct from *C. ventriarmatum*; the postcranial specimen conforms to the Linton species *Anthracodromeus longipes.* As the question of possible synonymy between these two nominal genera cannot be resolved on the evidence available, both names are retained *sub judice.* The Linton species designated *Cephalerpeton* aff. *C. ventriarmatum* (of late Westphalian D age) may have been derived from the Mazon Creek species (early Westphalian D) through enlargement of the mandibular teeth and resultant reduction of the dental formula. These agile, lizard-like small reptiles occur as rare erratics in the Linton deposit.

INTRODUCTION

The suborder Captorhinomorpha occupies a unique position in the early evolution of reptiles. The fossil record of this group extends from the Lower Pennsylvanian into the Upper Permian, forming one of the longest reptilian phylogenies within the Paleozoic. The Captorhinomorpha include the oldest known true reptiles (Eureptilia) and are

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closely related to the important synapsid (pelycosaur and therapsid) and diapsid (eosuchian, lepidosaur, and archosaur) lineages. The suborder can be divided into two families, the Protorothyrididae and the Captorhinidae. The protorothyridid genera were formerly included in the family Romeriidae (Carroll and Baird, 1972), but with the removal of the type genus *Romeria* to the Captorhinidae (Heaton, 1979) the family name Protorothyrididae Price, 1937 (emend. Gregory, 1950) becomes the correct designation for this group (Reisz, 1980).

Members of the more advanced captorhinomorph family, the Captorhinidae, occur in large numbers in terrestrial strata of Early to Late Permian age from the equatorial Laurasian land mass (Olson, 1952, 1954, 1962; Olson and Beerbower, 1953; Konzhukova, 1956; Heaton, 1979) and have also been found recently on the Gondwana land mass (Taquet, 1969; Kutty, 1972; Gaffney and McKenna, 1979). The captorhinids form a compact group of structurally similar, relatively specialized, slow, heavy-set reptiles. The structural changes that occur in this family include an approximately five-fold increase in size during the Permian and an increase in the numbers of rows of maxillary and dentary teeth.

The fossil record of the more primitive family, the Protorothyrididae, is restricted to a few specimens from the Pennsylvanian and Lower Permian deposits on the North American and European land masses of Laurasia. The known members of this family also form a compact group of structurally similar animals, but, in strong contrast to the captorhinids, the protorothyridids are relatively generalized, small, agile reptiles. Our current understanding of the Protorothyrididae is based primarily on the studies by Carroll (1964, 1969), Carroll and Baird (1972), and Clark and Carroll (1973).

The Pennsylvanian fossil record of this phylogenetically important group of reptiles appears to be restricted in variety and numbers by their preference for dry ground, away from the environments typically preserved during this period. Only as a result of preservation under unusual circumstances are we able to study a few remains of early protorothyridids. Specimens of *Hylonomus lyelli* and *Paleothyris acadiana* have been recovered from inside *Sigillaria* tree stumps that were preserved in standing position near Joggins and Florence, Nova Scotia, respectively (Carroll, 1964, 1969). A single skeleton of *Cephalerpeton ventriarmatum* has been found in an ironstone nodule from Mazon Creek, Illinois (Gregory, 1948, 1950; Carroll and Baird, 1972). Single, nearly complete skeletons of *Coelostegus prothales* and *Brouffia orientalis* from Nýřany, Czechoslovakia, and a poorly preserved, immature skeleton of *Anthracodromeus longipes* from Linton, Ohio, constitute the only protorothyridid material hitherto known from these famous coal-swamp deposits (Carroll and Baird, 1972). Although the coal-swamp faunas of Linton and Nýřany have been studied for more than a century, and thousands of specimens representing scores of fish and amphibian genera have been collected, only seven specimens of fully terrestrial reptiles have been found. These animals were probably erratics rather than customary members of the aquatic communities with which their remains are associated. The ecologies of the Westphalian coal-swamp deposits in which reptiles occur have been discussed by Westoll (1944), Rayner (1971), and most recently by Milner (1980). A revised list of the tetrapods present at Linton has been published by Hook (1981).

The purpose of this paper is to describe two additional specimens of protorothyridid reptiles that were recently collected at the Linton mine dump by Dr. Richard Lund, together with a previously misidentified specimen in the British Museum collection. Our study was based on high-fidelity latex casts (Baird, 1955) of skeletons preserved as natural molds in carbonaceous shale (Linton) or sideritic mudstone (Mazon Creek).

Abbreviations.—AMNH, American Museum of Natural History; BM(NH), British Museum (Natural History); CM, Carnegie Museum of Natural History; YPM, Peabody Museum of Natural History, Yale University.

Key to abbreviations used in the figures:

a = astragalus
ang = angular
c = calcaneum
ch = chevron
cr = caudal rib
d = dentary
f = frontal
fib = fibula
il = ilium
is = ischium
j = jugal
l = lacrimal
mt = metatarsal
mx = maxilla
p = parietal
pf = postfrontal
p for = parapineal foramen
pmx = premaxilla
po = postorbital
pp = postparietal
prf = prefrontal
prv = presacral vertebra
ptf = posttemporal fenestra
q = quadrate
qj = quadratojugal
sa = surangular
scl = sclerotic plate
sp = splenial
sq = squamosal
st = supratemporal
t = tabular
tib = tibia
v = vomer

Systematic Paleontology

Class Reptilia Linnaeus, 1758
Subclass Eureptilia Olson, 1947
Order Captorhina Olson, 1947
Suborder Captorhinomorpha Watson, 1917
Family Protorothyrididae Price, 1937
Cephalerpeton Moodie, 1912

Figured specimens.—CM 23055 (Fig. 1), a crushed, distorted skull; the left premaxilla, maxillae and lacrimals, right frontal and parietal,

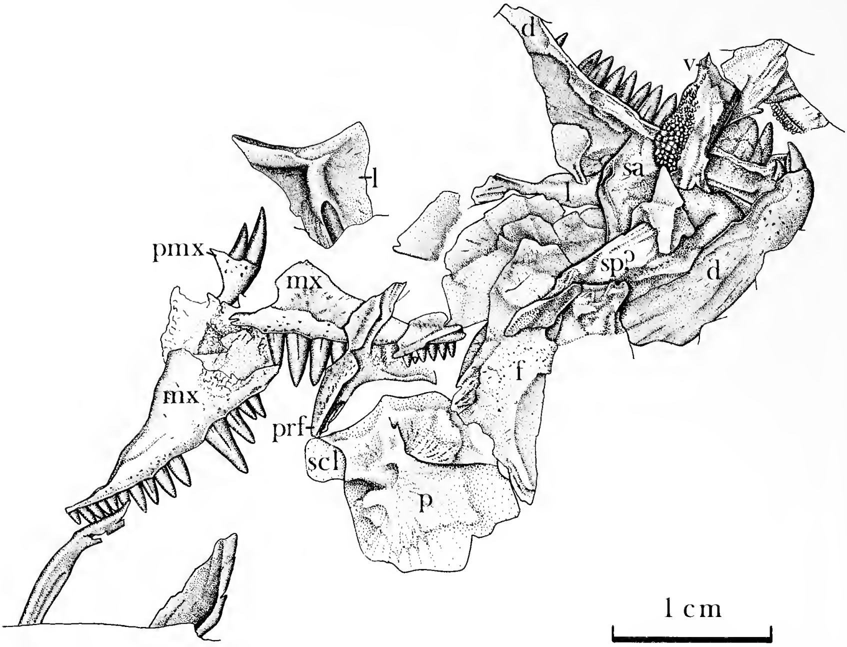

Fig. 1.—*Cephalerpeton* aff. *C. ventriarmatum,* CM 23055, a partial, disarticulated skull.

left prefrontal, right vomer, and a sclerotic plate are identifiable. The mandibles are represented by the dentaries, left surangular, and possibly right splenial. Other skull bones are present but are too badly fragmented for precise identification.

BM(NH) R.2667 (Fig. 2), the anterior part of a right mandible in lingual aspect (purchased as part of the J.W. Davies Collection, 1895). This specimen was mentioned by Steen (1931:885) as the "lower jaw of an Adelospondyl."

Description

Skull.—The identifiable portion of the skull CM 23055 resembles the type specimen of *Cephalerpeton ventriarmatum* (YPM 796) in a number of significant features. As in the type specimen, the maxillary process of the premaxilla is short, with places for only three teeth. Although Carroll and Baird (1972) reconstructed YPM 796 with a long maxillary process of the premaxilla, as is the case in other primitive captorhinomorphs, restudy of the premaxilla reveals that only three teeth can be accommodated on this bone. A three-toothed premaxilla

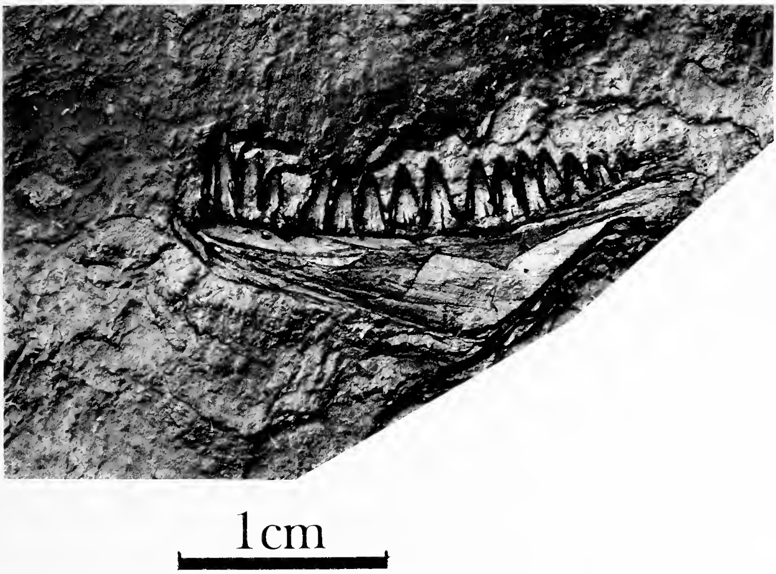

Fig. 2.—*Cephalerpeton* aff. *C. ventriarmatum,* BM(NH) R.2667, right dentary exposed in medial view.

was shown in earlier reconstructions by Gregory (1948, Fig. 2) and Baird (1965, Fig. 6).

The fact that the maxillae are exposed in lateral view in CM 23055, but in partial medial view in YPM 796, makes direct comparisons difficult. In CM 23055 the maxilla, completely separated from the other skull elements, has a large dorsal expansion above the caniniform teeth. The dorsally directed plate of bone is large enough to have extended dorsally to meet the nasal and to have covered the anterior process of the lacrimal that may have extended to the narial opening. In the type specimen of *Cephalerpeton ventriarmatum* the maxillae and lacrimals, exposed in medial view, have remained in articulation so that the external relationship of these bones cannot be established.

The similarity between the left lacrimals in the two specimens, both exposed in medial view, is striking. In YPM 796 the lacrimal duct opens to the interior near the mediodorsal margin of the maxilla and just anterior to the midpoint between the orbit and the external naris. The open groove for the lacrimal duct extends anteroventrally and its ventral margin forms a narrow ridge above the mediodorsal margin of the maxilla. The posterior part of the lacrimal has a long suborbital flange that may have excluded the maxilla from the orbit; much of the orbital margin of the lacrimal is covered medially by a long ventral process of the prefrontal. The same condition occurs in CM 23055. In this specimen the lacrimal duct is only partly covered by bone. A striated region on the medial surface of the lacrimal just ventral to the open region of the lacrimal duct indicates that this area was covered by a medial shelf of the maxilla to give the same arrangement as in *Cephalerpeton ventriarmatum.* A long groove in CM 23055 extends ventrally from the dorsal tip of the orbital margin to the level of the lacrimal ridge; this groove held the ventral process of the prefrontal. The suborbital flange of the lacrimal is also well developed.

The other elements of the skull roof in CM 23055 are not readily comparable with those in the type specimen of *Cephalerpeton ventriarmatum.* In CM 23055 these elements (prefrontal, frontal and parietal) are preserved so as to expose their external surfaces, whereas the same bones in YPM 796 are preserved with their medial surfaces exposed.

The roofing elements have a relatively well developed pattern of sculpturing of low ridges and small pits. The prefrontal has part of its anterior and posterior dorsal processes exposed, in addition to the long ventral process which forms part of the anterior orbital margin. The frontal has a pair of well developed, long grooves along its lateral margin for the attachment of the prefrontal and postfrontal. Between these grooves the frontal has a short, laterally directed process that forms part of the dorsal orbital margin. The medial margin of the badly crushed right parietal is overlapped by the frontal; its features are analyzed in detail in a subsequent section. Overlapping the posterolateral corner of the parietal is a sclerotic plate that is similar to those preserved in YPM 796; it is a thin, subrectangular bone with a bevelled edge.

Mandible.—Parts of the mandibles preserved in CM 23055 include both dentaries and fragments of the right surangular and splenial. Although both dentaries are partially covered by surrounding elements, sufficiently large portions of the left medial and right lateral surfaces are exposed to describe this element. The dentary is unusually deep dorsoventrally throughout its length. In association with this unusual depth, the anterior portion of the dentary near the symphysis is somewhat more massive than in other protorothyridids of similar size; more significantly, the dentary is twice as deep dorsoventrally at the level of the twelfth tooth than at the third. Although all skull elements are severely crushed, preservation cannot account for the unusual proportions of the dentary. The dorsal edge of the dentary is concave in lateral view, providing additional evidence of the unusual depth of the mandible in the posterior half of the dentary, and probably in the rest of the mandible. The alveolar shelf is also unusually large, as exposed on the left dentary, and its sutural surface with the splenial is extensive.

Only the left dentary is sufficiently exposed to indicate that it had places for 17 or 18 teeth. The thirteenth tooth of this dentary has been figured by Currie (1979, Fig. 13b), greatly magnified, to illustrate the pattern of vertical lingual striations on teeth of most Paleozoic reptiles. A nearly complete right dentary is exposed in medial view in BM(NH) R.2667 (Fig. 2). This element is identical to the left dentary of CM 23055, showing the typically deep subalveolar expanse of bone, and the large teeth with infolding of the enamel. As in CM 23055, there is only place on the dentary of BM(NH) R.2667 for seventeen teeth. Unfortunately the symphysis is not preserved.

The right surangular is partially exposed between the dentaries of CM 23055. Gentle striae on its surface radiate from the slightly grooved dorsal margin; the groove probably represents the area where the coronoid attached. The identification of another fragment lying between the dentaries as the right splenial is tentative. Longitudinal striations near its dorsal edge correspond to the expected sutured area with the alveolar shelf of the dentary.

Dentition.—The most significant similarity between CM 23055 and YPM 796 is their dentition. In both specimens there are places for three premaxillary and 16 maxillary teeth. This is far below the number in other primitive captorhinomorphs—*Hylonomus* has a dental formula of 5 + 36, *Paleothyris* has 6 + 35, and *Protorthyris* has 5 + 30 (Carroll and Baird, 1972; Clark and Carroll, 1973). In both specimens the first premaxillary tooth is large, roughly equal to the caniniform tooth on the maxilla, and much larger than in other primitive captorhinomorphs. The larger teeth show some infolding of the enamel. The palatal dentition is also quite similar in the two specimens, with closely packed small denticles covering most of the vomers.

Discussion

Similarities between CM 23055 and BM(NH) R.2667 from the Middle Pennsylvanian (late Westphalian D) deposit at Linton, Ohio, and YPM 796 from a slightly older horizon (early Westphalian D) at Mazon Creek, Illinois, indicate that these reptiles can be placed in the same genus. There are, however, some significant features that distinguish the Linton specimens from *Cephalerpeton ventriarmatum*. The preserved portion of the dentaries in CM 23055 and BM(NH) R.2667 demonstrates that the lower jaw was deeper dorsoventrally than the corresponding portions of the lower jaw in *C. ventriarmatum*. The teeth on the lower jaws of the Linton specimens are also larger and fewer in number than those of *C. ventriarmatum*. In the latter species the teeth on the dentaries are not substantially different from those in other protorothyridids, but there are places for only 21 or 22 teeth on the dentary, a much lower number than in other genera (Carroll and Baird, 1972). The dentaries of the skull from Linton (CM 23055) have places for no more than 18 large teeth (the exact number is uncertain), whereas the British Museum dentary has 17 (with possibly one more concealed at the posterior end). In these features the Linton specimen appears even more advanced than *C. ventriarmatum.* These differences are compatible with a postulated ancestor-descendant relationship in which the geologically older species is understandably more primitive in certain osteological features.

Anthracodromeus Carroll and Baird, 1972

Figured specimen.—CM 25282 (Fig. 3), consisting of one dorsal and ten caudal vertebrae, caudal ribs, chevron bone, scattered ventral scales, and parts of the pelvic girdle and hind limbs.

Description

CM 25282 includes a single posterior dorsal vertebra which has the general proportions characteristic of all protorothyridid captorhinomorphs. The centrum is a relatively long, low cylinder, pinched in at the middle. The neural arch is not swollen, and the neural spine is relatively tall and blade-like. The shape of the neural spine is remarkably similar to those of the dorsal vertebrae in the type specimen of *Anthracodromeus longipes* (AMNH 6940). As shown by Carroll and Baird (1972), neural spines of the dorsal vertebrae are hatchet-shaped, expanding anteroposteriorly from normal-sized bases to wide summits. This feature of the neural spines distinguishes *Anthracodromeus* from all other protorothyridids.

The lateral surfaces of the neural spines in the type specimen of *Anthracodromeus longipes* have a peculiarly "sculptured" or "hammered" appearance. In our opinion this very unusual feature can be accounted for by the poor ossification and manner of preservation of the type skeleton (which is obviously that of a very immature animal). In such a juvenile individual the perichondral bone sheathing the neural spines would be so thin that, when subjected to severe compression (as is typical in Linton material), it would become imprinted with the spongy texture of the interior. CM 25282 is nearly twice as large as the type specimen and is well ossified, so crushing during preservation has not produced the same appearance on its neural spines.

Seven anterior caudal vertebrae are preserved in nearly perfect articulation. Although they are incomplete, significant osteological features can be determined: The ratio of the length to posterior height of the centrum is almost 2:1. The centra have diminished in diameter, indicating that the tail was probably long and slender. The neural arches are long, narrow structures with slender zygapophyses and relatively tall neural spines. The best preserved neural spine, seen on the sixth

Fig. 3.—*Anthracodromeus longipes,* CM 25282, scattered vertebrae, pelves, hind limbs, and scattered ventral scales.

vertebra of the series, has the same height as that of the isolated dorsal vertebra, but its profile tapers upward so that its summit is less than half as expanded as that of the dorsal vertebra. The three most anterior vertebrae of the series have well developed transverse processes for the posteriorly curved caudal ribs. The two most posterior vertebrae have short, small lateral stumps on the centra which probably represent transverse processes. Three isolated caudal vertebrae are probably from the mid-portion of the tail; their centra are still quite long, but there are no remnants of transverse processes and the neural spines are very short.

All three elements of the left pelvis are partially exposed in lateral view; none of their sutures is visible. The only distinctive feature of this pelvis is the shape of the iliac blade, which expands posterodorsally above the acetabulum. The medial surface of the right iliac blade, also exposed in CM 25282, shows a series of grooves near its top that are probably for the attachment of epaxial musculature. In all these features this pelvis is similar to that of *Coelostegus prothales* Carroll and Baird (1972) from the coal-swamp deposits of Nýřany, Czechoslovakia.

The ilia in the type specimen of *Anthracodromeus longipes* appear to be quite different from that of CM 25282. As described and illustrated by Carroll and Baird (1972), they consist of a small acetabular portion joined to a long, narrow iliac blade. A re-examination of the specimen, however, indicates that what was interpreted as the entire blade is only its stout posterior ramus; anterior to this a thinner dorsal flange can be made out by collating the part and counterpart of the specimen. As re-interpreted, the iliac configuration appears to be compatible with that of CM 25282, if allowance is made for the great ontogenetic difference between the two individuals; its anteroposterior width is sufficient to accommodate two sacral ribs. This is at variance with Carroll and Baird's interpretation of the sacral region; their reconstruction of the ilium with a long, narrow, posterodorsally oriented blade could only accommodate one sacral rib. Two sacral ribs are, however, present in the type of *Anthracodromeus longipes,* giving added support to the above interpretation. We must emphasize the difficulty of interpreting an area that is feebly ossified, squashed flat against the vertebrae and femora, and obscured by pyritization.

All the limb elements are strongly crushed and distorted, making most morphological comparisons impossible. The femur appears to be long and slender. The tibia and fibula are considerably shorter than the femur, only about 56% as long; this proportion is characteristic of protorothyridids. The tibia has a wide proximal head and a slightly narrower distal end. The proximal end of the fibula appears narrow, whereas the distal end is broad and blade-like. The calcaneum, as in *Paleothyris,* (Carroll, 1969) is distinctive in having a distolateral notch. This notch, not found in other primitive reptiles, separates the distal surface of articulation with the fourth and fifth distal tarsals from the lateral edge of the calcaneum. The astragalus is partially obscured by the tibia, but it was undoubtedly L-shaped. The size of the distal end of the fibula indicates that the proximal fibular articulation of the astragalus was smaller than the tibio-astragalar articulation and that the neck of the astragalus was narrow, as in *Paleothyris.* The metatarsals are long and slender elements, the third metatarsal being nearly equal in length to the fibula, as in other protorothyridids.

Comparisons

The total eureptilian sample known from the Linton mine deposit, near Wellsville, Ohio, consists of seven specimens, three of which are pelycosaurian (Reisz, 1975) and four protorothyridid; all are fragmentary, and only the type of *Anthracodromeus longipes* includes the major part of the (very juvenile) skeleton. With such a small sample and such incomplete specimens it is difficult to judge the number of protorothyridid taxa present, either on anatomical evidence or on the basis of probabilities.

Once the apparent difference between ilia has been resolved, CM 25282 is reasonably assignable to "*Sauropleura*" *longipes* Cope, a species that was tentatively transferred to *Cephalerpeton* by Baird (1958) and was subsequently made the type species of *Anthracodromeus* by Carroll and Baird (1972). The skull specimen from Linton (CM 23055) and the isolated mandible (BM[NH] R.2667) are clearly assignable to the Mazon Creek genus *Cephalerpeton* although they differ significantly from the species *C. ventriarmatum.* The question thus arises: are there actually two protorothyridid genera present in the Linton fauna, or are *Cephalerpeton* and *Anthracodromeus* to be synonymized on the basis of the new evidence? To answer this requires a further examination of such anatomical features, both cranial and postcranial, as can be compared in the specimens at hand.

Skull.—As shown in Fig. 4, the type skull of *Anthracodromeus longipes* is truncated by the edge of the slab. During compression the cheek (with which the mandible remained articulated), was folded under the skull table, and the two sheets of delicate bone were compressed together so forcibly that the rim of the parapineal foramen embossed a circle on the jugal. The only skull element that is present in both this specimen and the new skull of *Cephalerpeton* from Linton is the right parietal.

In the latter specimen (Fig. 1), the disarticulated parietal lies with its dorsal surface uppermost and its anteroposterior axis pointing toward five o'clock; its medial margin is overlapped by the frontal so that only part of the heavily-rimmed parapineal foramen is exposed. The posterior margin of the parietal, which faces the prefrontal as the specimen lies, has its sculptured surface rabbeted by two semicircular embayments for the articulation of overlapping elements. These rabbets are floored by a posterior continuation of the parietal, as is indicated by the way the striations radiate from the center of ossification. This posterior configuration of the parietal is similar to that seen in *An-*

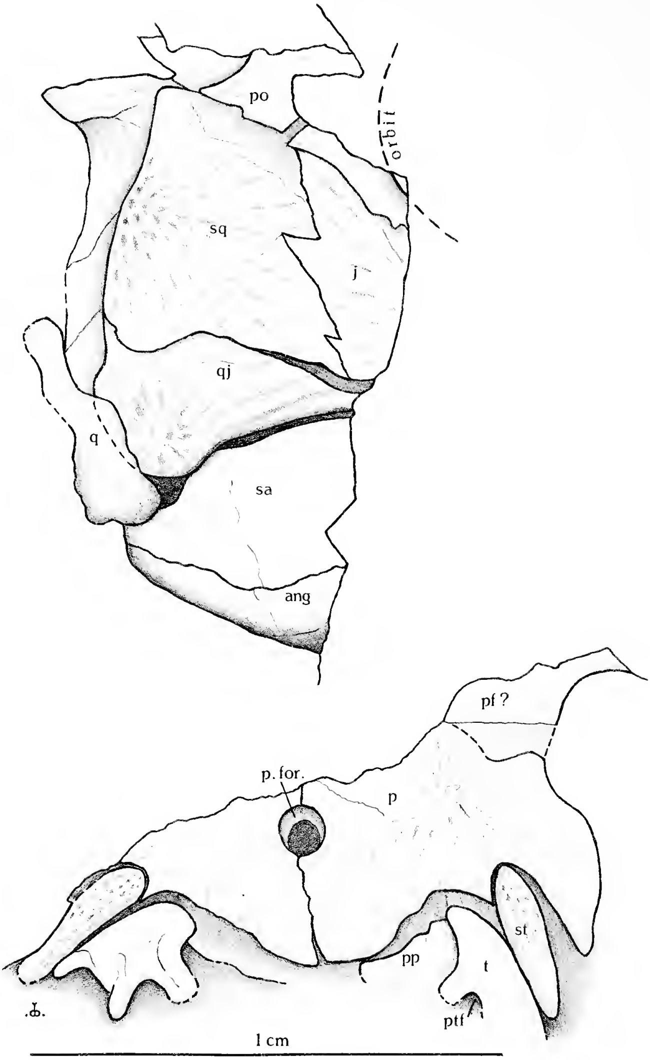

Fig. 4.—*Anthracodromeus longipes,* AMNH 6940, partial skull from holotype skeleton, part and counterpart.

thracodromeus longipes (Fig. 4), where the more lateral embayment accommodates the supratemporal, while the more medial one, which is doubly curved, accommodates both the postparietal and the dorsal process of the tabular. On the anterior margin of the parietal, in CM

23055, are shallow articular facets for the overlapping frontal and postfrontal, and on the anterolateral corner is one for the postorbital. The long parietal lappet seen in *A. longipes* is not in evidence in CM 23055, but this area is concealed by a sclerotic plate.

The parietal of CM 23055 has all the landmarks of the corresponding elements in the protorothyridid genera *Hylonomus, Brouffia, Coelostegus* and *Paleothyris,* although it differs significantly from them in proportions, being conspicuously short relative to its width. In the type of *C. ventriarmatum* the shape of the parietal has had to be reconstructed from the configuration of the surrounding elements (Carroll and Baird 1972, Fig. 2). The restoration shows it as broader than it is long; but a reconsideration of the palate indicates that the skull has been made too wide in this region. Thus the true proportions of the parietal in *C. ventriarmatum* are too conjectural for valid comparisons to be made. Similarly, in the type of *A. longipes* the parietal has been reconstructed as broad and short (Carroll and Baird 1972, Fig. 5); but as the anterior part of the bone is missing, its actual proportions remain uncertain. Thus the parietal, the only cranial element that permits the two skulls from Linton to be compared with the one from Mazon Creek, is too incompletely preserved to provide a sound basis for taxonomic judgement.

The cheek region is similar in the type specimens of *C. ventriarmatum* and *A. longipes.* It differs from the cheeks of other Pennsylvanian protorothyridids in being short anteroposteriorly. This shortening of the cheek would be consistent with a shortening of the skull table (for which, as noted above, direct evidence is lacking).

Mandible.—The only part of the mandible that can be compared directly in CM 23055 and the type of *A. longipes* is the posterodorsal area of the surangular. In both these specimens the mandible appears to be slightly deeper than in other protorothyridids. Given the incomplete nature of the cranial remains of these specimens little reliance can be placed on small proportional differences. In the type of *Cephalerpeton ventriarmatum* the lower jaw does not appear to be deeper than in other protorothyridids; this condition corresponds to the relatively unspecialized mandibular dentition present in this species.

Vertebrae.—As *Anthracodromeus* has been said to differ from *Cephalerpeton* in having hatchet-shaped neural spines and elongate limbs, these postcranial characters require reexamination. In the type specimen of *C. ventriarmatum* the neural spines are preserved only on the axis and the seven succeeding vertebrae, so our comparisons must be restricted to this region. Only in vertebrae 7 through 9 are the profiles of the neural spines clearly recorded: here the summits of the spines are *not* expanded anteroposteriorly. In the more anterior cervicals the situation is less clear. In the corresponding region of the type specimen of *A. longipes* the neural spines are irregular and their summits expanded, but to a lesser extent than those of the more posterior vertebrae (compare Figs. 1 and 4A in Carroll and Baird 1972). Thus the difference, though real, is not great, and it may be accentuated by the fact that the first specimen is three-dimensionally preserved while the second is crushed paper thin.

Forelimb.—In the type of *A. longipes* the humerus is 8 trunk-centra long; it articulates closely with a radius and ulna that are at least 5 trunk-centra long. The ends of all these elements are convexly rounded. In *C. ventriarmatum* an impression of the fleshy forelimb surrounds the bones, so their relative positions are probably close to natural. The humerus is 6.7 trunk-centra long; it is separated by a gap from a radius and ulna that are 4.7 trunk-centra long, and these in turn are widely separated from the metacarpals. The gaps between the bones are plain evidence of incomplete ossification. The ends of the limb bones are concave, indicating that the type of *C. ventriarmatum* may have been even more immature than the type individual of *A. longipes.* This difference in levels of ossification may account for the differences in limb proportions. On the other hand, the vertebrae of *A. longipes* appear to be more severely compressed than those of *C. ventriarmatum.* This difference in crushing would tend to impart greater apparent length to the centra of *A. longipes,* giving a falsely low limb to vertebral length ratio of this long limbed form. These probable differences in levels of ossification, preservation and compression, make comparisons between limb to central length ratios difficult.

The foregoing comparisons lead us to conclude that, although there are similarities between the type species of the nominal genera *Cephalerpeton* and *Anthracodromeus,* the evidence to justify a positive statement of synonymy or non-synonymy is either lacking or ambiguous. This is partly because the Protorothyrididae are inadequately represented in the fossil record, the morphological variation of particular taxa is unknown, and the known specimens are difficult to compare as a result of their fragmentary nature. It is not possible, therefore, to differentiate the morphological similarities that are indicative of relationships at the familial level from those that are indicative of relationships at generic or specific levels. In such a doubtful case the taxonomically *parsimonious* course would be to opt for a tentative synonymy, while the *conservative* course would be to retain both generic names until further evidence is forthcoming. Lacking strong convictions either way, we choose the second course. Rare though these reptiles are, their source localities are still yielding specimens to diligent collectors; so we may reasonably hope that future finds will clarify the issue.

In the preceding pages we have demonstrated the presence at Linton of a reptile that is unquestionably assignable to *Cephalerpeton* although it differs from *C. ventriarmatum* in species-level characters. In view of the possibility that this species may prove to be Cope's "*Sauropleura*" *longipes* we refrain from proposing a new specific name, but merely designate it as *Cephalerpeton* aff. *C. ventriarmatum* to indicate its distinctness from the type species.

REVISED DIAGNOSES

Cephalerpeton Moodie, 1912

Type species.—Cephalerpeton ventriarmatum Moodie, 1912

Diagnosis.—Protorothyridid captorhinomorph reptile characterized by short cheek, dorsally enlarged maxilla, very large marginal teeth with plicate enamel, reduced dental formula of three premaxillary and 16 maxillary teeth, heavily denticulated vomer, and long limbs.

Cephalerpeton ventriarmatum Moodie, 1912

Diagnosis.—Mandibular dentition relatively unspecialized; mandible shallower, with 21 or 22 teeth.

Horizon.—Ironstone nodules of Francis Creek Shale overlying Number 2 (Wilmington or Colchester) Coal, Carbondale Formation, Allegheny Group, Middle Pennsylvanian (early Westphalian D).

Locality.—Banks of Mazon Creek, Grundy County, Illinois.

Cephalerpeton aff. ***C. ventriarmatum***

Diagnosis.—Shorter maxillary enclosure of lacrimal duct than in *C. ventriarmatum*; dentition more specialized with relatively larger teeth; dentary deeper, with place for 17 teeth.

Horizon.—Carbonaceous shale underlying Upper Freeport Coal, Freeport Formation, Allegheny Group, Middle Pennsylvanian (late Westphalian D).

Locality.—Diamond Mine (Linton) near Wellsville, west bank near mouth of Yellow Creek, Saline Township, Jefferson County, Ohio: NE corner Sect. 13, T9N, R2W.

Anthracodromeus Carroll and Baird, 1972

Type species (monotypic).—*Sauropleura longipes* Cope, 1874.

Diagnosis.—Protorothyridid captorhinomorph reptile characterized by short cheek, hatchet-shaped dorsal neural spines, and very long limbs and feet.

Horizon and locality.—As for *Cephalerpeton* aff. *C. ventriarmatum.*

LIFE HABITS

Protorothyridid captorhinomorphs are considered to have been small, agile, terrestrial animals that fed largely on arthropods (Carroll, 1969; Carroll and Baird, 1972). Their gracile bodies, long limbs and high degree of ossification of the skeleton in the better known genera imply that protorothyridids were agile runners and tree climbers like the extant small, terrestrial and arboreal lizards. A terrestrial habitat is also suggested by the occurrence of the Pennsylvanian protorothyridids *Hylonomus* and *Paleothyris* in the hollows of upright *Sigillaria* stumps at Joggins and Florence, Nova Scotia. Too much should not be made of this point, however, for the same trees contain skeletons of evidently amphibious or aquatic labyrinthodonts—the edopoid *Dendrerpeton* and the embolomere *Calligenethlon* at Joggins, the edopoid *Cochleosaurus* and an unnamed embolomere at Florence (Museum of Comparative Zoology material).

Dietary habits of Paleozoic reptiles are difficult to establish in the absence of direct evidence, such as stomach contents. Speculations on preferred diets are generally based upon the known contemporaneous faunas as well as the skeletal morphology and dental patterns of the forms in question. It is generally assumed that the protorothyridids were insectivorous, although comparisons with modern lizards indicate that they were probably capable of preying on a variety of small terrestrial animals, including tetrapods. The marginal dentition seen in *Cephalerpeton* is considerably larger and more robust than those of other protorothyridids or of modern insectivorous lizards. The size and morphology of its skull and dentition indicate that *Cephalerpeton* was able to feed not only on arthropods, but also upon smaller terrestrial vertebrates, such as some of the lepospondyl amphibians, or young individuals of protorothyridids. An appropriate menu of insects occurs in association with the reptiles in the Mazon Creek and Nýřany deposits. At Linton, however, insect remains are absent, although the fauna includes infrequent specimens of more heavily sclerotized arthropods, such as diplopod myriapods (Baird, 1958*a*; Hoffman, 1963), and a pygocephalomorph crustacean (Brooks, 1962:199). It seems likely that the robust dentition of *Cephalerpeton* was able to deal with relatively hard-shelled arthropods of this sort. Myriapods are among the more common terrestrial arthropods in the Braidwood fauna of Mazon Creek, and many of them, such as *Euphoberia* and *Acantherpestes,* have spinescent exoskeletons that presumably developed as a defense against predation (Rolfe, 1980; Hannibal and Feldmann, 1981). The number of terrestrial predators against which such defenses might have evolved is limited, but it includes the dissorophid labyrinthodonts (Carroll, 1964), terrestrial microsaurs such as *Tuditanus* (Carroll and Baird, 1968), the smaller pelycosaurs (Reisz, 1972, 1975), and the protorothyridids.

On the other hand, millipedes are notoriously deliberate pedestrians, probably requiring little speed or agility to catch. As *Anthracodromeus* obviously had both a slender, lightly built body and long limbs it was able to capture agile invertebrates such as the fleet and nimble cockroaches (Blattaria) that abounded in fossil localities of Westphalian age. Although not preserved at Linton, cockroaches are plentiful in the Mazon Creek sediments where they constitute 21% of the insect fauna (Richardson, 1956). It seems most likely that these specialized protorothyridids had evolved their long limbs more as adaptations for predation than as a means to escape from predation. Their potential predators, primarily the haptodontine and ophiacodont pelycosaurs, were evidently much less agile than *Anthracodromeus.*

In addition to long legs, *Anthracodromeus* had feet that are remarkable for their length and areal extent when compared to its slight body weight. Both manus and pes are almost completely represented in the type specimen and have been reconstructed by Carroll and Baird (1972: Fig. 5). Although in life the feet would have been more compact laterally and the metapodials less splayed-out than they appear in that reconstruction, the reptile was doubtless able to scamper over boggy or muddy surfaces where other tetrapods would have become mired.

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