SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 151, NUMBER 1

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Research Fund

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(WITH 5 PLATES)

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PORT CITY PRESS, INC.
BALTIMORE, MD., U. S. A.

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ABSTRACT

The brachiopod genus *Stringocephalus* is reported in Indiana for the first time. This discovery is of great importance as it places this important Devonian marker of the Givetian Stage in the Devonian sequence of the eastern United States. The Indiana occurrence of *Stringocephalus* is below the Logansport Limestone, but overlies Silurian rocks. Comparison of the fossils accompanying *Stringocephalus* in Indiana with those of other formations in the United States and Canada indicates a close correlation with the Rogers City Limestone of Michigan and the Winnipegosis Formation of Manitoba. Correlation of *Stringocephalus* fauna in Indiana with that of Rogers City in Michigan indicates *Stringocephalus* in Indiana lies in the midst of the Cazenovia Stage of the Devonian.

One new species of *Subrensselandia* is described and the specimens of *Stringocephalus* are described and discussed.

INTRODUCTION

Since the discovery of Devonian rocks in eastern United States the exact position of *Stringocephalus* has been a matter of speculation because no specimens have hitherto been found. *Stringocephalus* is a large and distinctive brachiopod that is generally regarded as the leading fossil of the Givetian Stage of the Middle Devonian.[1] This genus is worldwide in distribution and is well known or common in many localities in Europe and Asia. It is also known from Australia

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[1] Also reported but rare in the Eifelian (Struve, 1961).

and north Africa and occurs more rarely in western United States and Alaska (Kirk, 1927). In western and northwestern Canada (Warren and Stelck, 1962; Crickmay, 1960) it is common in places and occurs through a fairly thick sequence of rocks. It has, however, until now, not been seen in the United States east of the Great Basin. Its report from Minnesota by Schuchert (1897, p. 417; Stauffer, 1922, p. 408) has never been authenticated. Consequently, the discovery of this important brachiopod by the second author helps to bring some of the stratigraphic problems of the Devonian of eastern United States into better focus. Some questions, however, are still left unanswered. It further supports the contention (Cooper, in Cooper et al., 1942, p. 1784) that the earliest occurrence of *Stringocephalus* in eastern United States is in the midst of the Cazenovia Stage.

In the winter of 1963 the second author reported to the U.S. National Museum discovery in the Wabash Valley of Indiana of a large brachiopod from limestone hitherto classified as Onondaga (Jeffersonville) by E. M. Kindle (1900) or Hamilton by Cooper and Warthin (1941). Although the first specimens submitted are mostly fragmentary and poorly preserved, they are unmistakably *Stringocephalus*. They indicate a shell about 3 inches wide, 2½ to 3 inches long, and 1 to 2 inches thick. The pedicle valve has an enormous, long, duplex septum which might be mistaken for the Silurian genus *Pentamerus*, often common in rocks subjacent to those containing *Stringocephalus* in Indiana. The brachial valve is provided with a long forked cardinal process.

A further discovery by the second author of the large brachiopod *Subrensselandia* in the same limestone that contains *Stringocephalus* adds additional information of great importance in the stratigraphy of the Devonian.

In June following the initial discovery, a party from the U.S. National Museum consisting of Drs. J. T. Dutro and W. A. Oliver, Jr., of the U.S. Geological Survey and G. A. Cooper was guided by Phelan to important localities. Although no first-rate specimens of *Stringocephalus* were taken, its position in the sequence is now established. Additional fossils were discovered that permit correlation of the *Stringocephalus*-bearing limestone with formations in the United States and Canada.

Localities.—*Stringocephalus* was taken from the upper 18 inches of a gray limestone abounding in stromatopores on the west side of the France Stone Company Quarry, on the north side of U.S. Highway 24, 2 miles east of the city limits of Logansport, Logansport (7½′)

Quadrangle, Ind. (USNM Cooper locality 381a). The west side of the quarry has long been abandoned and the exposed upper surface of the gray limestone has been weathering for many years, a fact that helped to make the *Stringocephalus* visible.

The following section of the gray *Stringocephalus*-bearing limestone was measured on the west wall of the quarry:

	Feet
Post-gray limestone	
C. Pinkish or cream colored coarsely granular limestone in patches	0.5
Gray limestone	
B. Gray, fine-grained limestone containing abundance of stromatopores (pl. 1, fig. 2) of all sizes up to 4 feet, a few corals, both solitary and colonial, and *Stringocephalus* in the upper 18 inches only. Corals and stromatopores usually upset or upside down; bedding crude or nonexistent. Uppermost surface with scattered fish fragments and sand patches	10
A. Gray sandy limestone, the sand grains frosted and well rounded, often in patches or in small channels, resting on an irregular surface with at least 6 inches of relief	5
Silurian (Kokomo) dolomite	

At this place the corals make up less than 10 percent of the coralline materials. The limestone might be described as a coralline conglomerate because the corals and stromatopores are essentially boulders in their helter-skelter orientation. On the west side of the quarry *Stringocephalus* occurs in two well-defined patches. The one on the southwest side is characterized by abundance of the twiglike stromatopore *Amphipora* (pl. 1, fig. 1), but this fossil does not occur at the patch on the northwest side.

The gray limestone is well displayed in the general vicinity of the quarry. Good exposures may be studied southwest of the quarry where the Pottawatomie Point Road, 1.35 miles east of Logansport city limits, cuts through 11 feet of the gray limestone about ¼ mile south of the intersection with U.S. Highway 24. On both sides of this cut and in the field and woods on the west side of the road *Subrensselandia* is abundant 6½ feet below the top (USNM Cooper locality 391b). The gastropods *Mastigospira* and *Buechelia tyrrellii* (Whiteaves) and the large, distinctive pelecypod *Liromytilus attenuatus* (Whiteaves) occur in the topmost layer. Good exposures also appear on the Fry Farm on the east side of the Cass Station Road, ¼ mile south of its junction with U.S. Highway 24, 3 miles east of Logansport City limits (USNM Cooper locality 391c). Here the large gastropod *Omphalocirrus manitobensis* (Whiteaves) occurs and large *Paracyclas* sp. is common.

A single valve of *Stringocephalus* (146119) was found on the upper surface of the gray limestone 0.2 mile west of Pottawatomie Point Road on a small knob (USNM Cooper locality 391e), demonstrating its presence above *Subrensselandia* but at the same level as *Liromytilus.*

Stratigraphic relationships of the gray *Stringocephalus*-bearing limestone.—The gray limestone rests unconformably on Silurian dolomite and is overlain unconformably by the Middle Devonian Logansport Limestone described by Cooper and Warthin (1941, p. 259). The Logansport Limestone, the fauna of which is well dated as lower Ludlowville in age by reference to the New York Devonian, thus gives a definite ceiling to this occurrence of *Stringocephalus* and *Subrensselandia.* The positioning of these two fossils in relation to beds lower in the Devonian can only be obtained by elaborate correlations as detailed below.

Cooper and Warthin (1941) selected as type section of the Logansport Limestone the good display at Pipe Creek Falls about 7 miles southeast of Logansport. This section includes 1 to 6 feet of stromatopore and coral-bearing gray limestone at the base followed by richly fossiliferous, cream-colored granular limestone. The basal bed has all the lithological characters of the *Stringocephalus-Subrensselandia*-bearing beds, but these important fossils were not seen.

In the France Stone Quarry the *Stringocephalus*-bearing gray limestone is overlain by granular limestone containing the characteristic fossils of the Logansport Limestone. Strong unconformity is shown at the contact of the Logansport and the *Stringocephalus*-bearing gray limestone by truncation of corals and stromatopores, sand patches, and scattered fish debris in the top of the gray bed. Cooper and Warthin included the gray limestone in their Logansport Formation, but it is evident that it must be divorced from this association. The fauna of the Logansport, which does not include that of the gray limestone from which Cooper and Warthin had only unidentified corals and stromatopores, has been clearly established to be the

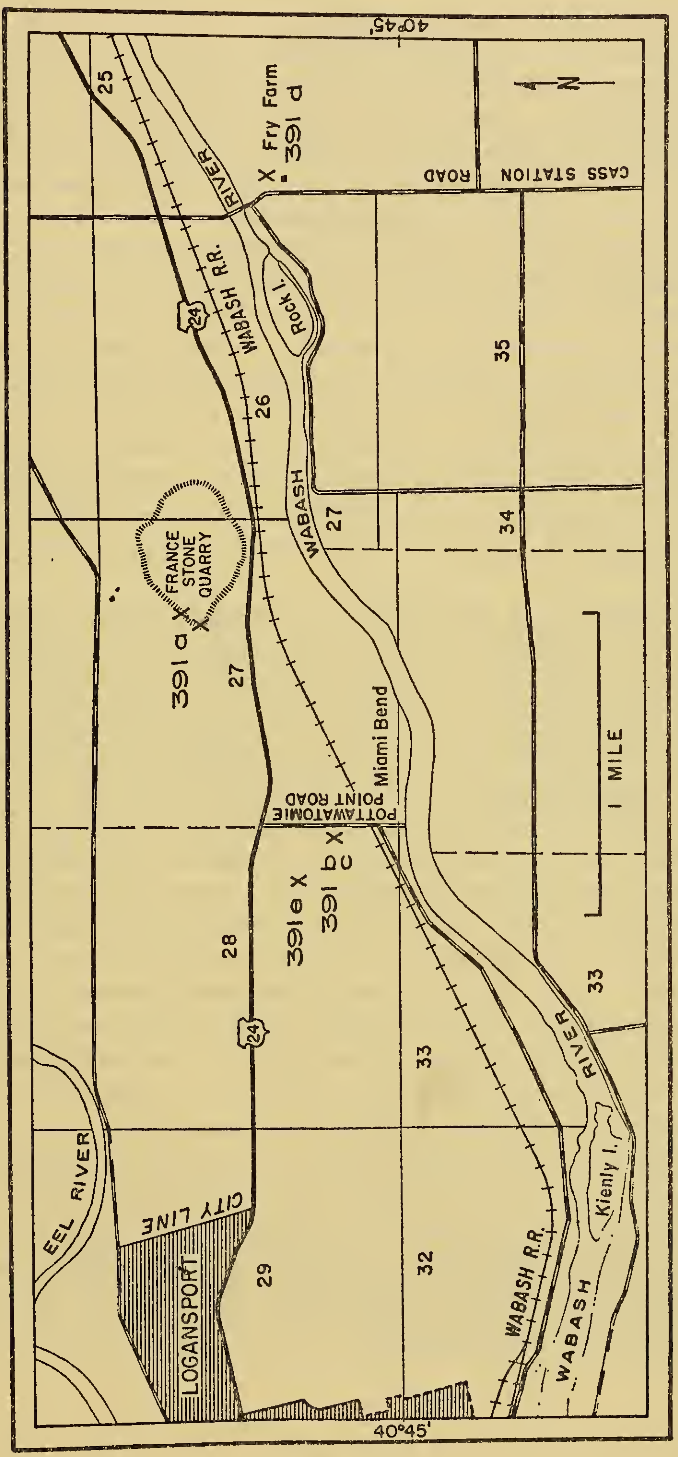

Fig. 1.—Map showing France Stone Quarry and surrounding country with localities of the Miami Bend Formation.

same as that of the Centerfield Member of the Ludlowville Formation of New York, the Hungry Hollow Formation of southwestern Ontario, Canada, the Four Mile Dam Limestone of eastern Michigan, and the Beechwood Limestone of the famous Falls of Ohio section in southern Indiana and northern Kentucky (Cooper and Warthin, 1942). Kindle (1900) originally dated all of the Logansport as Onondaga in age, equal to the Jeffersonville Limestone of the Falls of Ohio area. On the contrary, Cooper and Warthin (1941, p. 259) and Campbell (1942, p. 1068) showed that Kindle's leading Jeffersonville guide fossil, *"Spirifer acuminatus,"* is in reality one of the *Spinocyrta granulosa* tribe characteristic of the Hamilton group. Associated species also proved to be Hamilton rather than Onondaga species. They (Campbell, 1942, p. 886) also showed that the fauna accompanying Kindle's *"S." acuminatus* is the widespread Centerfield fauna. Thus the *Stringocephalus-Subrensselandia*-bearing gray limestone of Indiana is pre-Ludlowville and post-Upper Silurian, its fossils completely eliminating any possibility of Onondaga age of these beds.

Miami Bend, new formation.—From the above remarks it is evident that the *Stringocephalus-Subrensselandia*-bearing gray limestone must be separated from the Logansport and given its own name. We propose *Miami Bend* for it, from the community near the bend of the Wabash River slightly less than a mile southwest of the France Stone Quarry, Logansport-Anoka (7½′) Quadrangles. North of the bend 0.3 mile is located the *Subrensselandia* locality (USNM Cooper 391b) on Pottawatomie Point Road. The best exhibition of this limestone and the one best showing its relationships, however, is in the France Stone Company Quarry. We, therefore, select the west side of the quarry as the type section, but derive the name from Miami Bend. On the west side of the quarry the formation is 15 feet thick and is overlain by patches of the Logansport. On the southeast side of the quarry it is 11 feet thick and is overlain by 14 feet of Logansport Limestone. The same relationship appears on the west side of the Pottawatomie Point Road where the northwesternmost exposure, on the west side of a small isolated knob, is composed of Logansport Limestone. The two lithologies are readily separable because the Miami Bend is light gray and fine-grained limestone full of stromatopores, whereas the Logansport is coarsely granular, crinoidal limestone often cream yellow to pinkish, with only a few but different stromatopores and numerous corals.

GUIDE FOSSILS

The two principal fossils forming the subject of this discussion need further explanation to help make the correlation of the Miami Bend Formation clearer. *Stringocephalus* (Cloud, 1942, p. 104) is well known anatomically and needs no discussion of its morphology. Its occurrence in North America is poorly known and its stratigraphic range is not clearly understood. Furthermore, fossils accompanying *Stringocephalus* are poorly known individually and as a fauna. Consequently, remarks on these subjects may require revision as knowledge of them advances.

Stringocephalus, in spite of the fact that it is known to occur rarely in the Eifelian (Struve, 1961, p. 328), is still regarded as the leading fossil of the Givetian, which is often spoken of as the *Stringocephalus* zone. Identification of Eifelian *Stringocephalus* will largely depend on its accompanying fauna, whereas abundance of the genus is likely to indicate Givetian age. In North America, as elsewhere, *Stringocephalus* is a gregarious genus, occurring in banks or patch reefs and often in great abundance. A number of species of *Stringocephalus* have been created in Canada where it occurs throughout a fairly long sequence (Warren and Stelck, 1962; Crickmay, 1960 and 1962). Colonial genera, such as *Stringocephalus* and the pentamerids *Rhipidium* and *Pentamerus* that live in the same manner, are extremely variable locally, each patch often having its own species or subspecies. This leads paleontologists to create many species or to extreme conservatism depending on training or inclination. The North American occurrences are still too poorly known to have tested the usefulness of the described species. Obviously, this is a considerable handicap in correlation, especially between areas that are separated by long distances, as between Indiana and Manitoba and the Northwest Territories, Canada.

Subrensselandia (Cloud, 1942, p. 92) (type species *Newberria claypolii* Hall from the Hamilton Group in Pennsylvania) is an aberration of *Rensselandia* (formerly *Newberria*) differing from that genus only in the presence of small struts under the broad hinge plates of the brachial valve (pl. 2, fig. 4). Externally the two genera are identical. *Rensselandia* (Cloud, 1942, p. 94) occurs in Europe in close association with *Stringocephalus* and is probably as good a guide to the Givetian as that genus. It is not reported from the Eifelian. In the United States it is common in the Cedar Valley and Callaway Limestones of Iowa and Missouri. It is also known from Mackenzie Valley in the Northwest Territories and from the Nevada

	IOWA	CENTRAL MISSOURI	E. MISSOURI S.W. ILLINOIS	SOUTHERN INDIANA	INDIANA WABASH VALLEY	CENTRAL OHIO	MANITOBA	SOUTHEASTERN WISCONSIN	EASTERN MICHIGAN	SOUTHWESTERN ONTARIO	NORTHEASTERN OHIO	NEW YORK (GENERALIZED)	STAGE
	SWEETLAND CREEK	GRASSY CREEK	ALTO	BLAKISTON	DELPHI	OLENTANGY	MANITOBA GROUP (PART)	KENWOOD	SQUAW BAY	KETTLE POINT	HURON	GENESEE	FRASNIAN (FINGER LAKES)
GIVETIAN	CEDAR VALLEY WAPSIPINICON	CALLAWAY MINEOLA ASHLAND COOPER		BLOCHER	LITTLE ROCK CREEK ?	OLENTANGY (PART)	MANITOBA GROUP (PART)	NORTH POINT MILWAUKEE THIENSVILLE ?	THUNDER BAY POTTER FARM			GENESEO TULLY	TAGHANIC
									NORWAY POINT	IPPERWASH PETROLIA WIDDER		MOSCOW LUDLOWVILLE	TIOUGHNIOGA
			LINGLE	BEECHWOOD	LOGANSPORT	PROUT			FOUR MILE DAM	HUNGRY HOLLOW	TEN MILE CREEK	CENTERFIELD	
			ST. LAURENT	SWANVILLE SILVER CREEK		PLUM BROOK			ALPENA NEWTON CREEK GENSHAW FERRON POINT ROCKPORT QUARRY BELL	ARKONA	SILICA (PART)	SKANEATELES	CAZENOVIA
			BEAUVAIS		MIAMI BEND		ELK POINT WINNIPEGOSIS ELM POINT	LAKE CHURCH (PART)	ROGERS CITY				
EIFELIAN			GRAND TOWER = DELAWARE	DEPUTY SPEEDS		DELAWARE		LAKE CHURCH (PART)	DUNDEE	DELAWARE	SILICA (PART) BLUE BED DUNDEE	MARCELLUS	
?	SILURIAN	ORDOVICIAN	GRAND TOWER	JEFFERSONVILLE	SILURIAN	COLUMBUS	SILURIAN	SILURIAN	BOIS BLANC	ONONDAGA	DETROIT RIVER	ONONDAGA	UNDERLYING FORMATION

Fig. 2.—Chart showing the position of the Miami Bend Formation of the eastern United States and Canada and its correlation with other formations.

Limestone in the Great Basin. It has not been found with *Subrensselandia* except in Germany, but too little is known of either genus to say whether or not a time value may be attached to the presence or absence of supports under the hinge plates. Besides the type species another is known from the Middle Devonian of Germany. In the United States *Subrensselandia* occurs in central Pennsylvania, Missouri, and Michigan. The latter occurrence is known from a few specimens only and has not been described.

CORRELATION OF THE MIAMI BEND FORMATION

The obvious relationship of the Miami Bend Formation is with other occurrences of *Stringocephalus* and *Subrensselandia.* One salient point of comparison occurs in Canada and another in the northern end of the southern peninsula of Michigan. The Indiana formation shares the same fauna with these other two occurrences. Correlation with these two reference sections permits correct positioning of the Miami Bend in the Devonian. Other similar but less clear points of reference occur in Pennsylvania and Missouri.

Correlation with Manitoba sections, Lake Manitoba-Lake Winnipegosis area.—The Devonian in Manitoba is divided into two groups: The Elk Point Group and the Manitoba Group at the top. The former is divided in ascending order into the following formations: Ashern, Elm Point, Winnipegosis, and Prairie. The first and last, which is an evaporite, do not have fossils. The middle two are highly fossiliferous, the Elm Point characterized by *Atrypa arctica* Warren and the Winnipegosis abounding in *Stringocephalus.* This formation is of most concern in comparison with the Indiana occurrence.

The Winnipegosis Formation, besides *Stringocephalus,* contains the gastropods *Mastigospira, Buechelia tyrellii* (Whiteaves), and *Omphalocirrus manitobensis* (Whiteaves), and the elongated pelecypod *Liromytilus attenuatus* (Whiteaves), all of which occur in the Miami Bend Formation. *Subrensselandia* has not yet been reported from the Winnipegosis Formation, but the fossils recorded establish a satisfactory correlation with the Indiana fauna.

Correlation of the Miami Bend Formation in Michigan.—In Michigan, Ehlers and Radabaugh (1938) established a striking correlation with the Winnipegosis Limestone in their description and establishment of the Rogers City Formation. This formation, about 70 feet thick, contains a buff dolomite of 8 to 9 feet at the base that contains the brachiopod *Carinatina,* known also from the Lake Church Formation of Wisconsin and the Hume Formation of western

Canada. This bed is followed by about 8 feet of chocolate brown limestone containing exquisite, frilled *Atrypa* and *Subrensselandia.* The upper part of the next succeeding bed, 55 feet thick, contains the diagnostic Winnipegosis mollusks: *Mastigospira, Buechelia tyrrellii, Omphalocirrus manitobensis,* and *Liromytilus attenuatus* (LaRoque 1950). Although *Stringocephalus* has not yet been found in Michigan, the Rogers City Limestone, nevertheless, can be positioned in relation to the above sequence in Canada and in the Hamilton (Traverse) Group of Michigan.

The Rogers City Formation cannot be correlated with any formation east and south of Michigan except the Miami Bend, but it can be fixed in the standard New York section by establishing correlates in the Traverse Group above and the Hamilton Limestone below it. The Rogers City is underlain by the Dundee Limestone (*Brevispirifer lucasensis* zone) which for years has been correlated with the Delaware Limestone of Ontario and Ohio and via that formation to the Marcellus of New York. Thus the base on which the Rogers City rests is Marcellus. Further relations to New York are established through the Traverse Group which lies on the Rogers City.

The Traverse immediately overlying the Rogers City is definitely Hamilton in age except for the upper part which has been referred to the Taghanic Stage (Cooper et al., 1942, chart). In the midst of the Traverse is a great coral zone which is culminated by the Four Mile Dam Limestone. This contains *Fimbrispirifer venustus* (Hall) and many other fossils of the New York basal Ludlowville Centerfield Member (Cooper and Warthin, 1942, p. 886) and the Logansport of Indiana. Between this Centerfield equivalent and the Rogers City Formation several formations intervene, which by position and fauna are equated to the Skaneteles Formation of New York. The Rogers City and its partial equivalent, the Miami Bend Formation, are consequently placed between the Marcellus and Skaneateles Formations of the New York succession. It must be emphasized that the *Stringocephalus-Subrensselandia* sequence in question thus falls very low in the Hamilton Group (about middle Cazenovia Stage) and that the Skaneateles, Ludlowville, Moscow, and Tully Formations overlie it.

Other correlations of the Miami Bend in the United States.— The type species of *Subrensselandia* is common in parts of south central Pennsylvania (Perry County) where it occurs in the Montebello Sandstone (Ellison, 1963). According to Ellison, *Subrensellandia claypolii* (Hall) forms a zone in the Montebello Sandstone above beds with *Paraspirifer,* but below a coral biostrome that is equated with the Centerfield Member of the Ludlowville Formation. The presence of *Paraspirifer* suggests a level high in the Marcellus (Cooper, in Cooper et al., 1942, p. 1775). Thus *Subrensselandia* in Pennsylvania occurs in the same relative position that it occupies in Michigan. It is difficult in these fairly uniform clastics, such as the Montebello, to sort out and definitely identify the parts that are Marcellus and Skaneateles, except for the vague limits indicated by the occurrence of the mentioned fossils or faunas.

An occurrence of *Subrensselandia* in Missouri will complete the known areas occupied by the genus. In the much faulted Ste. Genevieve County area, *Subrensselandia claypolii* is reported in the Beauvais Sandstone (Croneis and Hoffman 1931) of uncertain position. This brachiopod was also found by Warthin and Cooper in the interesting section southeast of Union School in Perry County, Altenburg (15′) Quadrangle in eastern Missouri, where its position could be established. Here it occurs between a Delaware-Dundee equivalent containing *Brevispirifer lucasensis* (Stauffer) and the St. Laurent Limestone which has Skaneateles affinities. Its position is thus the same as that of the Rogers City Limestone of Michigan.

PALEONTOLOGY

SUBRENSSELANDIA SUBPYRIFORMIS Cooper and Phelan, new species

Large for the genus; shell thin except at the umbones; length about twice the width; valves of nearly equal depth, the ventral valve having a slightly greater depth than the other; outline inverted pyriform; profile the same. Sides posteriorly gently rounded but anteriorly nearly straight and tapering to about half the maximum width at the anterior; widest posterior to midvalve. Anterior commissure rectimarginate. Cross section forming a narrow ellipse. Pedicle valve beak small, incurved, and almost recumbent on the umbo of the brachial valve; foramen small. Surface smooth.

Pedicle valve interior with long, flaring dental plates; muscle scars moderately deeply impressed, the diductor scars subflabellate, and the adductors in a narrow groove between them. Vascula media long and broad. Genital markings subreniform, located in posterolateral shoulder.

Brachial valve interior with hinge plates supported by short struts; adductor field small, scars longitudinally striated. Vascula media short, indistinct.

Measurements in mm.—

	Length	*Brachial valve length*	*Maximum width*	*Anterior width*	*Thickness*
Holotype	54.7	52.0	24.0	17.0	31.0
146121 b	56.0	55.4	25.8	20.0?	31.3
146121 c	55.8	?	30.3	18.1	17.0?
146121 d	?	58.8	31.2	15.5	18.6
146121 e	53.4+	51.0+	32.9	21.0?	29.9
146121 f	50.1	48.4	25.0	15.5?	28.7

Stratigraphic occurrence.—Miami Bend Formation.

Locality.—Cooper 391b.

Diagnosis.—Large subpyriform *Subrensselandia* having a narrowly elliptical cross section at right angles to its length.

Types.—Holotype 146121a, figured paratypes 146121c-h, k, l, unfigured paratypes 146121b, i, j.

Comparison.—The only species to which *S. subpyriformis* can be compared is *S. claypolii* (Hall), the type species of the genus. Hall's species is also subpyriform and has an outline very similar to that of the Indiana species. The latter differs from the Pennsylvania species in having much deeper valves, thus producing an elliptical cross section in the direction of the thickness of the valves, i.e., dorsoventrally. The cross section of *S. claypolii* is the opposite to that of *S. subpyriformis* because its valves are much less deep and are more transverse.

Discussion.—The narrowly elongate form and shouldered appearance of this species are distinctive. In some specimens when adulthood is reached and the shell is no longer growing anteriorly and laterally, shell layers are added at almost right angles to these directions and the brachial valve then tends to grow ventrally and add depth to the shell. Some pedicle valves show a tendency to dorsad growth in the late stages.

Preservation of the Miami Bend *Subrensselandia* is not good for exterior details. The matrix adheres so closely to the shell surface that it is almost impossible to obtain the beak and the exterior, except for the one specimen figured. Internal moulds, however, are excellent and afford good details of the muscle scars, pallial and genital marks. The vast majority of specimens are detached valves, often shingled together and difficult to separate. Complete specimens are rare and are usually at an angle to the crude bedding of the separated shells. In some instances they lie across the bedding or are transversely fractured by jointing or weakness in the rock.

Furthermore, some of the complete specimens are crushed in various directions with the result that only a few are available for description. Actually, we do not have a perfectly formed specimen with both valves attached.

This species of *Subrensselandia* is not likely to be confused with any known species of *Rensselandia.* The enormous *R. missouriensis* (Swallow) is much larger and much thicker and wider; *R. johannis* (Hall) is smaller and not pyriform in either profile or outline; *R. laevis* (Meek) is still larger than the Indiana species, is more robust, and has more rounded outlines and profile; it is distinctly not pyriform; *R. cordiforme* Stainbrook is a small rounded form.

As reported above, specimens of *Subrensselandia* have been taken in eastern Missouri along the Mississippi and from the Rogers City Formation in Michigan. Specimens from these places in the national collections are too fragmentary for description.

It is interesting to note that occurrences of this genus, like those of *Rensselandia* and *Stringocephalus,* often occur as bioherms or biostromes consisting mostly of individuals or detached valves of one species, often exhibiting great variation. Similar "banks" of large pentameroids, such as *Pentamerus* and *Rhipidium,* are known. A bank of the latter in southern Perry County, Tenn., consists of 20 feet of limestone mostly composed of *Rhipidium.* Occurrences of great numbers of *S. claypolii* occur in the Montebello Sandstone of Pennsylvania.

STRINGOCEPHALUS, species A

Large, roundly but transversely elliptical in outline with the maximum width at about midvalve; hinge narrower than the midwidth and producing distinct shoulders at the extremities; posterolateral extremities narrowly rounded; sides strongly rounded; anterior margin broadly rounded but the anterolateral extremities broad. Valves unequally convex, the pedicle valve having the greater convexity. Beak small, short, sharply pointed, and forming an angle of 94° to 110°. Beak ridges sharp; interarea narrow; deltidial plates concave and foramen small and oval. Surface smooth.

Pedicle valve moderately convex in lateral profile and broadly convex in anterior profile with the median region somewhat narrowly convex. Median region in young specimens somewhat narrowly swollen, the swelling dying out anteriorly; posterolateral flanks steep.

Brachial valve gently convex in anterior and lateral profiles; somewhat more convex in the posterior region; posterior margin nearly straight. Median region somewhat flattened but lateral regions sloping gently to the margins.

Pedicle valve interior without dental plates but with a long prominent septum duplex that extends from the apex for three-fourths the length toward the anterior margin. Septum highest about 0.6 the length from the beak where it has a sharp crest, then falls off rapidly with a steep slope to its end.

Brachial valve interior with a short, low median septum, highest posteriorly and extending slightly anterior to midvalve; cardinal process huge and forked in the large specimens with a broad, stout shaft and short prongs that diverge at about an angle of 24°. Cardinal process in a specimen 55 millimeters long, measuring 18 millimeters in length. Hinge plates stout. Loop not seen.

Measurements in mm.—

	Length	*Brachial valve length*	*Maximum width*	*Hinge width*	*Thickness*
146122 a	56.4	48.8	75.5*	46.0*	27.4
146122 b	68.3	58.5?	80.8*	52.5?	28.0+
146122 c	69.3	?	76.5	?	?
146122 d	63.0?	53.0?	86.0?	50.0?	32.0?
146122 e	?	?	98.9	95.0?	50.0+

Stratigraphic occurrence.—Top of Miami Bend Formation.

Localities.—391a, 391e.

Diagnosis.—Medium-sized to large *Stringocephalus* having a short narrow beak, gentle convexity, a wide hinge, and moderate thickness.

Types.—Figured and measured specimens: 146122 a, b, e, f; measured specimens: 146122 c, d; unfigured specimens: 146122.

Comparison.—Of the many species of *Stringocephalus* recently described only two are like that from the Miami Bend Formation: *S. chasmognathus* and *S. aleskanus* Crickmay, both from the upper part of the Ramparts Formation = Beavertail Formation. Both species are characterized by considerable width and a very short beak. The measurements of the holotype of *S. chasmognathus* are similar to those of the Miami Bend specimens, especially 146122b, except for the thickness which appears to be greater in the Canadian species. Crickmay's sections (1960, p. 886) of this species indicate less massive internal structures than those inside the Indiana specimens. The measurements of the holotype of *S. aleskanus* are very similar

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* Based on half measure.

to those of our specimen 146122b except for the thickness. Our specimen has definitely been crushed and the true thickness is not known. The interior structures of *S. aleskanus* cannot be compared with ours because Crickmay's sections are not cut through the cardinal process to show the forks. The structures that are shown seem to be less massive than those in our specimens. The Indiana specimens seem to us to compare more favorably with *S. chasmognathus* of the two Canadian species. The proportions and short beak are similar but the beak of the Indiana form is slightly longer, more erect and sharper. Furthermore, the Indiana species seems to have been slightly more slender.

Discussion.—The preservation of the *Stringocephalus* from the Miami Bend Formation is very poor. The shells are partly cemented to the matrix in many cases so that one must resort to grinding with dental abrasive wheels to free them. In others where the shell and matrix make contact the shell is wholly or partly disintegrated and an irregular seam of clay appears. In such cases that part of the shell in contact with the clay is completely destroyed.

Only one complete specimen had both valves in contact. Several of our specimens are single valves. Consequently, we were unable to make any sections through the shell.

STRINGOCEPHALUS, species B

A single poorly preserved specimen indicates another species of *Stringocephalus*. This specimen is 83 millimeters long by 65 millimeters wide at its widest part somewhat anterior to midvalve. The beak is fairly long and strongly incurved like that of *S. burtini*. The deltidial region is estimated at about 23 millimeters in length and is strongly concave. The exterior is not preserved but a good view of the septum may be had. This is extremely long, measuring 120 millimeters along the curve of the valve and terminating about 10 millimeters posterior to the anterior margin. The septum is duplex and thickest about one-third its length from the beak.

This specimen has some features, especially the strongly incurved beak, reminiscent of *S. sapiens* Crickmay and *S. vernaculus* Crickmay. The former species seems not to have been as large as the Indiana one and its median septum is indicated as shorter (60 to 70 percent of the length). *Stringocephalus vernaculus* is also not so large as the Indiana specimen but it has a strongly incurved beak like it. The median septum, however, is only 70 percent of the length, whereas in the Miami Bend specimen it is fully 90 percent of the length.

Stringocephalus axius is another large species described but not well illustrated by Crickmay. It is of the same order of size as the Indiana specimen but its beak was shorter and strongly incurved. *Stringocephalus axius* is also indicated as a rather narrow species.

The occurrence of worn and weathered *Stringocephalus* in which the duplex septum is exposed could readily be mistaken for *Pentamerus* and the beds enclosing them inadvertently be assigned to the Silurian.

Stratigraphic occurrence.—Top of Miami Bend Formation.

Locality.—391a.

Types.—Figured specimen 146120.

LOCALITIES OF MIAMI BEND FORMATION

Logansport (7½′) Quadrangle, Indiana

391a.—Upper 18 inches of Miami Bend on the west side of France Stone Company Quarry, SW ¼, NE ¼, sec. 27, T 27 N. R 2 E, on north side of U.S. 24, 2 miles east of Logansport city limits.

391b.—Beds with *Subrensselandia,* 6½ feet below the top of the Miami Bend Formation, in the road cut and in the woods, 150 feet west of the Pottawatomie Point Road, ¼ mile south of its junction with U.S. Highway 24, NE ¼, SE ¼, SE ¼ sec. 28, T 27 N, R 2 E, 1.35 miles east of city limits of Logansport.

391c.—Beds with *Liromytilus,* 6½ feet above *Subrensselandia* at the top of the formation, 150 feet west of Pottawatomie Point Road road cut, ¼ mile south of junction of Pottawatomie Point Road and U.S. Highway 24, NE ¼, SE ¼, SE ¼, sec. 28, T 27 N, R 2 E, 1.35 miles east of city limits of Logansport.

391d.—Miami Bend Formation on Fry Farm, east side of Cass Station Road, 0.4 mile south of its junction with U.S. Highway 24, NW ¼, NW ¼, SW ¼ sec. 25, T 27 N, R 2 E, 3.4 miles east of the city limits of Logansport.

391e.—Top of the Miami Bend Formation on the Oscar Miller property, 0.2 mile south and 0.2 east of the junction of U.S. Highway 24 and Pottawatomie Point Road, NW ¼, SE ¼, SE ¼ sec. 28, T 27 N, R 2 E, 1.35 miles east of Logansport city limits.

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EXPLANATION OF PLATES

PLATE 1

Surface of Miami Bend Formation and France Stone Quarry

Fig. 1. Surface of the Miami Bend Formation in the France Stone Quarry, south side locality 391a showing a cross section of a large *Stringocephalus* with numerous specimens of the stick-like stromatopore *Amphipora.*

Fig. 2. Surface of the Miami Bend Formation on the west side of the France Stone Company Quarry (locality 391a) showing large stromatopores.

Fig. 3. South wall of the France Stone Company Quarry (June 6, 1964) showing the Silurian at the base, the Miami Bend Formation (MB) and the Logansport Formation (L) at the top.

PLATE 2

Subrensselandia

Subrensselandia subpyriformis Cooper and Phelan, new species

Figs. 1-3. Respectively dorsal, side, and ventral views of a paratype, ×1, USNM 146121e, a more robust specimen than usual. Fig. 4. Interior of brachial valve, ×2, showing supports of the hinge plate, USNM 146121-1. Fig. 5. Anterior view showing rectimarginate commissure and narrowly tapering anterior region, ×1, paratype USNM 146121h. Fig. 6. Dorsal view of a long, tapering brachial valve, ×1, paratype USNM 146121d. Figs. 7-10. Ventral, posterior, side, and dorsal views of a large tapering individual, ×1, holotype USNM 146121a. Fig. 11. Posterior view of a complete specimen showing muscle scars, ×1, paratype USNM 146121k (see plate 3 for other views of this specimen).

All specimens from locality 391b.

PLATE 3

Liromytilus and Subrensselandia

Liromytilus attenuatus (Whiteaves)

Fig. 1. Rubber impression of two large left valves showing characteristic ornamentation and remains of the snail *Buechelia,* ×1, figured specimen USNM 146123a.

Locality 391b.

Subrensselandia subpyriformis Cooper and Phelan, new species

Figs. 2, 3. Ventral and brachial views of an imperfect specimen showing the pallial and muscle marks, ×1, paratype USNM 146121k (see plate 2 for posterior view). Fig. 4. Posterior of a fragmentary specimen showing the beak and small foramen, ×2, paratype USNM 146121g (see plate 4 for dorsal view). Figs. 5-7. Three views of the same pedicle valve, one in dorsal view, one tilted laterally and the last tilted toward the observer, all showing the genital markings and the long dental plates (as slots), ×1, paratype USNM 146121c.

Locality 391b.

PLATE 4

Stringocephalus and Subrensselandia

Stringocephalus, species A.

Fig. 1. Posterior view of an incomplete brachial valve showing forked cardinal process, ×1, figured specimen USNM 146122. Fig. 2. Interior of a large specimen excavated from the anterior to show the enormous, stout cardinal process, ×1, figured specimen USNM 146122e.

Stringocephalus, species B.

Fig. 3. Pedicle valve of a large, elongated individual, with outer shell partly worn away and revealing the long, duplex septum, ×1, figured specimen USNM 146120.

Locality 391a.

Subrensselandia subpyriformis Cooper and Phelan, new species.

Figs. 4-7. Dorsal, ventral, posterior, and side views of a young and slender specimen, crushed slightly on one side, ×1, paratype USNM 146121f.

Locality 391b.

PLATE 5

Stringocephalus and Subrensselandia

Stringocephalus, species A.

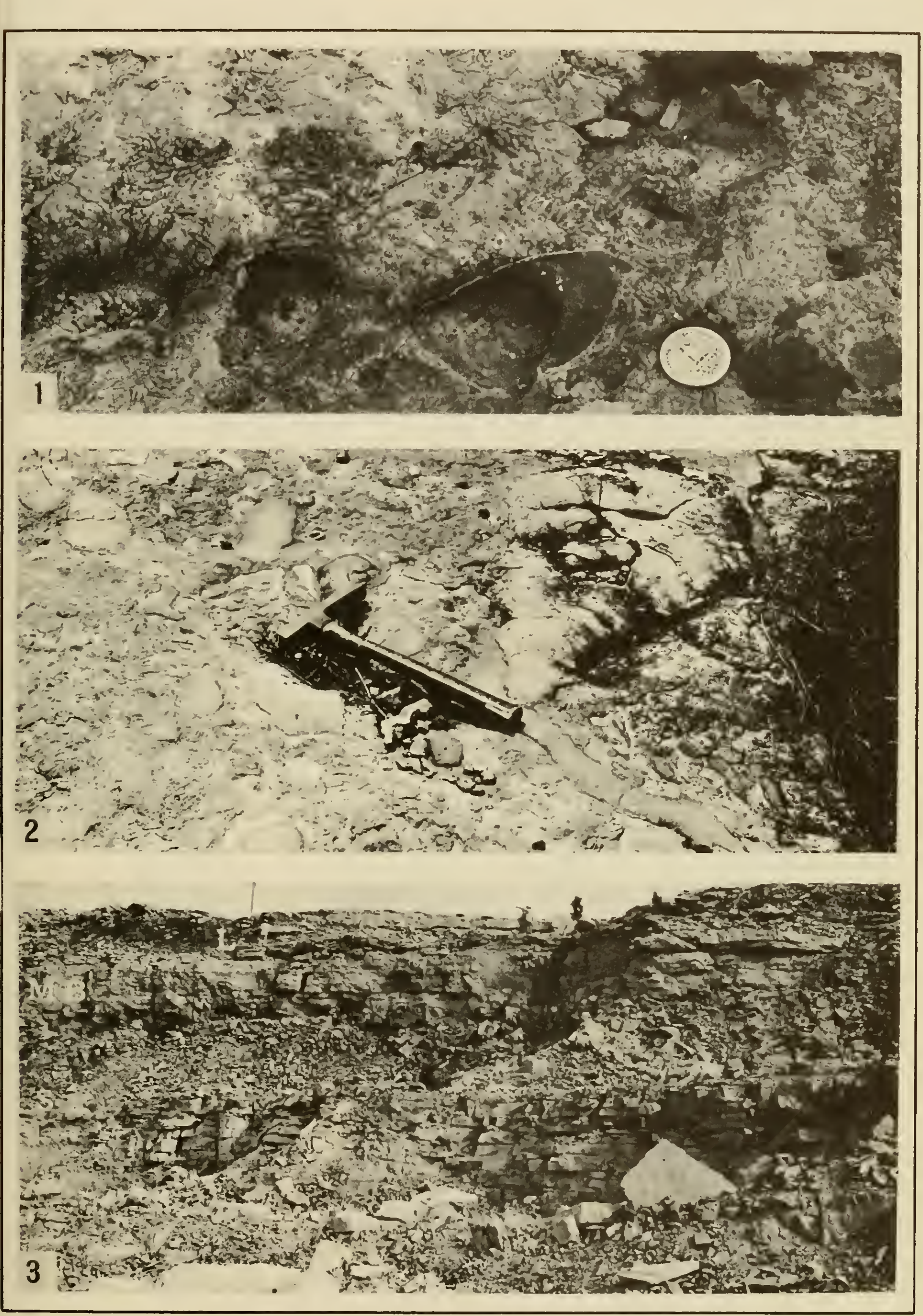
Figs. 1-4. Respectively posterior, ventral, dorsal, and side views of an imperfect specimen preserving both valves, with outline restored, showing the septum of the brachial valve, ×1, figured specimen USNM 146122a. Fig. 5. Large pedicle valve showing the long, median septum, ×1, figured specimen USNM 146122b.

Locality 391a.

Subrensselandia subpyriformis Cooper and Phelan, new species.

Figs. 6, 7. The posterior part of specimen showing the beak, beak ridges, and foramen, respectively ×1, ×2, paratype USNM 146121g (see plate 2 for posterior view).

Locality 391b.

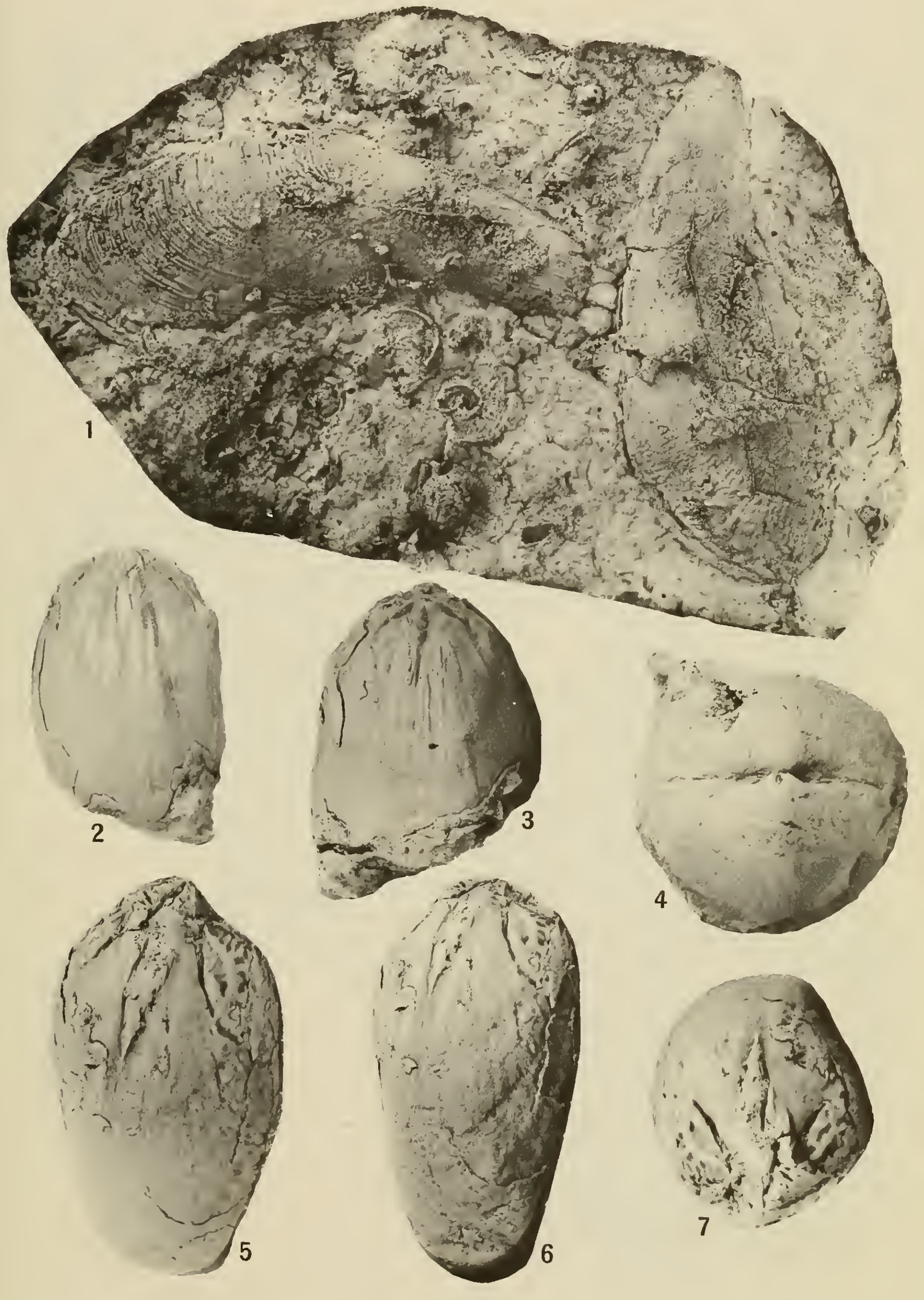


Miami Bend Formation, France Stone Company Quarry

(See explanation of plates at end of text.)

SUBRENSSELANDIA

(SEE EXPLANATION OF PLATES AT END OF TEXT.)



LIROMYTILUS AND SUBRENSSELANDIA

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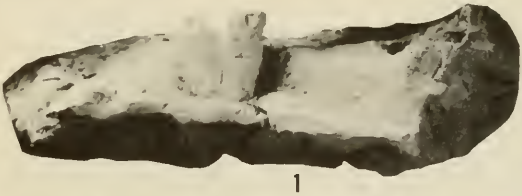
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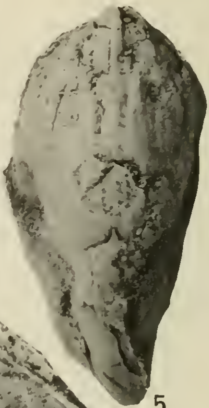
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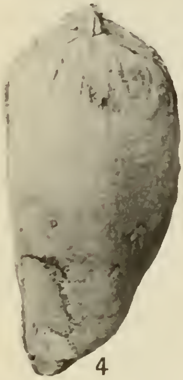
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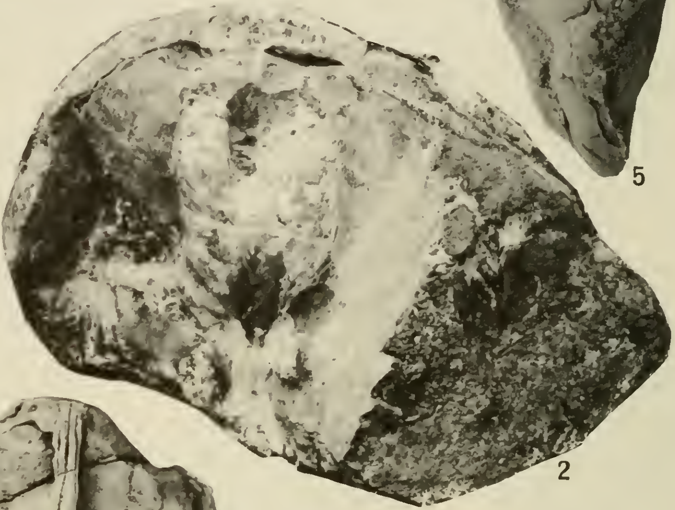
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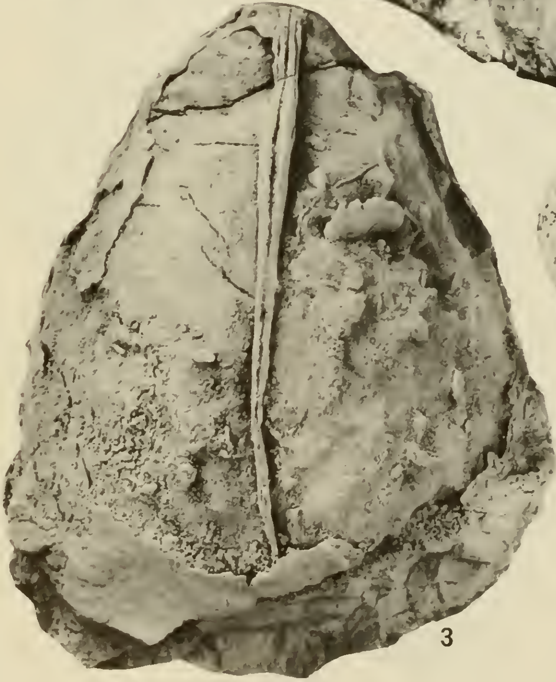
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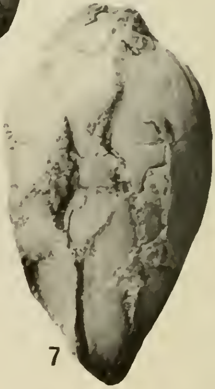
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STRINGOCEPHALUS AND SUBRENSSELANDIA

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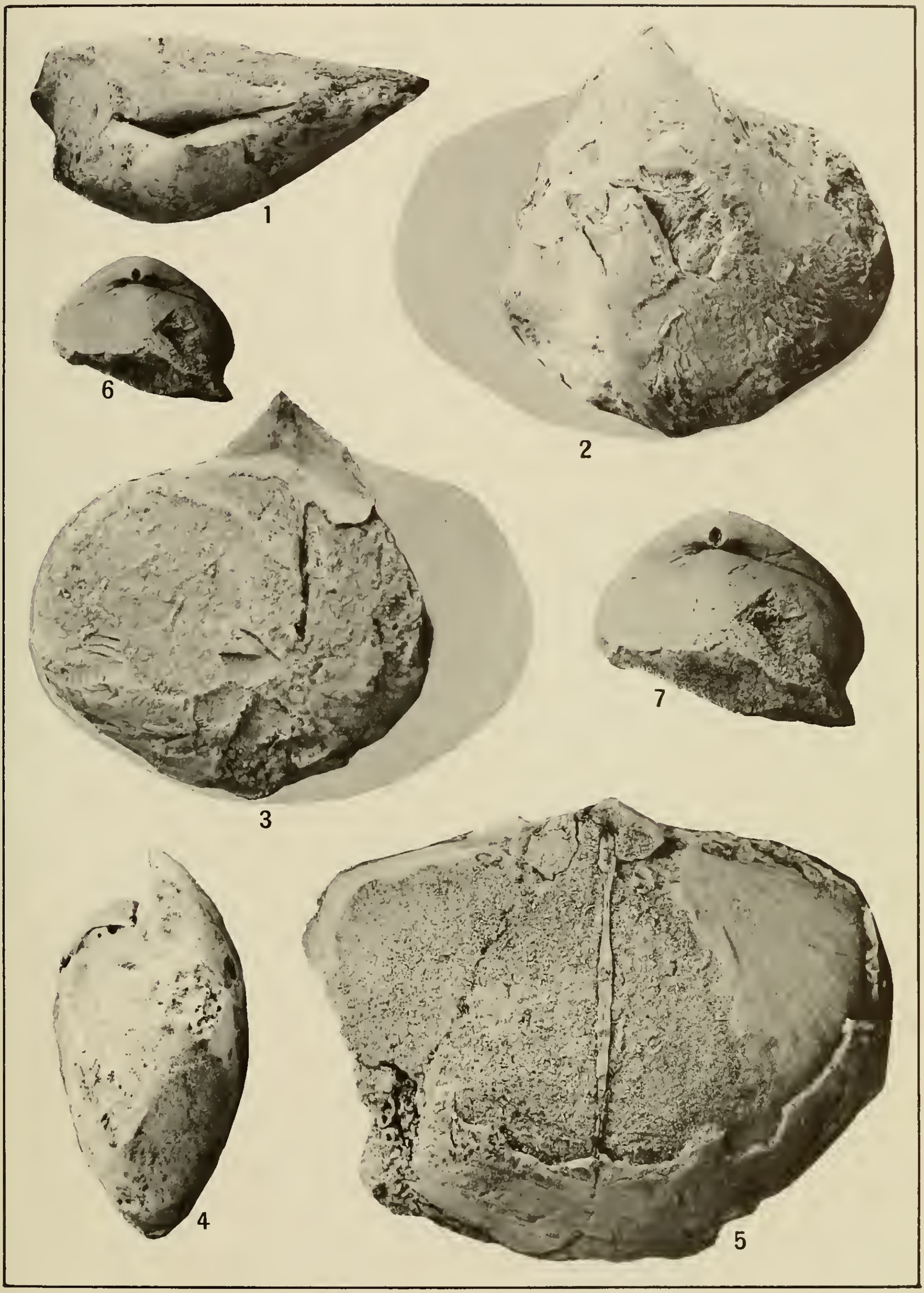

STRINGOCEPHALUS AND SUBRENSSELANDIA

(SEE EXPLANATION OF PLATES AT END OF TEXT.)

SMITHSONIAN MISCELLANEOUS COLLECTIONS
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INTRODUCTION

Tropidurus torquatus Wied is one of a small number of lizard species in South America that range from the open temperate savannalike cerrados of southern Brazil into the semidesert caatingas in northeastern Brazil and through the Amazonian rain forest to reach the Caribbean coast in the Guianas and Venezuela. The widely distributed populations usually are considered to belong to a single species (Burt and Burt, 1933; Cunha, 1961) with great geographical variation that is currently under study by Dr. P. E. Vanzolini.

Because of the wide range of climatic conditions and plant formations from which this species is recorded, its ecological relationships are of great interest.

The authors spent 4 weeks in Belém, Pará, near the mouth of the Amazon, during July and August 1963 (the first part of the dry season), collecting information on the ecology of this species, particularly its distribution in different habitats, its use of the structure of the environment, and its temperature relationships.

Our observations were made primarily on the grounds of the Museu Goeldi where we conducted repeated censuses of the *Tropidurus torquatus* present and on a number of days watched those in one small area. Though we marked no lizards, some in this area were recognizable as individuals. We also made a number of short excursions in the vicinity of Belém, particularly to Utinga and the grounds of the Instituto Agronomico do Norte, where we examined a number of different habitats and collected temperature data.

We want to thank Dr. Dalcy Albuquerque, director of the Museu Goeldi, Dr. Fernando C. Novaes, chief of the vertebrate division, and

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Dr. Oswaldo da Cunha, herpetologist, for their kind assistance in providing facilities and in many other ways, in Belém. We must also thank Dr. P. E. Vanzolini of the Departamento de Zoologia, São Paulo, for suggesting this project and for reading and discussing the manuscript.

HABITAT

Tropidurus torquatus is a common lizard at Belém near the mouth of the Amazon, but not an inhabitant of the Amazonian rain forest or even of the various types of second-growth forest. All of the several hundred individuals of this species that we saw were in or on the edge of clearings.

T. torquatus was common in a variety of situations: on rocks in a bulldozed bare quarry, but not in the second growth bordering it; on piles of scrap metal at the edge of a grassy pasture and on fenceposts and telephone poles through pastures, but again not in the nearby second growth; on trees surrounded by waist-high grass at the edges of a plantation of rubber trees, but not on the rubber trees within the plantation; on fallen logs in a sparsely vegetated flat that had been cleared near a lake, but neither in the second growth nor in the primary forest which surrounded this clearing; on the wall surrounding the Bosque Municipal (a patch of tall forest within the city), on the open playground in this park, and on a large fallen tree that had opened a clearing about 10 by 30 meters when it crashed down, but not in the forest even along the narrow trails; in the open part of the park of the Museu Goeldi, but only very rarely in the parts of the park where the trees grew more closely and formed a complete canopy.

There seem to be two major factors in determining where *torquatus* occurred—one associated with microclimate, probably temperature, and the other associated with the structure of the environment, particularly the presence of suitable perches.

Structural niche.—Most of the *torquatus* observed were sitting up on some sort of perch a few centimeters to several meters above the ground, and no *torquatus* were found in places where perches were not available to them. These lizards require a perch which allows them to climb a few centimeters to a couple of meters above the ground, and one which is not of small diameter. Trees are used as perches, but the fact that the tree extends its trunk above 2 or 3 meters for an additional 10 to 30 meters seems to be irrelevant to the lizard except with respect to its escape behavior (see below).

A wide variety of things were used as perches. Rocks, bricks, cement blocks, curbs, walls, logs, and the trunks of trees were most commonly used. With two exceptions, both in a dense hedge, no lizard was seen on a slender perch (i.e., less than 3 cm. in diameter).

The usual height at which lizards were seen during a series of censuses around the grounds of the Museu Goeldi is shown in table 1. In each of seven, approximately 50-minute censuses two of us followed the same course, walking slowly and recording for each lizard the height above the ground at which it was first seen. (Heights were measured with a steel tape.) The number of lizards seen during a census varied from 26 to 47. Since perch height did not vary at different times of day, all the censuses are combined.

TABLE 1.—*Perch height. The number of individual* Tropidurus torquatus *observed at various heights above the ground during censuses.*

Height above ground (cm)	Number of individuals		
	On trees	On other perches	Total
400-449	2		2
350-399			
300-349	4		4
250-299	6		6
200-249	6	1	7
150-199	14	3	17
100-149	15	11	26
50-99	36	23	59
1-49	28	43	71
On ground			38
Total	111	81	230

On these censuses no lizard was seen above 4½ meters and most were below 1½ meters. Relatively few—only 38 out of 230—were seen on the ground, and most of these were small individuals.

Many individuals were seen on perches other than trees, such as rocks, walls, etc., where the height to which they could climb was limited. A lower proportion of the available trees than of these other sorts of perches were used. The *torquatus* on trees which would allow them to climb higher than 5 meters still are usually seen within 2 meters of the ground (table 1).

Temperature.—The association of *torquatus* with open areas and its avoidance of forests may be associated with its temperature requirements.

Tropidurus torquatus is a heliotherm that, when weather conditions permit, uses variation in environmental temperatures to raise its body temperature considerably above that of the air and maintain it within a relatively narrow range.

The temperatures of 51 individuals were taken with a Schultheis quick-reading thermometer immediately after they had been shot with .22 caliber dust shot. These temperatures were taken on sunny days when the lizards had the opportunity to thermoregulate. The air temperature in the vicinity was taken immediately after capture.

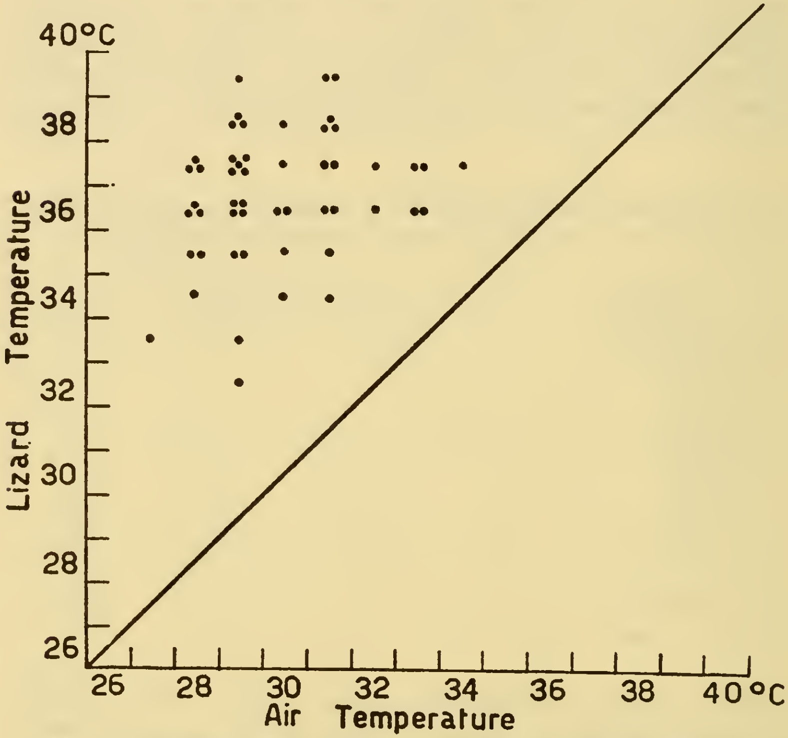

Fig. 1.—*Tropidurus torquatus* temperatures: lizard body temperatures plotted against ambient air temperatures.

The temperatures were recorded over an air temperature range of 8°C, from 26.6° to 34.4°. The lizard temperatures also ranged over 8°, from 31.6° to 39.4°. However, 80 percent of the records fall within a 4° range from 34.6° to 38.4° and 58 percent in a 2° range from 35.6° to 37.4°. The body temperatures are plotted against air temperatures in figure 1.

An even more striking way of demonstrating the behavioral thermoregulation in these animals is to plot the air and body temperatures simultaneously against time of day (figure 2). This shows a regular rise in air temperature as the day progresses but no corresponding trend in the lizard temperatures.

DAILY ACTIVITY

This species is strictly diurnal. None was active at night, and activity began after sunrise and ceased about sunset.

Early morning.—One morning was devoted to watching three *torquatus*, a large male and two females, as they began their daily routine. These three lizards had been located asleep the night before, flattened close together against the side of the trunk of a small tree about 3¼ meters above the ground.

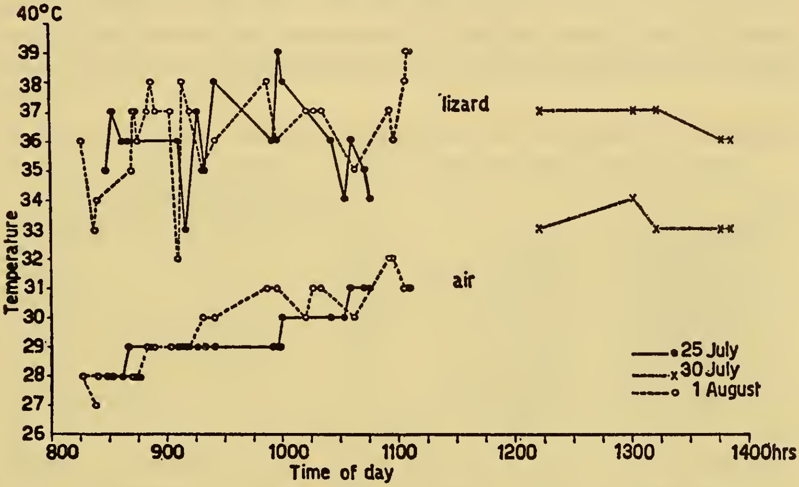

FIG. 2.—*Tropidurus torquatus* temperatures: lizard body temperatures and ambient air temperatures plotted against time of day.

Observations were started at 0550 hours, after dawn but before sunrise (0620 hrs.) They remained asleep until about 0640 when their eyes were noticed to be open. Five minutes later one of the females lifted her head from the trunk slightly. The first patch of sun reached the tree about 0715. The first female moved around the trunk at 0722 and at 0743 up into a patch of sun. The large male lifted his head at 0736 and moved into the sun at 0752. The second female moved into the sun at 0759. At 0820 the first female ran down the tree and across the ground to her usual perch. The male and the other female remained sunning for some minutes longer before leaving the tree where they had slept.

Other observations supported the general picture that the lizards remained in their sleeping sites after sunrise. They were usually sunning by 0800 but seldom much before this.

Sunning and thermoregulation.—Once a *torquatus* has left its sleeping site it may move into the sun directly or it may move to a perch where there is no sun. Usually it does not remain long on a shaded perch but moves again into the sun. During the morning the lizard's activities may take it into the shade but usually it moves back into the sun. Later, during the heat of the day, the *torquatus* are more frequently seen perching in the shade. In the late afternoon as the air cools the lizards again are seen basking and also sitting on substrates which have been warmed by the sun, though these may no longer be receiving direct sunlight. This reaction to warm substrates is particularly noticeable when clouds hide the sun in the afternoon (a common occurrence during our stay in Belém).

Table 2.—*The relation between time of day and number of* Tropidurus torquatus *seen in the sun during censuses.*

		Number of lizards		
Time of census	Date	Sun	Shade	Part sun
0900-0952	19 VII	30	4	2
0908-0957	2 VIII	30	9	3
1100-1150	17 VII	6	19	3
1100-1150	29 VII	11	12	7
1300-1352	23 VII	8	21	1
1527-1635	15 VII	4	19	0

The relationship between time of day and sunning is shown in table 2.

Even more striking than whether the animals are in the sun or not are the changes in posture at different times of the day and under different conditions.

In the morning when the animals begin to sun and also in the afternoon when they seek sun, if available, or warm substrates (e.g., cement walks that have been in the sun all day), they flatten themselves against the substrate so that all of their ventral surfaces are in contact with it—belly and chest, throat, tail, arms, and legs. When they are on warm substrates this probably raises their temperature, though it cannot do so in the early morning. As the day progresses and both lizard and environment heat up, the lizard seldom assumes this flattened posture, but usually sits with at least its head and chest raised.

In the middle of the day when a lizard is sitting on a very warm substrate, it assumes a posture which is almost the exact opposite of the flattened one. The animal raises itself so that it is in contact with the substrate as little as possible. Not only are the head and body raised but also the tail (though the tip may sometimes touch). Even the toes and fingers are raised so that the only parts of the animal to touch are the palms of the hands and the soles of the feet. This presumably reduces the amount of heat which is transferred from the hot substrate to the body of the animal.

We have the impression that when the animals are sunning in the morning they orient themselves to expose the maximum surface to the sun.

This species shows little color change and none which we could see associated with temperature or sunning.

Reaction to rain.—These *T. torquatus* remained active during cloudy periods during the day, but on one occasion when it began to rain they behaved differently. They ignored the first sprinkle except to wiggle when struck by a raindrop as if they had been crawled on by an ant. When it began to rain somewhat more heavily, most, but not all, of the lizards moved into concealed hiding places. In one case the hiding place was that used for sleeping, in two other cases it was not. These hiding places concealed them and also protected them from the rain.

Late afternoon.—*T. torquatus* seem to have definite places to sleep. We watched three *torquatus* go to their sleeping sites: one, a female, climbed up to her sleeping site on a tree at 1805 hours; one, a larger female, climbed to hers in a brick pile at 1804; and one, a large male, climbed up a tree to sleep at 1820. These lizards sought their sleeping places as it began to get dark but while we could still see them clearly. On cloudy afternoons they remained active until about sunset, but probably went to sleep earlier than on bright afternoons. In all of the cases observed the lizard slept in a place it did not visit when active except as a hiding place. Going to the sleeping site was simple and direct with few pauses.

Sleeping sites.—Four sleeping sites were found: (1) Between the vertical sides of two bricks in a brick pile about one-half meter above the ground; used by a single lizard. (2) On the trunk of a tree three-fourths meter in diameter about 3 meters above the ground under the leaves of an epiphyte which hung down along the trunk; used by a single lizard. (3) On the 12-centimeter trunk of a tree 3¼ meters above the ground behind a small branch which grew parallel to the trunk and just above where it joined the trunk; usually used by two and on one occasion by three lizards. (4) In a deep but narrow crevice in a very large tree, about 1 meter above the ground; used by three lizards on occasion at least. All four of these sleeping sites were used repeatedly, almost surely by the same lizards. The crack in the large tree and the brick pile were used by lizards as hiding places from us. The two more exposed spots on the tree trunks were not so used.

These places have in common that they were above the ground and that they more or less hide the lizards (in two cases quite well, and in two cases only moderately so) and that they were on the west side of the structure.

MAINTENANCE ACTIVITIES

Posture.—*T. torquatus* on tree trunks or other vertical surfaces frequently rests head downward with its neck bent so that the head is almost parallel to the ground. On lower perches such as rocks it usually climbs to the top of the perch and rests in a horizontal position. It also is frequently seen on the side of a rock with its body vertical and its neck bent forward so that the head is over the top of the perch and parallel to the ground.

Feeding and foraging.—*T. torquatus,* like most other iguanids, does not search actively for its food, which is primarily insects.

Some prey was captured when it lit on the lizard's perch or passed near the lizard; in other cases the lizard left its perch and traveled some distance to the insect. The longest excursion seen was by a large male that ran 4 meters across the ground to seize a large fluttering dragonfly. We have the impression that *torquatus* traveled farther for large than for small prey. In the case of the dragonfly, the lizard ran directly to it and seized it. Another lizard approached a large butterfly more slowly in a series of short runs, keeping his head and body close to the ground as if he were stalking it. Several times we saw a *torquatus* jump into the air to snap at a flying insect and one lizard on two successive days stationed himself in an area where many small flies were hovering and repeatedly leaped up at them. Most of these attempts were unsuccessful but we saw him make several captures. In these leaps the front feet certainly and perhaps the hind feet left the ground.

One *torquatus* was seen to pick an insect off a green leaf and another to reach under a leaf and seize one. This latter insect was probably seen by the lizard as it crawled under the leaf.

Many times a *torquatus* on the ground picked up a number of insects, six or seven within a half minute, from the same place. These probably were ants, since ants were the only insects present in concentrations and lizard feces contained large numbers of ants. However, a lizard sitting on its perch ignored a great many ants that we could see running up and down his perch and even over him.

On one occasion we saw a *torquatus* run a short distance and seize a seed with white plumes that drifted to the ground.

Small insects were picked up with the tongue and swallowed immediately. Larger insects were picked up with the jaws as well, and were chewed before being swallowed. A lizard which had come to the ground to capture one of these larger insects frequently carried it back to its perch or to another perch before eating it.

Though most of the lizard's time was spent on an elevated perch and some insects were caught on it, most of the captures we saw were made on the ground. The lizard either left its perch to capture an insect seen from its perch, or encountered an insect while on the ground.

During the periods when the lizards were active we observed frequent captures and attempted captures of prey, certainly at the rate of several an hour.

Fecal pellets collected in the park of the Museu Goeldi contained a large variety of orders of insects. The commonest item was ants which were present in all but one pellet that contained instead a number of termites. Most of the food taken was small, up to 1½ centimeters in length, though one large male was seen to eat a dragonfly with a body of approximately 7 centimeters.

All but one of the food items were of groups that are active in the open during the day. The only exception was the fecal pellet full of soldier termites. During the day these usually are found in their nests or foraging in covered tunnels. However, when a tunnel is broken the soldiers rush out and probably the lizard had encountered a freshly broken tunnel.

A considerable amount of plant material was found in the feces. Some of this was probably taken incidentally with insects. Some may have been taken when mistaken for an insect as described for the plumed seed above. We saw no other lizard eat any plant material.

Water.—No *torquatus* were seen drinking. They may occasionally do so but certainly not as frequently as they feed. Water is available to them during rains and as dew on some occasions, but since they seem to hide during rains and do not become active in the early morning much of their necessary water must come from the food which they eat.

Defecating.—Waste material is defecated in the form of a pellet, roughly cylindrical with bluntly tapered ends about four to five times as long as wide and with a white cap more or less loosely attached to one end. Fecal pellets vary from about 1 to about 3 centimeters in length; some of this variation related to the size of the animal defecating. A fresh pellet is dark, almost black in color, damp, and soft to touch, and contains much moisture. The white cap is nearly dry when extruded and represents the material excreted by the kidneys.

Defecation seems to occur in the morning, within an hour or two after the *torquatus* become active but we did see one individual defecate at midday. How frequently an individual defecates is unknown.

Defecation seems to occur wherever the lizard is at the time and fecal pellets accumulate on and around the most frequented perches until the pellets are broken up by ants or disintegrated by rain.

A lizard may defecate when on either a vertical or a horizontal surface. In the three cases noted closely, the lizard flattened against the substrate and raised its tail base and vent and the fecal pellet was extruded white cap first. In one case the tail was jerked upward slightly during this, as if the lizard were straining. Once the pellet has been extruded, it may fall to the ground if the lizard is on a vertical surface, or may hang attached if the lizard is on a horizontal surface; in the latter case the lizard moved a few steps away, lowering the vent to the ground so that the fecal pellet was brushed off.

The *torquatus* took no interest in their freshly defecated pellets or in those of others.

Escape reactions.—The escape reactions of *torquatus* seemed to depend largely on the position of the animal when disturbed.

The initial reaction seemed to be to run, frequently out of sight, sometimes toward but seldom into a hiding place. A *torquatus* on a rock or a tree usually ran around to the other side; one on the ground might run to a tree and a short ways up it, it might run to a rock pile, or it might just run away a few meters. If followed or approached again the *torquatus* on trees usually ran up out of reach; most of the others hid in a crack or crevice or behind or under something.

In its initial run a *torquatus* sometimes ran toward some particular hiding place even if it stopped before reaching it. On one occasion a lizard ran toward and past us to disappear through a broken window into a basement. In their reactions the lizards seem to make use of a knowledge of their surroundings and a lizard on a tree might leave the tree at our approach to run across the ground to another tree or to something under which it could hide. Though the lizards tolerated our presence at 10 meters or more, and sometimes at 3 or 4 meters, closer approach usually sent them running and at even 10 or 15 meters they seemed aware of our presence.

Predators.—We have no information at all on the predators of this species but it is probably taken, at least occasionally, by most diurnal predators that hunt in open areas and also probably is found by nocturnal predators occasionally.

Shedding and comfort movements.—A number of individuals were seen in the process of shedding. In this species the skin is not shed all at once. Instead pieces of old skin a few square centimeters in area come off separately. Many individuals have part of their body brightly patterned where the old skin has sloughed off while other parts are very dull and dark where the old skin still adheres. We have no data on how long the whole shedding process takes or the interval between sheddings.

Individuals were seen occasionally making what seem to be comfort movements. One scratched briefly at its right shoulder with its right hindleg in what looked to be a rather ineffective manner. Several times a lizard wiped or scraped its jaws or lips on the ground or perch; once the lizard had a bit of loose skin on its jaws, once it had a plume of a seed caught in its mouth and another had just seized a small insect which may have had an unpleasant taste or have stung him.

Another sort of comfort movement was a twitch or shake of leg or head. This seemed to be in response to an ant crawling on the lizard, though frequently ants crawling on them were completely ignored, and sometimes when a lizard twitched or shook a leg no ant could be seen.

One female was seen sitting in the shade with one hindleg extended almost straight up in the air, the body twisted to allow this. This was seen only once and its significance is completely unknown.

HOME RANGE

Each *torquatus* seemed to restrict its activities to a small area centering on a few perches and their vicinity.

One male whom we recognized as an individual was observed over our 4-week stay in Belém in the same small area. We recorded his movements during several periods in different days. These observations for 6 different days are presented in figure 3, a total of 1023 minutes with the lizard under observation 91 percent of the time. One can join the most distant points at which the lizard was seen to form a convex polygon with an area of 195 square meters, but from figure 3 it is evident that his activity is concentrated in only a small part of this. The lizard spent most of his time (63 percent) on three perches, a rock pile, a stump, and a palm tree (perches labeled 1, 2, and 3 in figure 3), and moved frequently from one of these to another.

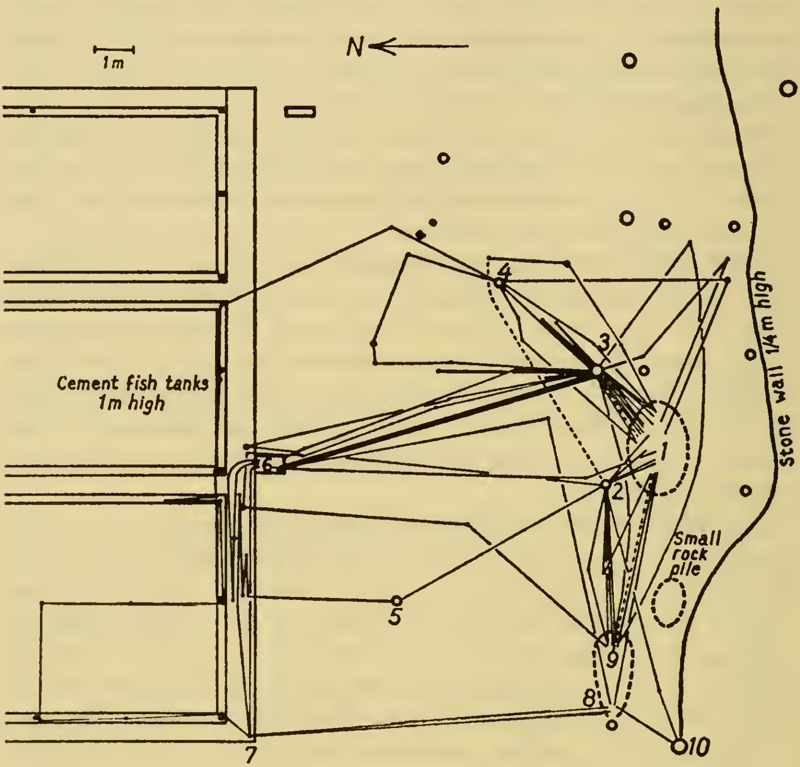

FIG. 3.—Habitat utilization in *Tropidurus torquatus*. The movements of one adult male during 936 minutes in nine observation periods over 6 days. Heavy lines indicate structural features, and circles represent trees. Fine solid lines show observed movements; fine dashed lines show movements not observed, but deduced. Small dots indicate stops of less than 5 minutes; large dots stops of longer than 5 minutes. The time spent on the numbered perches is shown in table 3. Movements of less than 1 meter have been omitted.

He also made numerous excursions from these perches to other places in the vicinity, repeatedly visiting certain perches and not visiting others which seemed similar. He spent an additional 18 percent of his time on these perches. The remaining 19 percent of the time was spent on the ground or on perches which he visited only once during these observations. This data is presented in table 3. The region of greatest concentration is not in the center of the home range but to one side of it and consists not of a central point but of three different perches. We think the lizard ranged to the north rather than to the south because the area to the south was more heavily shaded.

The route the lizard took during one observation period is shown in figure 4. In this period he moved from one to another of his three principal perches four times for no apparent reason. He made several longer excursions, chasing another male three times and approaching a female once. He also made shorter excursions (not indicated) in the immediate vicinity of his major perches to catch insects. It is striking how much of the total area visited in 6 days (fig. 3) he visited in this one 3-hour period.

Table 3.—*Habitat utilization: Time spent on certain perches by a large male* Tropidurus torquatus *during nine observation periods on 6 days, July 11-19* (see figures 3 and 4).

Perch	Number of minutes on perch	Number of days on which perch was visited	Number of visits to perch
1. Rock pile	274	5	14
2. Stump	168	6	10
3. Palm	150	6	15
4. Tree	58	3	5
5. Tree	35	2	2
6. Small pile of scrap sheet iron	28	3	5
7. Southwest corner of cement walk	23	2	3
8. West end of sandpile	25	2	3
9. East end of sandpile	20	4	4
10. Large tree away	6	1	1
from major perches	149		
Total	936		

After the observations described were made, a tree was felled so that the trunk lay near the base of the palm which the lizard used frequently. By the next day he was using this trunk as one of his favored perches.

This male shared his home range with at least three adult females and we occasionally saw another adult male invade it from the east.

Several times we saw the resident chase this intruding male away, particularly when it approached one of the perches which the resident used most frequently.

Immediately before we left Belém we found this lizard in a prolonged fight with another male of his size and watched him be defeated. On the following 2 days, he was absent from his usual perches which were now occupied by another male, probably the one which had defeated him, and the original resident was seen a few meters farther north.

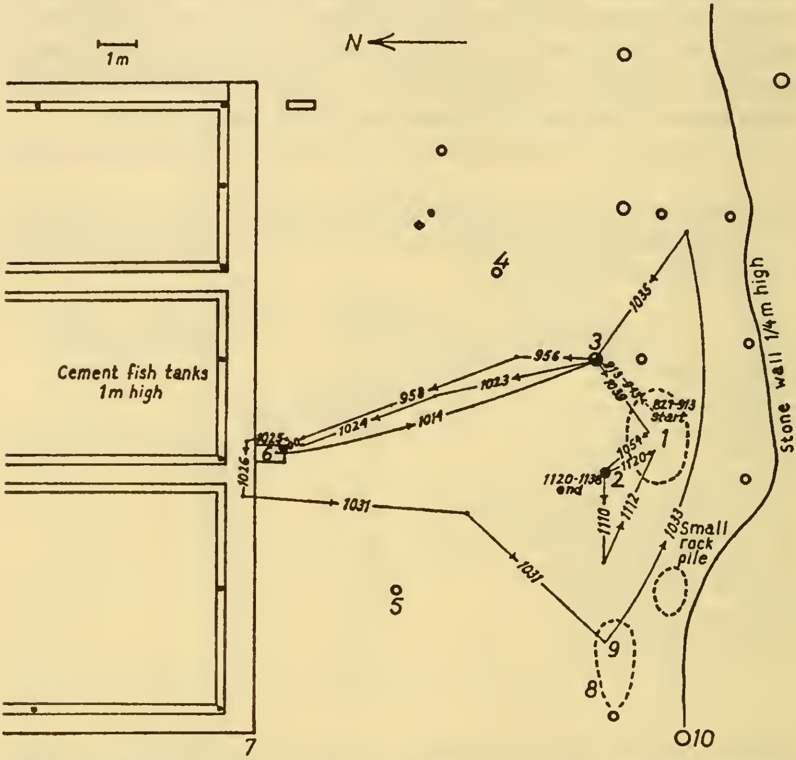

FIG. 4.—The movements of the male *Tropidurus torquatus* in figure 3 during a single 191-minute observation period. Figures show the time at which each move occurred and the arrows the direction. Other conventions are as in figure 3. The shifts at 0956-8 hours, 1023-4, and 1033 were to chase another male; that at 1110 was to investigate a female.

DISCUSSION AND CONCLUSIONS

The high eccritic temperature of *T. torquatus* may be a major factor in its restriction to open areas and its absence from the forest around Belém. Sun is present even in the tallest, most dense, tropical rain forest but because of the behavior of *torquatus* most of it is not available to this species.

Because these lizards seldom climb more than 3 or 4 meters above the ground they are excluded from the well-lighted canopy. The sunlight which reaches the lower levels of the forest does so as isolated patches, the positions of which are continuously changing as the sun moves and as branches and leaves in the canopy are blown by the wind. Consequently, the surfaces of the sunlight patches are not heated to anywhere the extent that the sun heats surfaces in the open, and thus opportunities to use heated substrates for thermoregulation are strongly restricted in the forest. Inger (1959) has shown that a skink living in the rain forest in Borneo is able to maintain a body temperature above the surroundings by basking in the patches of sunlight (though the temperature it maintains is still 4° or 5°C below that measured for Belém *torquatus*).

T. torquatus restricts its activities to a small area, probably usually less than 200 square meters, and spends most of its time on a few perches within this area. This behavior would certainly interfere with following the movements of the sun on the forest floor necessary to using them for thermoregulation.

Certainly the insect food which *torquatus* takes is available in the forest, particularly since it includes a large number of ants and these seem always to be abundant. Water is more available in the forest than in the open. The influence of predators on this species is completely unknown, but it seems unlikely that the predator pressure in the forest is sufficiently great to exclude them from it completely. The availability of suitable egg-laying sites in the forest is impossible to evaluate without much more information, and this may be an important factor in preventing populations establishing themselves there. But the absence of any individuals more than a very short distance inside the forest suggests that the factors operating do so throughout the life of the individual.

From these arguments it seems likely that *torquatus* is absent from the forest basically because its thermoregulatory behavior is such that it cannot maintain a sufficiently high body temperature under forest conditions. It probably is absent not because the necessary radiant energy does not exist in the forest, but because the animals' behavior is not adapted to taking advantage of it.

Even in open areas *torquatus* is not uniformly distributed. The lizards only occur where suitable perches are available. Thus the animals are absent in absolutely bare fields, clearings, and in grassy pastures and meadows that lack trees or fenceposts.

The lizards are arboreal in Collette's (1961) sense in that they spend much of their time above the level of the ground. They are not arboreal in the sense that they are more closely associated with trees as such than with any other surface irregularity. Lizards are frequently seen on top of low perches as well as the vertical sides of taller ones.

These two requirements—suitable perches and suitable conditions for thermoregulation—seem basic to the ecology of the *Tropidurus torquatus* at Belém. This species does not occur where either of these is absent. Together they seem to provide a suitable habitat for the species. Other factors are undoubtedly important (e.g., food supply, egg-laying site, etc.), but these latter seem less critical in determining the distribution of *Tropidurus torquatus* at Belém.

At the present, suitable habitats for *Tropidurus torquatus* at Belém have almost entirely been created and maintained by man. The only exception that we saw was a small clearing created by the fall of a large forest tree which was close to the edge of the forest.

Tropidurus torquatus is definitely a component of the fauna of the Belém area but not of the forest. Presumably it is a species that evolved in more open environments and subsequently penetrated the forest in clearings and along the edges. It may have invaded the Belém area only after there were manmade clearings. It is also possible that it has a longer history in the region, and before man began to modify the environment may have lived in natural clearings, perhaps those caused by fallen trees, those along the banks of the rivers, or others. Whichever is true, it is certain that man has provided a much greater extent of suitable habitats than ever have occurred in the area before.

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SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 151, NUMBER 3

Charles D. and Mary Vaux Walcott Research Fund

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(With 14 Plates)

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ABSTRACT

A study of the Orgueil meteorite shows that three main periods of mineral formation can be recognized: an early stage with minerals like troilite that are stable at several hundred degrees centigrade; a middle stage with minerals like chlorite and limonite formed below 170°C; and a late stage with carbonates and sulphates formed below 50°C. A physico-chemical analysis of the mineral-forming conditions indicates that oxidized phases like sulphate and limonite cannot be formed as a result of a local equilibrium but that an oxidizing substance must be brought into the system.

Volatiles like CO, CO_2, and H_2O may emanate from the interior of a meteorite parent body but none of these can oxidize troilite to limonite and sulphate. A possibility is that water at the surface of the parent body was dissociated by ultraviolet light to hydrogen and oxygen compounds, of which the lighter hydrogen escaped whereas at least some fraction of the oxygen or peroxides reacted with solid phases on the surface of the meteorite parent body.

1. INTRODUCTION

The carbonaceous meteorites have attracted much interest lately. The organic compounds in particular have been extensively analyzed because of the suggestion (Claus and Nagy, 1961) that part of this material may be of extraterrestrial biogenic origin. However, the characteristics of the inorganic compounds which constitute some 90 to 95 percent of these meteorites are still little known. This is due to the fact that carbonaceous chondrites mainly contain extremely fine-grained minerals, some of which are poorly crystallized and have varying chemical composition. Moreover, sample material is relatively hard to obtain, and the opacity of petrographic thin sections due to the presence of organic compounds renders microscopical observations difficult.

The mineral associations in carbonaceous chondrites have been studied recently by DuFresne and Anders (1962), Mason (1962), Nagy et al. (1963a), and Fredriksson and Keil (1964). DuFresne and Anders attempted to show, mainly by means of *e*-pH diagrams, that low temperature minerals in meteorites like Orgueil and Murray formed from high temperature minerals during an aqueous stage were close to equilibrium. Fredriksson and Keil on the other hand showed that Murray consists of at least two parts, which have been mechanically mixed together, one of high and one of low temperature origin.

In the present work the available data on the Orgueil meteorite are summarized (sections 2 and 3) and used for a physico-chemical treatment to estimate the conditions that governed the formation of the minerals in this particular carbonaceous chondrite. The relations derived give some indications of the surface conditions of the parent body. The material studied was obtained from the Swedish Museum of Natural History and from the "Nagy sample" (Nagy et al., 1964). In both cases it was ascertained that the samples had the original texture and did not contain gross contaminations (Anders et al., 1964).

2. MINERALOGICAL COMPOSITION OF THE ORGUEIL METEORITE

The Orgueil meteorite can be described as a bituminous clay with a clastic texture. This bituminous clay shows a breccia structure (fig. 1), the fragments and the matrix having identical composition when compared under the microscope and microprobe.

Approximately three-fourths of the meteorite consists of a sheet silicate (table 4c). A number of accessory minerals are listed in the same table. The meteorite is traversed by thin veins, mainly containing sulfates, which seem to be the last crystallized minerals.

Mineralogical and paragenetical evidence given in sections 2 to 4 is summarized in table 5. Below, the amount and composition of each mineral is discussed in detail.

Chlorite.—The major phase has long been considered to be "like serpentine or chlorite" (Pisani, 1864). Mason (1962) preferred serpentine because of the low aluminum content. On the basis of X-ray analysis, Nagy et al. (1963a) concluded that the mineral probably was a chlorite; this conclusion is supported here. In the present work the chemical composition of the groundmass was determined by electron microprobe X-ray analysis. The thin sections used for the analysis were moved at a rate of 8 micron/min. under the electron beam and the X-ray intensities for Si$K\alpha$, Mg$K\alpha$, Fe$K\alpha$, Ni$K\alpha$, S$K\alpha$, and Al$K\alpha$ were integrated over periods of 20 sec. (Fredriksson and Keil, 1964).

In order to obtain a representative composition for the predominant phase, three parts, each approximately 15 μ long, were selected in which all six elements varied less than ±10 percent. These parts were selected from several hundred microns of such microprobe tracks. Table 1 shows the composition of this phase in weight percent. Calcium was not accurately determined, since its concentration is low compared with the other elements and most of it is present in other minerals. Further, since Ca is 8-coordinated it should not enter the chlorite structure to any large extent.

A partial analysis by Jarosewich (1965, see table 2) shows that probably all of the sulphur in table 1 is present as a water-soluble sulphate, mainly a magnesium sulphate. This is to be expected since the amount of sulphate in silicates is low (Ricke, 1960). Probably the sulphate is present in a finely divided form or is absorbed on the layer lattice silicate.

Provided that aluminum is mainly present in 6-coordinated positions and after the water-soluble quantities of magnesium and sulphate as found by Jarosewich (see table 2) have been deducted, the probe analysis of the chlorite can be written either

$$(\mathrm{Mg, Fe^{2+}, Ni, Al})_{5.93}\,\mathrm{OH}_{7.86}\,\mathrm{O}_{0.14}\,\mathrm{Si}_4\,\mathrm{O}_{10}$$

or

$$(\mathrm{Mg, Fe^{3+}, Ni, Al})_{5.93}\,\mathrm{OH}_{5.75}\,\mathrm{O}_{2.25}\,\mathrm{Si}_4\,\mathrm{O}_{10}$$

the formulas representing the extreme cases. According to table 2 it is evident that most iron in the chlorite is ferric, since much of the ferrous iron must be present in magnetite, troilite, and breunnerite.

Approximately 1 percent sodium is probably present (fig. 9), and this to some extent accounts for the deficiency in cations. Small amounts of potassium, chromium, and manganese are probably present (compare p. 12). Potassium and manganese have also been found in sulphates and carbonates (Nagy and Andersen, 1964).

The electron micrograph (fig. 2) and the electron diffraction patterns from several grains (fig. 3) also make it probable that the groundmass consists of a chlorite. Using MgO as a standard, one of the pseudohexagonal patterns (fig. 3) gave the cell dimensions in table 3, which compare well with data given by Kerridge (1964). In the same table, unit cell dimensions of substances with a chemical composition similar to that of the major phase are given. Compared with this observed unit cell, ordinary chlorites (the nomenclature of Deer, Howie, and Zussman, 1962, and Brindley and Youell, 1953, is followed) have fairly large cell dimensions that increase with the iron content according to the formulas by Hey (1954) for a, b, and c. The cell dimensions indicate that the mineral probably is a ferric chamosite in good agreement with Jarosewich's data. The broad undefined (001) reflection (Nagy et al., 1963) indicates a stacking disorder.

The quantity of chlorite in the meteorite has been estimated at about 75 volume percent according to microprobe traverses, areal estimates of microradiographs (fig. 5), electron probe scanning (fig. 7), and microscopic observations on five thin sections, about 5-10 microns thick. The values in table 4c are based on the calculation discussed in sections 3 and 4.

Magnetite.—Fe_3O_4 is one of the phases in Orgueil that is easy to observe and isolate. X-ray microradiographs (the method is described by Fredriksson, 1958), figures 5a, and 5b, illustrate the distribution, relative amount, and shape of the magnetite grains. It appears that the magnetite occurs in two forms: (a) as micron-sized, irregular grains, and (b) as spherical particles from a few microns to some 40 microns in diameter, several of them being hollow (figs. 6a and 6b). A few of the spherules have been analyzed with the microprobe, both in thin sections and as isolated grains. (The latter were kindly given to us by Dr. D. Parkin). The spherules consist of an unusually pure magnetite. The Ni content is at most 100 ppm but probably less than 50 ppm, and the Mn content is only about 400 ppm. This is exceptional since most terrestrial magnetite (including our microprobe standard) contains 10 times more Ni, Mn, and Cr. The high purity of the meteorite magnetite suggests that the magnetite spherules were formed at low temperatures, possibly by alteration of rounded aggregates of ferric hydroxide (see below and p. 7). Such recrystallization would explain, by shrinkage, why the spherules are hollow.

Some of the magnetite, however, may be an early high temperature phase, perhaps even preceding the troilite. If the small irregular magnetite grains are of this type or are primordial condensates (Wood, 1963), they should contain considerably more trace elements, e.g. Ni, than the spherules. Mason (1962) indicated that the magnetite in Orgueil has an unusual large unit cell and concluded that the composition might be close to trevorite ($NiFe_2O_4$). This appears to be in agreement with a high temperature origin for the major part of the "magnetite." Finally, there seems to be a very late magnetite in the sulphate veins (Nagy, personal communication). Although this type of magnetite has not been found in the present study, it might be contemporaneous with the magnetite spherules.

It should be pointed out that the magnetite spherules morphologically resemble the cosmic spherules (Murray and Renard, 1891; Pettersson and Fredriksson, 1958; Castaing and Fredriksson, 1958; Hunter and Parkin, 1960; Thiel and Schmidt, 1961; and others) as well as volcanic magnetic spherules (Fredriksson and Martin, 1963). However, the Orgueil spherules contain less nickel than the cosmic spherules, and less manganese than the terrestrial ones, and can consequently be distinguished by careful analysis. This offers an opportunity to ascertain the total influx to the Earth of carbonaceous meteorites of the Orgueil type by extracting and counting such spherules from slowly deposited deep-sea sediment (e.g. Petterson and Fredriksson, 1958), provided no authigenesis of similar spherules takes place in the deep-sea sediments. To distinguish between terrestrial spherules and cosmic spherules that are formed in the atmosphere by ablation of meteorites (Castaing and Fredriksson, 1958) and spherules from Group 1 carbonaceous chondrites (Wiik, 1956) they must all be analyzed. Such an estimate seems most desirable, for it is probable that only few carbonaceous meteorites survive the passage through the atmosphere and those which do are hard to retrieve, whereas their resistant magnetite spherules mostly would survive. If the suggestion is accepted that some material with a composition close to that of Orgueil is the parent material for most meteorites (Mason, 1960; Ringwood, 1961; Fredriksson, 1963), there is good reason to believe that the number of carbonaceous meteorites entering the atmosphere is much higher than recovered falls indicate. The abundance of magnetite in Orgueil can be estimated from X-ray microradiographs (e.g. fig. 5) at approximately 4 volume percent. This agrees well with the calculated value in table 4c but is almost an order of magnitude lower than the estimate by DuFresne and Anders (1962, p. 1091) and Anders (1964, p. 630). If these values were correct no iron would be left for the chlorite, breunnerite, and troilite (compare section 3 below). In 1864 Cloetz and Pisani found a content of 20.63 and 15.77 weight percent respectively of magnetite, determined as insoluble in HCl, but these values were shown to be too high by Cohen (1894).

Troilite.—FeS (Fitch et al., 1962) occurs largely as euhedral, corroded crystals from a few microns to a few hundred microns in diameter (figs. 4, 5, and 7). The habit suggests a hexagonal symmetry which indicates that the mineral is troilite. The monoclinic modification of FeS, smythite (Erd et al., 1957), has also a hexagonal habit, but smythite is rare and has never been observed in meteorites. An X-ray powder-pattern of the FeS-phase in Orgueil shows several of the strong troilite lines, whereas none of the strong smythite lines was present. Microprobe analysis of a number of grains indicates that 1.3 to 1.6 percent Ni substitutes for Fe. As shown in figures 4 and 7, the troilite is frequently altered to ferric hydroxide, FeOOH, with some Ni and Cl (Nagy et al., 1963b). Some brownish, highly refractive hexagonal particles which have been described as "organized elements" may also be alteration products of troilite (see further p. 10). The corroded troilite crystals are frequently associated with native sulphur (see fig. 4).

The microradiographs (figs. 5a and 5b) as well as X-ray diffraction data indicate that troilite is less abundant than magnetite (i.e. 2 percent).

Sulphur.—S occurs in native form (DuFresne and Anders, 1962). Figure 4 shows a few sulphur globules. They were first found in the magnetic fraction (size 44-88 microns) of a powdered sample, since they to a large extent are associated with corroded crystals of magnetic troilite. It seems clear (fig. 4) that the troilite is an earlier mineral than the free sulphur. Some of the "globules" show crystal faces. They can be found in practically any untreated, newly broken up part of Orgueil. This contradicts the hypothesis that this type of sulphur globules may be an artifact produced by various sample treatments (Fitch et al., 1962). Microscopic observation suggests that the crystals are orthorhombic. A chemical analysis of the meteorite by G. Jarosewich (table 2) showed the presence of 1.6 percent free sulphur, which is in good agreement with analyses by Anders et al. (pers. com.). This value is considerably higher than the estimate made from direct microscopic observations, indicating that some of the sulphur may be very fine grained.

Ferric hydroxide.—Described by Nagy et al. (1963b) under the name limonite, occurring in some of the particles described as organized elements. Since the real identity of the ferric hydroxide is unknown, the name limonite ($FeOOH \cdot nH_2O$) will be retained here in accordance with the recommendation of Palache, Berman, and Frondel (1944). The limonite contains minor amounts of nickel and chlorine. Figures 4 and 7 show that it is an alteration product of troilite, although in some cases it appears to be redeposited in available pores, for instance in the bubbles of "organized elements." The limonite is older than the veins and probably also older than the previously mentioned (p. 4) magnetite spherules. Since the chlorite contains ferric iron it is possible that limonite and chlorite were formed simultaneously. Dr. B. Mason (pers. com.) has suggested that the limonite might have formed by terrestrial oxidation, e.g. from lawrencite $(Fe,Ni)Cl_2$ or troilite $(Fe,Ni)S$. This appears unlikely because of the frequent association with "organized" elements and because the magnetite spherules discussed on page 5 seem to be recrystallized limonite.

It has been shown that the compound $FeOOH$ may incorporate Cl ions (Chow, 1964). The Cl content (up to 3 percent) of the Orgueil limonite indicates that the troilite was altered in an aqueous environment containing chlorine. A possibility that gaseous Cl_2 was in part responsible for this oxidation cannot be disregarded and, as will be shown in section 5, some "external" sources of oxidizer seem necessary.

Direct observations of the quantities of limonite present are difficult to make, but it is only a minor constituent, probably occupying less than 1 volume percent of the meteorite.

Breunnerite and dolomite.—Breunnerite, $(Fe,Mg)Co_3$, was first discovered in Orgueil by Pisani (1864). A microprobe analysis by Nagy and Andersen (1964) showed 20 percent Mg and 12 percent Fe. According to microscopic observations some 5 volume percent of the meteorite is made up of strongly birefringent minerals presumably identical with the carbonates breunnerite and dolomite. Dolomite, $CaMg\,(CO_3)_2$, has been found in Orgueil by DuFresne and Anders (1962) but has not been observed by the present authors or by Nagy and Andersen (1964). The abundance is not easily ascertained. According to the calculations in section 3 dolomite may be completely missing and at most be present only in small amounts; otherwise, considerably less magnesium and calcium would be available for chlorite, epsomite, breunnerite, and gypsum, and consequently more sodium sulphate would form (see section 3). The carbonates are not found in veins but may nevertheless be formed late since they commonly are fresh and well crystallized.

Gypsum.—$CaSO_4 \cdot 2H_2O$ is present as small individual grains according to Nagy and Andersen (1964). Compared with the theoretical formula for anhydrite, their probe analysis shows a deficiency of Ca and S which may be interpreted as indicating that the mineral is indeed gypsum ($CaSO_4 \cdot 2H_2O$) and not anhydrite ($CaSO_4$). It is not unlikely that this is the original form, and if so it was probably formed below 50°C (Posnjak, 1938, 1940). The mineral seems to be present only in minute amounts, less than 1 volume percent, but since it is difficult to identify microscopically, it is not easy to estimate its abundance.

Magnesium sulphate.—$MgSO_4 \cdot nH_2O$ and a sodium-containing sulphate have been observed in the veins (fig. 9). The magnesium sulphate has been definitely identified (Cohen, 1894; DuFresne and Anders, 1962) but it is difficult to ascertain how much water of crystallization was present originally. The presence of a sodium sulphate has been inferred from mineralogical studies and analysis of water extracts of Orgueil sample (DuFresne and Anders, 1962) showing that sodium may well be present in some double salt, e.g. bloedite, $Na_2\ Mg(SO_4) \cdot 4H_2O$. Figure 9 illustrates the distribution of Na^{23}, Mg^{24}, Mg^{25}, and Si^{28} in the veins. It seems that the sodium-containing salt crystallized before the magnesium sulphate, but it might also have formed in late cracks since many sodium salts are very soluble. The amount of sulphates has been estimated as high as 17 percent (DuFresne and Anders, 1962), and indeed, exposed surfaces of certain samples (e.g. the main mass in Paris) show an abundant network of sulphate veins. The present work on thin sections indicates that such veins are less abundant than the carbonates, which is in agreement with observations by Nagy (pers. com.). Sulphates in veins are estimated at 2 to 3 percent by volume, while the total amount of water soluble $MgSO_4 \cdot 7H_2O$ should be about 13.1 weight percent according to analysis by E. Jarosewich (see table 2). This value is in good agreement with data by DuFresne and Anders (1962) and Anders (pers. com.). Consequently it seems reasonable to assume that the sulphur found in the chlorite analyses in table 1 is present as finely divided or absorbed sulphates, mostly of magnesium but also of some other cations, e.g. iron, nickel, calcium, and sodium.

Calcium phosphate.—Described in Orgueil by Nagy and Anderson (1964) and tentatively identified as merrillite, $Na_2Ca_3(PO_4)_2O$, since the measured absolute mass concentrations of calcium and phosphorus are a little too low to suggest whitlockite, $\beta Ca_3(PO_4)_2$. However, sodium was not analyzed for (op. cit.) and the mineral may consequently be whitlockite, which is a common phosphate in many meteorites (Fuchs, 1962). No direct estimates of its abundance exist, but if all available phosphorus is ascribed to this mineral, a maximum of 0.8 volume percent can be calculated (see table 4c). This amount does not influence the sodium or calcium balance significantly.

Brucite or Periclase.—$Mg(OH)_2$ MgO. A single 10μ cube-shaped grain of a mineral with a high Mg-content was found with the microprobe (fig. 10). Subsequent analysis showed 50 percent Mg and approximately 1 percent Fe and 1 percent Si. The Mg content is too high for any likely compound other than periclase, MgO, or brucite, $Mg(OH)_2$. Theoretically brucite has 41 percent Mg and the high value of the present analysis may be explained if it is assumed that the vacuum in the probe and the heat from the electron beam boiled off water from brucite. Probably also some excitation of the surrounding chlorite took place. This assumption is supported by the observed amounts of silicon. Periclase is not stable in the aqueous environment which seems necessary to explain the late vein minerals (p. 13) in Orgueil, and this fact also supports the assumption that the mineral indeed is brucite, $Mg(OH)_2$.

Olivine.—$(Mg, Fe)_2 SiO_4$ has not been found with certainty. One 40μ large grain analysed with the microprobe showed Mg, Fe, and Si contents corresponding to an olivine with 95 percent forsterite. The particle was lost and the identification could not be confirmed. J. F. Kerridge (1964) has inferred from electron diffraction data that Orgueil contains micron size grains of olivine. It is difficult, however, to understand how olivine, particularly in small grains, could survive in the aqueous environment in which the last-formed Orgueil minerals originated.

Several workers (e.g. Urey, 1957, and DuFresne and Anders, 1962) have suggested that the Orgueil was formed by alteration of some material of chrondritic composition. During informal discussions some petrographers (e.g. Griffith in La Jolla, 1964) have suggested that some fragments like that in figure 1 may be pseudomorphs after olivines or pyroxenes. Probe analyses showed that the fragment in figure 1 has basically the same composition as the main mass except for a slight increase in nickel and sulphur. Consequently this particular fragment is apparently not an alteration product of a meteoritic olivine since these have generally extremely low nickel content. (Compare the discussion of the Murray carbonaceous chondrite by Fredriksson and Keil, 1964.) It should be pointed out, however, that the presence of a few olivine pseudomorphs would not contradict the tuffaceous character. On the other hand, if fresh olivine is still present it is almost necessary to assume that Orgueil is a mechanical mixture of high and low temperature phases similar to Murray (Fredriksson and Keil, 1964) and that fine grained olivine would have to be emplaced at a very late stage.

Carbonaceous compounds and organized elements.—No efforts have been made to identify any of the organic compounds. Some preliminary electron microprobe analyses by C. Andersen * have indicated the presence of rounded aggregates, 10 to 30 microns in diameter, enriched in carbon, perhaps up to 30 percent. No direct correlation with any organized elements could be established. The possibility exists that these aggregates contain graphite, because this mineral has been observed in Ivuna (Vdovykin, 1964). This work is presently being extended.

The results of some electron microprobe work reported by Nagy et al. (1963b) have been confirmed with respect to the rounded aggregates of limonite coated with what appears to be a thin film of organic material. One of us (K.F.) has repeatedly in discussions offered the explanation that these "plastic shells" were formed by evaporation and recondensation of organic material on the walls of bubbles created by vapors. Subsequently limonite was deposited in voids after some low-boiling organic compounds. Alternatively organic material could be adsorbed on the surface of the limonite aggregates. It will be shown that the primitive material which ultimately became Orgueil must have been exposed to at least several hundred degrees centigrade, e.g. for the formation of euhedral troilite crystals. Consequently a distillation of organic compounds present in the accumulation of primitive matter appears likely.

It is now obvious that the type V organized elements (Claus and Nagy, 1961) or Sexangulatus Celestites (Staplin, 1962) mainly are altered troilite crystals (see figs. 7 and 11 and p. 6). Mueller

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(1962) and Anders and Fitch (1963a) reached the same conclusion. The later suggestion by Fitch and Anders (1963b) that the type V organized elements are deformed pollens is, like the proposition of extraterrestrial fossils (Claus and Nagy, 1961), based entirely on a morphological argument.

3. QUANTITATIVE RELATIONS

In section 2 and table 4c figures for the quantities present of some minerals are given. They have been derived by means of volumetric estimates from electron micrographs and microscopical observations and from the complete and partial chemical analyses of Orgueil (Wiik, 1956; Jarosewich, table 2) and of various minerals. A second analysis of Orgueil by Wiik (in Mason, 1962) gave virtually the same results.

In these petrochemical calculations some arbitrariness was necessary. The following steps were followed in the calculation:

1. The analyses by Wiik (1956) and Jarosewich (see table 2) were recalculated to an ignition loss free basis, assuming that both samples had the same amount of ignition loss. The number of moles available per 1000 g of this ignition loss free matter is given in table 4a. The number of moles of native sulphur, S, water soluble sulphate, SO_4^{2-}, and magnesium, Mg^{2+}, are given in table 4b. The figures in tables 4a and 4b are more accurate than is warranted by the chemical analyses but have been used in order not to introduce calculation errors.

2. The amount of negative sulphur is then found to be 0.542 moles, S according to table 4b.

3. From step 2 and the quantities of sulphates * in table 4b it is found that the amount of FeS can at most be 0.517 moles.

4. All phosphorus is used to form 0.021 moles merrillite of the composition $Na_2Ca_3(PO_4)_2O$.

5. All silicon is used to form chlorite (the composition is given in table 1 and with the formula given on p. 3). This process also consumes all nickel.

6. All water soluble magnesium is used to form 0.559 moles magnesium sulphate of the composition $MgSO_4$.

7. All remaining magnesium and some iron form 0.314 moles breunnerite of the composition $Mg_{0.8}Fe_{0.2}CO_3$.

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* It is possible that the content of SO_4^{2-} in the meteorite is larger than Jarosewich found since some sulphates like gypsum are not very soluble.

8. All remaining calcium forms 0.169 moles gypsum of the composition $CaSO_4 \cdot 2H_2O$.

9. All remaining sulphate forms 0.043 moles sodium sulphate of the composition Na_2SO_4.

10. All remaining iron forms 0.260 moles magnetite, Fe_3O_4, and 0.051 moles limonite, FeOOH. (There is no way to find these abundances from chemical data, but microprobe analyses approximately suggest their relative quantities.)

11. All remaining carbon forms 2.441 moles graphite,* C.

12. After steps 1-11 there remain (except oxygen and hydrogen)

element	*moles*
Na	0.127
K	0.016
Cr	0.051
Co	0.009
Al	0.065
Ti	0.009
Mn	0.029

which make up only 1.05 percent of ignition loss free material. Part of these metals (particularly sodium) are probably present in the chlorite, which has a slight deficiency in metal ions (see p. 3). Some manganese and potassium is probably present in carbonates and sulphates (Nagy and Andersen, 1964).

4. TEMPERATURE AND PRESSURE CONDITIONS DURING THE FORMATION OF THE MINERALS

The temperatures that controlled the formation of the minerals in Orgueil can be estimated by the following relations.

There are hexagonal, tetragonal, and monoclinic modifications with approximately the composition FeS. The hexagonal form is stable from 743°C down to at least 325°C (Arnold, 1962), whereas the monoclinic form is unstable above 265°C (Moh and Kullerud, 1964). This indicates that the FeS-phase in Orgueil was formed above 265°C, but an exact minimum temperature is difficult to ascertain since the stability field for the intermediate FeS form is unknown (Moh and Kullerud, 1964). Since Orgueil is water rich, it can be expected that a high water pressure will change the stability relations. Studies of the system Fe-S-H_2O indicate that $FeS \cdot nH_2O$,

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* Vdovykin (1964) found graphite in Ivuna but whether it exists in Orgueil is not known.

hydrotroilite, may be stable at 100°C, which also indicates that the troilite formed at high temperatures (Moh and Kullerud, 1964).

Fe_3O_4 can be stable from very high temperatures, the melting point being 1591°C down to low temperatures (see figs. 15 a-b and 16 a-b), but the extent of the stability region depends on the partial pressures of oxygen, carbon dioxide, and hydrogen sulphide.

Fe_3O_4 and FeS are stable together at least from 675°C (Kullerud, 1957) down to 325°C. Between 675 and 560°C (see fig. 12) FeS and Fe_3O_4 are stable together with either FeO or FeS_2 but not with Fe, Fe_2O_3, or S. Below 560°C (see fig. 13) FeS and Fe_3O_4 are stable together with either Fe or FeS_2 but not with Fe_2O_3 or S. It therefore seems evident that troilite and some of the magnetite in Orgueil represent an early association (see p. 5) that is not in equilibrium with native sulphur or limonite in the groundmass.

The stability conditions of chlorite are little known. According to Nelson and Roy (1958) 14Å chlorites may alter to 7Å chlorites when the temperature sinks below 350-500°C. The broad diffuse (001) peak and the absence of a well formed 14Å peak in the X-ray diffraction pattern of the Orgueil chlorite (Nagy et al., 1963a) indicate a stacking disorder in the structure. This suggests that the chlorite was formed at low temperature. It is probable that the iron content of the Orgueil chlorite will change these relations somewhat, since the phase diagrams by Nelson and Roy (1958) refer to iron-free chlorites. The period of formation of the chlorite is uncertain but probably it acquired its present appearance about the same time as limonite was formed since both indicate an aqueous environment rich in ferric iron.

Limonite probably was formed at low temperatures since goethite decomposes above 170°C at 900 bars (Schmalz, 1958). Limonite and native sulphur are clearly later than troilite (see figs. 4 and 7) and probably formed simultaneously with the chlorite.

The presence of gypsum in the veins indicates that they were formed at temperatures below 100°C, probably in the range 0-42°C according to the results by Posnjak (1938, 1940). MacDonald (1953) showed that gypsum will precipitate out of seawater at all temperatures below 34°C (at one atmosphere) if the deposition is an equilibrium process. He further showed that variations in the pressure have only small effects; thus a pressure of 100 bars only raises this temperature to 35°C. Both Posnjak and MacDonald showed that at these low temperatures gypsum and not anhydrite was the stable form even in salt solutions 4.8 times more saline than seawater. It cannot be denied, however, that anhydrite might have been the primary mineral in Orgueil and that gypsum was formed by hydration during sample preparation or some other time after the fall.

The low temperature of formation and their occurrence in the veins indicates that the sulphates are among the latest formed minerals in Orgueil. The period of formation for the carbonates is less evident but their fresh appearance makes it highly probable that they also belong to the latest formed minerals in Orgueil.

No good geologic manometer is present so far as we presently know. The brecciation of the meteorite before the formation of the veins indicates that the lithostatic pressure was not very high when the minerals in Stages II and III (see table 5) were formed.

Table 5 summarizes the mineralogical and paragenetical evidence given in sections 2 to 4.

5. STABILITY CONDITIONS AND THE FORMATION OF THE MINERALS

The natural approach would be to study the formation of the minerals in a chronological order but this is difficult to do without any preconceived idea of the parent material for Orgueil. It is possible, however, to start with a study of the late minerals that were formed during Stage III (see table 5). Once possible stability conditions for these are established their formation is easier to explain. This study shows that the veins most probably were formed in an open system, perhaps with free oxygen or peroxide as oxidizer. The tuffaceous structure and the presence of hydrous phases in the Orgueil meteorite indicate that the minerals may have been formed at the surface of a meteorite parent body.

To analyse the mineral forming conditions DuFresne and Anders (1962) and Nagy et al. (1963a) used *e*-pH diagrams. Like acid-base and redox diagrams * they show the stability relations between various chemical species, but they fail to indicate in what quantities the substances take part in the reactions (Boström, 1965). Further the sizes of various stability areas for different compounds in an *e*-pH diagram, for example, depend on the activities of various chemical species in the solution. For this reason the order of magnitude of these activities must be known before diagrams can be constructed for

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* The reader is assumed to be familiar with the construction and use of such diagrams. They are extensively discussed elsewhere, e.g. Hägg (1940), Delahay, Pourbaix, and van Rysselberghe (1950), Sillén (1952, 1959), and Boström (1965).

the discussion below. The notation that will be used in the following is given in the Appendix.

The activities can be found in different ways. If the association is quantitatively very small compared with the solution with which it is in contact, it would be justified to assume that the composition of the solution changes little during the reactions so that consumption and production of various ions such as H^+ and OH^- can be disregarded (Boström, 1965). Another solution is possible for closed systems where we know how much has been consumed and produced of various species. It is then sometimes possible to find the activity distribution in the solution (op. cit.).

These approaches cannot be used in the present case since there is no evidence to justify the first approach, and there are no safe indications of the quantitative relations before the vein-forming reactions started. However, at equilibrium with a solution all solid phases must have their solubility products satisfied, and electroneutrality must hold for the solution. By means of these relations the activities can be calculated and *e*-pH diagrams can be drawn, after which it is possible to analyze the mineral-forming conditions. The physicochemical constants are given in tables 6a-6c. The variation in the stability constants is small between 0° and 42°C, in which range gypsum can be expected to form (see p. 8), and we can therefore with good approximation use data for 25°C and 1 atm. for the main part of the discussion. How the constants are calculated is described in the appendix, p. 24. The ionic strength is unknown and the activity coefficients therefore have to be assumed to be close to unity.

From the descriptions above it seems natural to test whether epsomite, gypsum, breunnerite, and dolomite can be stable together. The stability relations between the three first mentioned minerals will be studied first.

It may be objected that the degree of hydration is unknown in the sulphates and that some hydration took place after the fall of the meteorite. However, if the minerals were formed at low temperatures in an aqueous environment, the sulphates probably would be precipitated in hydrated form.

For the late minerals the following formulas will be used.

epsomite	$Mg\,SO_4 \cdot 7H_2O$
gypsum	$Ca\,SO_4 \cdot 2H_2O$
breunnerite	$Mg_{0.8}Fe_{0.2}CO_3$
dolomite	$Ca\,Mg\,(CO_3)_2$

In the aqueous solution electroneutrality must hold, that is:

$$2(Mg^{2+})+2(Fe^{2+})+2(Ca^{2+})+(H^{+})=$$
$$2(SO_4^{2-})+2(CO_3^{2-})+(OH^{-})+(HSO_4^{-})+(HCO_3^{-})$$

Further, from the assumption that breunnerite behaves as an ideal solid solution and from the activity products in table 4 and by setting $(Fe^{2+})=x$ we get: *

$$(Mg^{2+})=4x$$
$$(CO_3^{2-})=\frac{3.2\times 10^{-9}}{5x}$$
$$(SO_4^{2-})=\frac{4.2\times 10^{-5}}{4x}$$

If brucite should also be in equilibrium with the solution we have the additional condition:

$$(OH^{-})=\sqrt{\frac{8.9\times 10^{-12}}{4x}}=\frac{4.72\times 10^{-6}}{\sqrt{x}}$$

From the relations above and the fact that (table 4b)

$$\frac{(CO_3^{2-})(H^{+})}{(HCO_3^{-})}=4.69\times 10^{-11}$$

we further derive:

$$(HCO_3^{-})=\frac{2.88\times 10^{-8}}{x}$$

and:

$$(Ca^{2+})=\frac{2.4\times 10^{-5}}{4.2\times 10^{-5}}\times 4x=2.28x$$

(HSO_4^{-}) and (H^{+}) can be neglected (see fig. 14) since there are no indications of strongly acid conditions under which limonite or carbonates would be unstable.

Substituting the activities in the electroneutrality condition with the expressions derived for the various activities we get:

$$x^2-3.26\times 10^{-7}x=1.44\times 10^{-6}$$
$$x=1.21\times 10^{-3}$$

The calculated activities are given in table 7 for various pH values in the solution. Column *a* gives the activities in the solution when

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* It can be objected that (Mg, Fe) CO_3 is not an ideal solution. However, even if the ratio $\frac{(Mg^{2+})}{(Fe^{2+})}$ is varied between 1 and 10 the calculations below are little affected.

pH and (Mg^{2+}) are high enough to form brucite. Columns *b-d* give the activities in other solutions which fulfill the relations deduced above except that brucite is not stable. A check shows that electroneutrality holds for all these solutions and that breunnerite, gypsum, epsomite, and dolomite all have their activity products satisfied.

These calculations do not consider the valence changes in the sulphur or iron compounds. Figures 16a-b show in what areas of the system $Fe\text{-}H_2O\text{-}H_2CO_3$ the derived relations are valid. (Since the activity of $MgCO_3$ in breunnerite is larger than the activity of $FeCO_3$ the stability field for breunnerite should be larger than that for $FeCO_3$ in figs. 16a-b, but this difference is so small that it can be neglected for this study.) The shaded area indicates where the carbonates and sulphates can be stable together. By combining the calculated activities with the information in figures 16a-b we find that at 25°C the carbonates can only be at equilibrium with substantial quantities of sulphate when ($H_2CO_{3\ tot}$) $> 10^{-3}$. High temperature requires even larger carbonic acid activity. When ($H_2CO_{3\ tot}$) is about 10^{-2} at 25°C this condition is fulfilled between $pH = 5\text{-}7$. Of interest is also that under these conditions magnetite is a stable phase.

Under these neutral or slightly acid conditions breunnerite, gypsum, epsomite, dolomite, and magnetite can be stable together. The activities in table 5 further show that compounds such as calcite and melanterite, $FeSO_4 \cdot 7H_2O$, are not stable under such conditions. It is an interesting fact that neither of these minerals has been observed in Orgueil or carbonaceous meteorites in general. The calculations further show that the carbonates and sulphates discussed above are not stable with brucite.

The presence of sodium sulphate has not been considered above, since the total amount of sodium sulphate present seems to be very small, as indicated on page 8.

This study does not prove that the vein minerals were formed simultaneously with the carbonates but it is possible and seems very likely. Figures 15, 16, 17, and the data in table 4 further show that the association of brucite, troilite, native sulphur, sulphates, and carbonates is unstable. Thus, for instance, brucite only should be stable at $pH = 10.1$, a value that will be only slightly decreased by the Fe^{2+} content of the solution. It is therefore obvious that the conditions in Orgueil do not represent equilibrium between all the coexisting phases, which is also clearly illustrated by figure 7 and by the stability data given in section 4.

The seemingly simplest explanation of how the low-temperature minerals were formed would be to assume that they were formed as a result of reactions between phases in the present groundmass.

Redox processes among limonite, troilite, and native sulphur are possible (figs. 15 and 17), forming SO_4^{2-} Fe^{2+} and Fe_3O_4. The following equations for the limiting cases can be written (the figures below the formulas indicate the number of moles consumed or formed during the reaction, assuming that 0.77 moles SO_4^{2-} is formed by the process):

$$\begin{array}{lccccccccccc}
1. & 26\,\mathrm{FeOOH} & + & \mathrm{FeS} & + \rightarrow & \mathrm{SO_4^{2-}} & + & 9\mathrm{Fe_3O_4} & + & 12\mathrm{H_2O} & + & 2\mathrm{H^+} \\
 & 20.02 & & 0.77 & & 0.77 & & 6.93 & & 9.24 & & 1.54
\end{array}$$

$$\begin{array}{lccccccccccc}
2. & 18\,\mathrm{FeOOH} & + & \mathrm{S} & + \rightarrow & 6\mathrm{Fe_3O_4} & + & \mathrm{SO_4^{2-}} & + & 8\mathrm{H_2O} & + & 2\mathrm{H^+} \\
 & 13.86 & & 0.77 & & 4.62 & & 0.77 & & 6.16 & & 1.54
\end{array}$$

$$\begin{array}{lccccccccccc}
3. & 8\,\mathrm{FeOOH} & + & \mathrm{FeS} & + & 4\mathrm{H_2O} & \rightarrow & 9\mathrm{Fe^{2+}} & + & \mathrm{SO_4^{2-}} & + & 16\,\mathrm{OH^-} \\
 & 6.16 & & 0.77 & & 3.08 & & 6.93 & & 0.77 & & 12.32
\end{array}$$

$$\begin{array}{lccccccccccc}
4. & 6\,\mathrm{FeOOH} & + & \mathrm{S} & + & 2\mathrm{H_2O} & \rightarrow & 6\mathrm{Fe^{2+}} & + & \mathrm{SO_4^{2-}} & + & 10\,\mathrm{OH^-} \\
 & 4.62 & & 0.77 & & 1.54 & & 4.62 & & 0.77 & & 7.70
\end{array}$$

Considering the large quantities of H^+ or OH^- formed, the assumption of a local equilibrium, as shown by reactions 1 to 4, is unlikely. By combining reactions 1 and 3, and 2 and 4 the following formulas are derived in which the production of hydrogen and hydroxyl ions is negligible:

$$\begin{array}{lccccccccccc}
5. & 24\,\mathrm{FeOOH} & + & \mathrm{FeS} & \rightarrow & 8\mathrm{Fe_3O_4} & + & \mathrm{Fe^{2+}} & + & 12\,\mathrm{H_2O} & + & \mathrm{SO_4^{2-}} \\
 & 18.48 & & 0.77 & & 6.16 & & 0.77 & & 9.24 & & 0.77
\end{array}$$

$$\begin{array}{lccccccccccc}
6. & 16\,\mathrm{FeOOH} & + & \mathrm{S} & \rightarrow & 5\,\mathrm{Fe_3O_4} & + & \mathrm{Fe^{2+}} & + & \mathrm{SO_4^{2-}} & + & 8\mathrm{H_2O} \\
 & 12.32 & & 0.77 & & 3.85 & & 0.77 & & 0.77 & & 6.16
\end{array}$$

The observed proportions of SO_4^{2-}, Fe^{2+}, and Fe_3O_4 among the late minerals do not agree with these results. According to Nagy (pers. com.) some magnetite occurs in the veins, but according to equations 5 or 6 magnetite should be a common vein mineral, which is not the case. Further, processes like 1 to 6 require more iron than is present according to the bulk composition of the meteorite. It may be objected that sulphate-forming processes have been taking place in large volumes of the parent body and that the mobile sulphate has been enriched in certain parts of the parent body, but this can probably only account for some vein sulphate and not for the main part of the sulphate which is found in the groundmass.

Another explanation could be that the original groundmass had a chemical composition identical with the present gross composition of the meteorite. Aqueous solutions attacked the walls of fissures and reprecipitated dissolved fractions as sulphates without major redox processes. Such a leaching process might have taken place late in the development of the meteorite, but it cannot explain how other late minerals or the original nonequilibrium assemblages of minerals in the groundmass were formed. The assumption of a closed system thus seems to be impossible.

Consequently the minerals were probably formed in an open system. The problem is to find an oxidizer to explain the formation of both sulphate and limonite.

It is possible that after primordial dust had formed a parental meteorite body, reduction processes took place in the central part of the body (Ringwood, 1961) or in other hot zones (Anders, 1963; Fredriksson, 1963). Gaseous emanations like CO_2, CO, and H_2O moved from these hot zones to the outer parts of the parent body. This may explain the origin of the water and CO_2. However, CO_2 is too weak an oxidizer to form goethite and sulphate from troilite, as can be observed in figure 17 and equation 7.

7. $H_2O_{(\ell)} + CO_{2(g)} + FeS \rightarrow FeOOH + CO_{(g)} + 1/2\ H_{2(g)} + S_{(s)}$

$$\Delta G_r = +22.41\ \text{Kcal}$$

Nor is it likely that thermal decomposition of water into oxygen and hydrogen can explain the redox processes, since the presence of goethite and gypsum shows that the reactions took place at very low temperatures where the dissociation of water can be considered negligible (Wagman et al., 1945; see table 4c). Nor is it likely that any of the reactions 8 to 12 played any important role, because of the large positive values for the free energy of reaction:

	Reaction	*Free energy of reaction* ΔG_r (Kcal)
8.	$S + H_2O_{\ell} \rightarrow H_2S_{(g)} + \frac{1}{2}\ O_2$	+47.5
9.	$S + 4H_2O_{\ell} \rightarrow H_2SO_{4aq} + 3H_{2(g)}$	+49.42
10.	$2H_2O_{(\ell)} + Fe_3O_4 \rightarrow 3FeOOH + \frac{1}{2}\ H_{2(g)}$	+0.68
11.	$FeS + 2H_2O_{(\ell)} \rightarrow FeOOH + S_{(s)} + 1\frac{1}{2}\ H_{2(g)}$	+15.60
12.	$FeS + 2H_2O_{(\ell)} \rightarrow FeOOH + H_2S_{(g)} + \frac{1}{2}\ H_{2(g)}$	+7.71

Certainly equation 10 could explain how limonite was formed from magnetite, but it does not explain the formation of native sulphur or sulphates or the corroded nature of the troilite. Equations 11 and 12 can to some extent explain this, but the free energies of reaction seem to be fairly large, particularly for 11, which is the only one that might explain the formation of both limonite and sulphur from troilite. Nor has this reaction been observed in any hydrothermal experiments; instead FeS seems to alter to hydrotroilite (Moh and Kullerud, 1964).

However, since the system is open, the hydrogen formed may escape from the system and thus make reactions like 11 more likely, but this would also mean that water can escape.

Another explanation would be that oxides present in primordial dust acted as oxidizers, but as was pointed out by Latimer (1950) the primordial dust must in the main have been characterized by rather reducing conditions since the quantities of oxygen present were small. Another strong argument against such an explanation is that the Orgueil meteorite as we see it today is the result of long and complex processes. It therefore seems unlikely that the oxidation state of the primordial dust could have any influence on late mineral-forming processes in the meteorite parent body.

Consequently it seems questionable that emanations from the inner part of the meteorite parent body or the composition of the primordial dust can explain the redox processes in the Orgueil meteorite.

A third possible explanation would be that water on the surface of the meteorite parent body has been exposed to ultraviolet radiation from the sun. This dissociates some of the water into several chemical compounds and radicals. The fast-diffusing hydrogen may escape from the surface at a more rapid rate than the heavier radicals and compounds of oxygen, part of which dissolve in the surface water and oxidize the upper layers of the meteorite parent body. This process was suggested by Poole (1941) as a geochemically important process for the earth. These reactions have been more extensively discussed by Harteck and Jensen (1948) and Dole (1949). It seems likely that these processes could occur on a meteorite parent body. Some support for such an assumption is found in the tuffaceous structure of the meteorite and the hydrated nature of the minerals, indicating that they have been formed close to the surface. Further, the mixture of redox states in the Orgueil meteorite resembles the surface conditions on the earth. In terrestrial unconsolidated rocks and soils, oxidized and reduced phases like limonite and bitumen are often mixed together. This depends on the fact that at low temperatures and pressures many systems approach equilibrium very slowly. The process can explain the observed quantities of sulphate, magnetite, and limonite, but it requires that the gravitational field be sufficiently large to retain the gaseous oxidizing emanations and liquid water, at least for some time. A geologically short period of oxidizing conditions should suffice to explain the processes discussed above, perhaps some thousand years, as is indicated by the crystallization time for dolomite as suggested by DuFresne and Anders (1962,

p. 1085). For such a short time even fairly small celestial bodies should be able to retain an atmosphere according to the calculations by Spitzer (1952) and Sytinskaya (1962), but it seems questionable that this celestial body can have been much smaller than the moon.

It could be proposed that oxygen was formed by living organisms as a product of carbon dioxide assimilation. However, the evolution of life and the subsequent formation of oxygen as a result of biological activity is a process that demands much longer time than the interaction between water and ultraviolet radiation, or some other kind of energetic radiation that can dissociate water. This also means that the parent body must be able to retain the atmosphere longer, perhaps some hundred thousand years, and consequently must be of larger size under otherwise identical conditions.

Oxidation processes involving free oxygen may lead to acid conditions. This is evident from the reactions 13 to 15. Organic matter could react with oxygen, forming water and carbon dioxide. The resulting acids could react with several phases, like brucite, forming late sulphates and carbonates according to reactions 16 and 17:

	Reaction	*Free energy of reaction* ΔG_r (Kcal)
13.	$2H_2O + 2S + 3\ O_2 \rightarrow 2H_2SO_4$	-241.3
14.	$2H_2O + 2FeS + 9/2\ O_2 \rightarrow Fe_2O_3 + 2H_2SO_4$	-371.8
15.	$3H_2O + 3FeS + 13/2\ O_2 \rightarrow Fe_3O_4 + 3H_2SO_4$	-534.4
16.	$H_2SO_4 + Mg(OH)_2 + 7H_2O \rightarrow MgSO_4 \cdot 7H_2O + 2H_2O$	< -17.3
17.	$H_2CO_3 + Mg(OH)_2 \rightarrow MgCO_3 + 2H_2O$	-11.1

Certainly many processes like 13 to 17 can be considered. There is as yet little evidence of these reactions, and therefore the qualitative discussion given above must suffice.

It should be remembered that these conditions do not imply that an oxygen-rich atmosphere or a strongly acid surface layer was formed; it seems more probable that the oxygen and the acids were consumed immediately after their formation.

It is also probable that redox processes were acting when the chlorite in its present state was formed, since chemical analysis (table 1) as well as diffraction data suggest a high content of ferric iron (see pp. 3-4). The parent material of the chlorite is not known but might have been a well-ordered ferrous chlorite, formed together with troilite and magnetite under hydrothermal conditions. Later oxidizing processes formed solutions rich in ferric iron and sulphate which could react with the early chlorite and transform it to the present chlorite. The sulphate and ferric ions may be delivered from the oxidation of troilite, which at the same time also could form native sulphur and limonite. Some oxygen may also have reacted directly with ferrous chlorite forming ferric chlorite. Limonite has not been observed in the veins; it is therefore probable that the oxidizing processes were declining in intensity or had ceased completely when the veins were formed. However, another explanation for the absence of limonite in the veins may be that since the solubility product for ferric hydroxide is very small the ferric iron could not migrate long distances before it was precipitated. It may also be suggested that limonite was formed from lawrencite, $FeCl_2$, after the fall of the meteorite. It is difficult to visualize, however, how lawrencite could survive the redox processes that formed ferric chlorite.

It has been suggested that alteration of olivines and pyroxenes of chondritic composition could form chlorite and brucite (Kerridge, 1964), but the high content of volatile elements like mercury, lead, and bismuth (Anders, 1964) makes it unlikely that the present groundmass has been exposed to magmatic temperatures. Another suggestion would be that periclase and olivine were mixed with the low-temperature phases, a process similar to the one that formed Murray (Fredriksson and Keil, 1964) and that periclase later was hydrated to brucite.

6. CONCLUSIONS

From the above discussions it is apparent that the Orgueil meteorite does not represent original solar material. On the contrary the meteorite has undergone extensive hydrothermal and low-temperature alterations, although these processes seem not to have changed the bulk chemical composition of the primitive, that is the pre-Orgueil, material seriously. The reason for this conclusion is that it has still a bulk composition that resembles the assumed solar composition (Suess and Urey, 1956; Aller, 1961; Anders, 1964). As has been discussed above, a high temperature magmatic pre-Orgueil stage can be practically ruled out, at least for the major fraction.

The following sequence of events for the development of the Orgueil may be suggested. A presumed primitive accumulation of dust, frozen gases, ice, etc. (Urey, 1952, 1963; Ringwood, 1960; Anders and DuFresne, 1962; and others), probably of the size of a large asteroid or possibly as big as the moon, develops hot zones either by short-lived radioactivity or possibly by slow collisions, that is, between bodies of which at least one has a very low density. One of the colliding objects might even have been a comet head as advocated by Urey (1963) and Urey and Murthy (1963). Conceivably, in such a collision, the energy may be dissipated relatively slowly within the larger body. Once formed it seems possible that such hot zones could be enforced by chemical reactions, possibly between free radicals* (Urey, 1952). If the dust planetoid was penetrated deep enough by the shockwaves, large quantities of magma may have been generated and retained for a sufficient time to give rise to processes resembling volcanism. As suggested by Ringwood (1961), Fredriksson (1963), and Fredriksson and Ringwood (1963), chondrules may well be the product of such explosive volcanism. Some chondrules may also form directly as splash drops (Urey and Craig, 1953, and others). The heat from the hot zone would influence the surrounding primitive material (Anders, 1963); hot gases will be driven toward the surface creating pneumatolytic to hydrothermal conditions such that troilite (FeS) might crystallize together with other minerals, probably layer lattice silicates. The latter minerals probably were the parent material for the present Orgueil matrix silicate, the chlorite. During the cooling-off period the troilite oxidizes to limonite, sulphur, and sulphate. At the same time the late carbonates and sulphates formed and the chlorite acquired its present composition. As has been shown it is probably necessary to assume an external source of oxidation, possibly free oxygen. This oxygen would be supplied by dissociation of water induced by ultraviolet light at the surface of the body. The surface is continuously reworked by the impact of smaller bodies or secondary objects produced in larger collisions. Such processes are vividly suggested by the Ranger pictures of the moon. The reworking of the surface would expose a considerable amount of Orgueil material to sunlight. Close to the pseudo-volcanic area (or areas) where pre-Orgueil material may be mixed with chondrules and heated to higher temperatures, similar processes may further account for meteorites like Murray (Fredriksson and Keil, 1964), which is a mixture of chondrules and mineral fragments of high temperature origin (Fredriksson and Reid, 1965) and low temperature phases similar to the bulk of the Orgueil.

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* Recently free radicals were found in the Mighei, group II, carbonaceous chondrite (Vinogradov et al., 1964).

APPENDIX

1. Notation

(A)	Activity of A
F	Faraday constant
G_r	Free energy of a reaction
H_f	Heat of formation
K	Thermodynamic equilibrium constant
P	Pressure
R	Gas constant
S	Entropy
T	Absolute temperature
e°	Standard electrode potential
n	Number of Faradays
pA	Negative decadic logarithm of (A); thus $\mathrm{pH} = -\log_{10}(\mathrm{H})$ $\mathrm{pFe_{tot}} = -\log_{10}(\mathrm{Fe_{tot}})$
pK	Negative decadic logarithm of K
ln	$\log_e$

2. Calculation of the physico-chemical constants

The standard redox potential and the equilibrium constant for a reaction are found by the expressions:

$$e^\circ = \frac{\Delta G_r}{n\,F}$$

and

$$\ln K = \frac{\Delta G_r}{-R\,T}$$

Almost all values for ΔG, ΔH, and S for 25°C, 1 atm. are derived from Latimer (1952) with exception for the values $\Delta H_f = 813.13$ K cal, S = 87.7e.u. for $MgSO_4 \cdot 7H_2O$ that were calculated by means of data in Kelley (1937, p. 101) and Latimer (1952, pp. 316, 359-369), and the value $\Delta G_f = -117.0$ K cal for goethite (Schmalz, 1958).

Most of the calculations are for 25°C, 1 atm. conditions. A few 100°C calculations have been made by means of data from Kelley (1960) and by the formulas for the variation of ΔG with temperature given in Kortüm (1960, pp. 398-410).

ACKNOWLEDGMENTS

The authors are greatly indebted to Profs. H. C. Urey and G. Arrhenius for much encouragement and helpful discussions. Drs. B. Mason, A. M. Reid, and G. Switzer read the manuscript and contributed many valuable suggestions. Discussions with Drs. E. Anders, E. P. Henderson, K. Keil, B. Nagy, and D. Weill are gratefully acknowledged. Mrs. B. Boström kindly did the electron microscope work. The work was generously supported by grants NsG 317-63 and NsG 688 from the National Aeronautics and Space Administration and an equipment grant G 12325 from the National Science Foundation. The electron microscopy work was supported by grant B 8069 from the National Science Foundation.

TABLES

TABLE 1.—*Electron probe analysis (in weight percent) of chlorite in the Orgueil meteorite* *

Si	14.9
Fe	15.6
Mg	12.9
Ni	1.4
Al	1.0
S	2.7

* Analyst, K. Fredriksson

TABLE 2.—*Partial analysis of the Orgueil meteorite* *

	Percent of total sample
Carbon tetrachloride and ether extracts	3.2
Sulphur in this extract	1.6
Water-soluble matter	18.2
Sulphate from this extract	6.9
Magnesium from this extract	1.3
Fe^{2+}	5.6
Total Fe	18.3
Fe^{3+} (by difference)	12.7

* Analyst, E. Jarosewich, Division of Meteorites, Smithsonian Institution, Washington.

TABLE 3.—*Cell dimensions (in Å)*

	a	b	c	d_{001}
Found in Orgueil	5.28±0.05	9.14±0.09		7-14*
Serpentines **				
Chrysotile (ortho-)	5.34	9.2	14.63	
Lizardite	5.31	9.20	7.31	
Septechlorites **				
Amesite	5.31	9.19	14.01	
Ferrous chamosite	5.415	9.38	7.11	
Ferric chamosite	5.255	9.10	7.062	

Chlorites ***

$a = 5.320 + 0.008\ (Fe^{2+} + Fe^{3+})$

$b = 9.202 + 0.014\ (Fe^{2+} + Fe^{3+})$

$d_{001} = 13.925 + 0.115\ (Si\text{-}4) \text{-} 0.025\ Fe^{3+}$

* The d_{001} value from Nagy et al. (1963, p. 544).

** From Deer, Howie, and Zussman (1962, pp. 167, 174).

*** Simplified from Hey (1954).

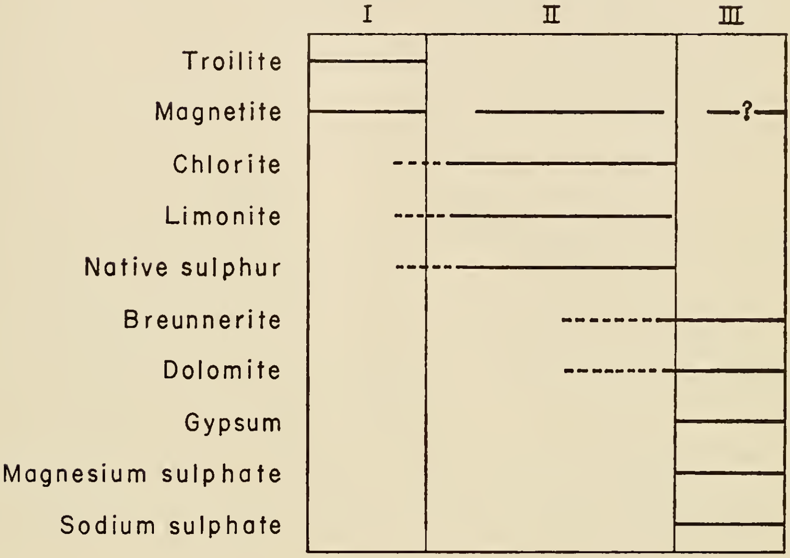
TABLE 4.—*Composition of the Orgueil meteorite*

	4a. Moles per 1000g (ignition loss free matter)
Fe	3.522
S	1.830
Si	4.009
Ti	0.009
Al	0.346
Mn	0.029
Mg	4.185
Ca	0.232
Na	0.255
K	0.016
P	0.042
H_2O	11.784
Cr	0.051
Ni	0.176
Co	0.009
C	2.755

4b. Moles per 1000g (ignition loss free matter)	
native sulphur	0.542
sulphate, SO_4^{2-}	0.771
water-soluble magnesium, Mg^{2+}	0.559
ferric iron, Fe^{3+}	2.444
ferrous iron, Fe^{2+}	1.074

4c. Calculated quantities of the minerals in Orgueil	
chlorite	62.6
magnetite	6.0
troilite	4.6
sulphur	1.7
limonite	0.5
merrillite	0.8
breunnerite	2.8
magnesium sulphate—x H_2O	6.7
gypsum	2.9
sodium sulphate	0.6
graphite	2.9
remaining metals	1.1
	93.2

Table 5.—*The succession of the Orgueil minerals*



The succession of the various minerals is indicated by full lines; dashed lines indicate possible extensions. I indicates early period with formation of high temperature minerals, the controlling temperature being several hundred degrees centigrade. II is a later stage with moderately high temperatures, probably not above 170°C, and water-rich environment. III represents late vein mineralizations formed in an aqueous environment at low temperature, probably below 40°C.

TABLE 6.—*Stability constants at 25° C, 1 atm.*

6a. Aqueous equilibria

$(Mg_{0.8}^{2+}\ Fe_{0.2}^{2+})\ (CO_3^{2-}) = 3.2 \times 10^{-9}$ (breunnerite) *
$(Ca^{2+})\ (Mg^{2+})\ (CO_3^{2-})^2 = 4.5 \times 10^{-20}$
$(Ca^{2+})\ (CO_3^{2-}) = 4.7 \times 10^{-9}$ (calcite)
$(Ca^{2+})\ (SO_4^{2-})\ (H_2O)^2 = 2.4 \times 10^{-5}$
$(Na^{+})^2\ (SO_4^{2-})\ (H_2O)^{10} = 8.7 \times 10^{-2}$
$(Mg^{2+})\ (SO_4^{2-})\ (H_2O)^7 = 4.2 \times 10^{-5}$
$(Mg^{2+})\ (OH^{-})^2 = 8.9 \times 10^{-12}$
$(Fe^{2+})\ (SO_4^{2-})\ (H_2O)^7 = 1.3 \times 10^{-12}$
$(Ni^{2+})\ (SO_4^{2-})\ (H_2O)^7 = 3.5 \times 10^{-2}$

* Assuming $FeCO_3$ and $MgCO_3$ to form an ideal solid solution.

6b. Other equilibria

$4\ CO_2 + 3\ Fe \rightarrow Fe_3O_4 + 4\ CO$	$K = 3.1 \times 10^{-3}$
$HCO_3^- \rightarrow H^+ + CO_3^{2-}$	$K = 4.69 \times 10^{-11}$

6c. Dissociation constant of water at various temperatures *

Reaction	*T° K*	*Equilibrium constant of formation,* K_f
$H_{2(g)} + \frac{1}{2}\ O_{2(g)} \rightarrow H_2O_{(g)}$	300	6.1×10^{39}
	400	1.7×10^{29}
	500	7.7×10^{22}
	600	4.3×10^{18}

* Data from D. D. Wagman et al. (1945).

TABLE 7.—*Activities of ions at various pH values in an aqueous solution in equilibrium with the solid phases* $Mg_{0.8}\ Fe_{0.2}\ CO_3$, $Mg\ SO_4 \cdot 7H_2O$ *and* $Ca\ SO_4 \cdot 2H_2O$.

	A	B	C	D
pH	10.1	7	5	4
(Fe^{2+})	1.2×10^{-3}	1.2×10^{-3}	3.8×10^{-3}	9.4×10^{-3}
(Mg^{2+})	4.8×10^{-3}	4.8×10^{-3}	1.5×10^{-2}	3.8×10^{-2}
(Ca^{2+})	2.7×10^{-3}	2.7×10^{-3}	8.7×10^{-3}	2.1×10^{-2}
(SO_4^{2-})	8.7×10^{-3}	8.7×10^{-3}	2.8×10^{-3}	1.1×10^{-3}
(CO_3^{2-})	5.3×10^{-7}	5.3×10^{-7}	1.7×10^{-7}	6.8×10^{-8}
(HCO_3^{-})	8.3×10^{-7}	1.1×10^{-3}	5.0×10^{-2}	1.3×10^{-1}
pH_2CO_{3tot}	5.9	2.9	1.3	0.9

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EXPLANATION OF PLATES

Figs. 1 A and B. Photomicrograph of thin section of Orgueil. Magnification 60×. Nicols half crossed in 1 B to increase contrast. According to the probe analysis the fragment has a composition similar to the matrix except for somewhat higher nickel and sulphur. Note the parallel structures around the fragment, suggesting that the fragment was harder than the surrounding material during agglomeration.

Fig. 2. Electron micrograph of overlapping crystals of the layer lattice silicate (chlorite, see p. 3), which constitutes approximately three-fourths of the meteorite. Note the pseudohexagonal habit of the crystals. Whole area: 3 x 2.2 microns.

Fig. 3. Electron diffraction pattern of one of the crystals in figure 2. The deduced latice spacings (in Å) $a = 5.28$, $b = 9.14$ agrees fairly closely with ferric chamosite (see page 4 and table 3).

Fig. 4. Photomicrograph of the magnetic fraction, 44-88μ, of a powdered sample of Orgueil. The shiny globules are native sulphur (S) closely associated with hexagonal troilite (FeS). Note particularly the corroded troilite crystals, two of which have holes. Two opaque black spherules as well as some of the aggregates consist of magnetite (Fe_3O_4).

Figs. 5 A and B. X-ray microradiographs of a thin section of Orgueil in CuKα radiation (A) and in CrKα radiation (B). The particles indicated with A consist of magnetite (Fe_3O_4) and those with B of troilite (FeS with some Ni). The absorption in magnetite as compared with the matrix is considerably decreased for CrKα, while troilite, B, shows same or increased contrast in this radiation. Note the corroded hexagonal plate of troilite, lower right.

Figs. 6 A and B. Microradiographs (compare fig. 5) showing rounded hollow particles of magnetite (Fe_3O_4). The small hexagonal particle upper left is troilite.

Fig. 7. Photomicrograph and electron probe scanning pictures of corroded troilite, partly altered to ferric hydroxides, limonite. The back scattered electron picture (BSE) indicates the average atomic number of the phases present, the three other scan pictures show distribution of iron, sulphur, and nickel. Most of the opaque grains are magnetite. Note that nickel is homogeneously distributed in the matrix; the concentration is approximately 1 percent, almost the same as in troilite and limonite (see p. 6). Sulphur is also present in the matrix but less evenly distributed than nickel; the sulphur probably occurs as a sulphate impregnation of the layer lattice silicate. The scanned area is 50 x 50 microns.

Figs. 8 A and B. Photomicrograph of thin section of powdered sample of Orgueil; magnetic fraction 44-88 microns. A is transmitted light, B reflected light. The pictures illustrate the close association of native sulphur, transparent in A, whitish gray in B, with troilite. B further illustrates the extremely corroded state of the hexagonal troilite crystals, which explains their odd shapes and colors.

Fig. 9. Distribution of Na^{23}, Mg^{24}, Mg^{25}, and Si^{28}, in polished sections of Orgueil. The pictures were obtained by means of secondary ion emission spectroscopy (Castaing and Slodzian, 1962a and b, and 1963). The pictures illustrate composite veins of magnesium and sodium sulphates. The veins are enriched in sodium, particularly at the vein walls. The matrix material also contains small amounts of evenly distributed sodium. Note that no direct comparison between different *elements* can be made on the basis of the recorded intensities. The black grid represents strips of aluminum evaporated onto the sample to overcome its low conductivity. The size of the square holes is approximately 50 x 50 microns.

Fig. 10. Electron probe scanning pictures of polished section of Orgueil, showing one grain ~10 microns, of periclase MgO, possibly formed by vacuum and heating in the electron microprobe (see p. 9). All the iron-rich grains, white in the back scattered electron (BSE) as well as in the iron picture, are magnetite, as concluded from the deficiency in sulphur. Sulphur is rather homogeneously distributed through the matrix. The magnesium-rich grain to the right is probably brucite, $Mg(OH)_2$, partly altered to periclase, MgO, by the electron beam. Scanned area approximately 100 x 100 microns.

Fig. 11. Photomicrograph of thin section of Orgueil showing several hexagonal limonite particles representing completely altered troilite crystals, the largest of which is approximately 25 microns. Compare figures 5 and 7 and page 6. These particles seem indistinguishable from organized elements, group V (Claus and Nagy, 1961).

Fig. 12. Phase relations in the system Fe-O-S below 560°C and 675°C (after Kullerud, 1957).

Fig. 13. Phase relations in the system Fe-O-S below 560°C (after Kullerud, 1957).

Figs. 14 A and B. pH diagrams at 25°C, 1 atm. A: for the system H_2CO_3-H_2O. B: for the system H_2SO_4-H_2O.

Figs. 15 A and B. *e*-pH diagram for the system Fe-S-H_2O. There are no thermodynamic data available for hydrotroilite, $FeS \cdot nH_2O$, which seems to be the stable form at 25°C and 100°C. The field for FeS in the diagram thus gives the minimum extension of the stability field for hydrotroilite. The stability field for goethite, FeOOH, is not indicated but is somewhat larger than that for Fe_2O_3. Small figures attached to the lines indicate to what pS_{tot} value the lines refer; $pFe_{tot} = 2$. A: for 25°C, 1 atm. B: for 100°C, 1 atm.

Figs. 16 A and B. *e*-pH diagram for the system $Fe\text{-}H_2CO_3\text{-}H_2O$. Small figures attached to the lines indicate to what $pH_2CO_{3\,tot}$ value the lines refer; $pFe_{tot} = 2$. Shaded areas indicate where carbonates and sulphates may be stable together. A: for 25°C, 1 atm. B: for 100°C, 1 atm. The stability field for geothite, FeOOH, is not indicated but is somewhat larger than that for Fe_2O_3.

Fig. 17. *e*-pH diagram for the system $S\text{-}H_2O$ at 25°C, 1 atm. Small figures attached to the lines indicate to what pS_{tot} value the lines refer.

Fig. 18. *e*-pH diagram with the systems $Fe\text{-}H_2O$ and $H_2O\text{-}C$ superimposed on each other at 25°C, 1 atm.; $pFe_{tot} = 2$. The stability field for FeOOH, is not indicated but is somewhat larger than that for Fe_2O_3.

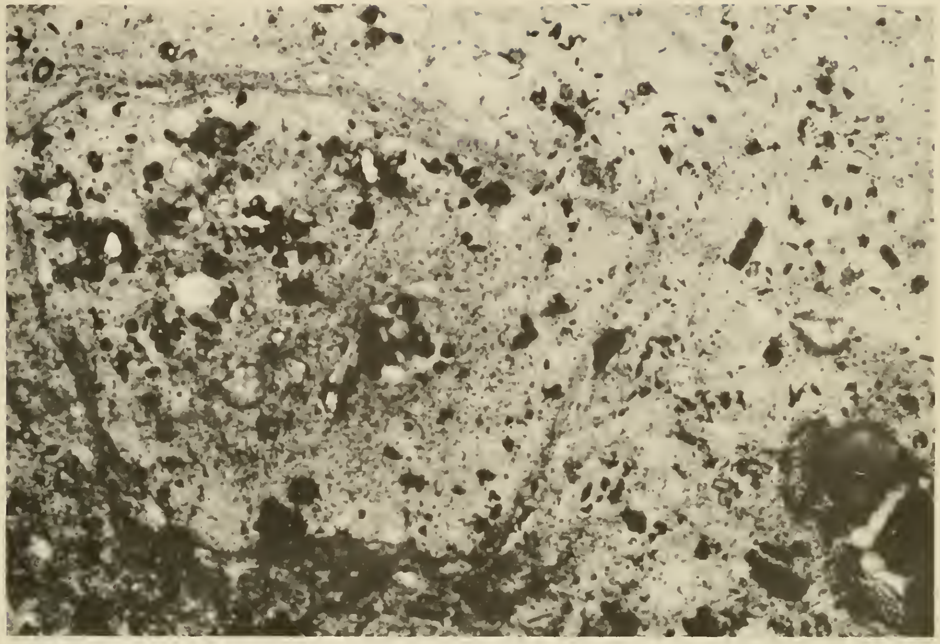


Fig.-1a

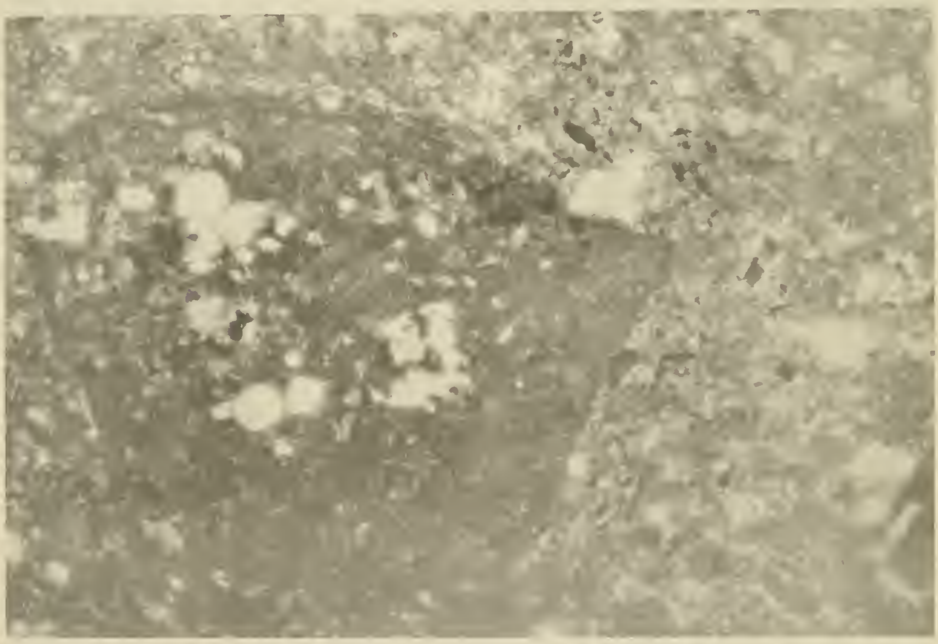


Fig.-1b

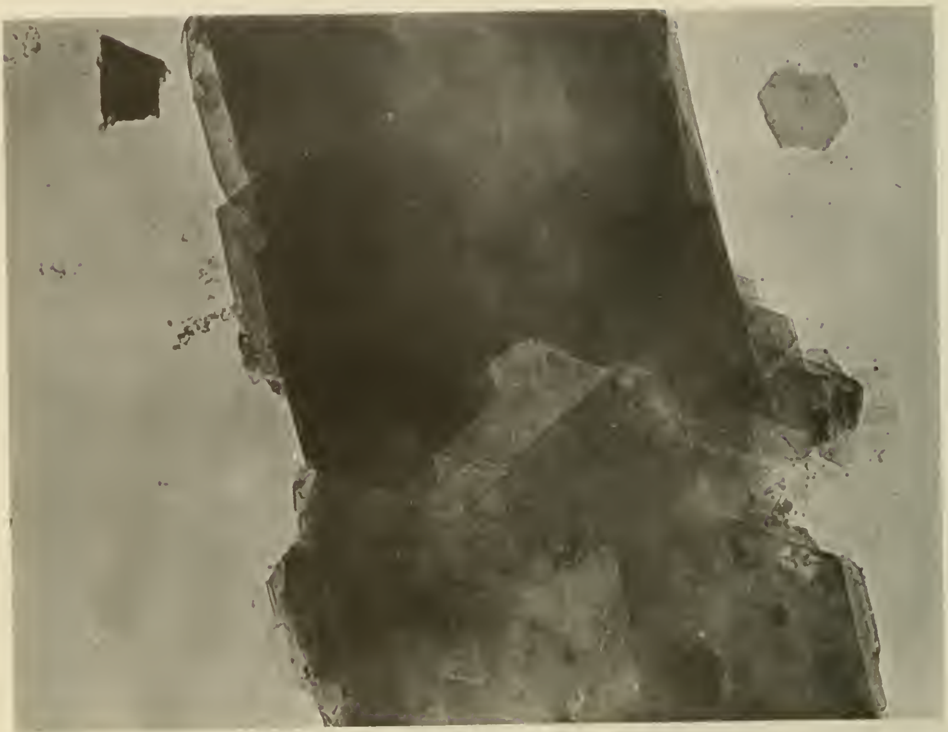


Fig.-2

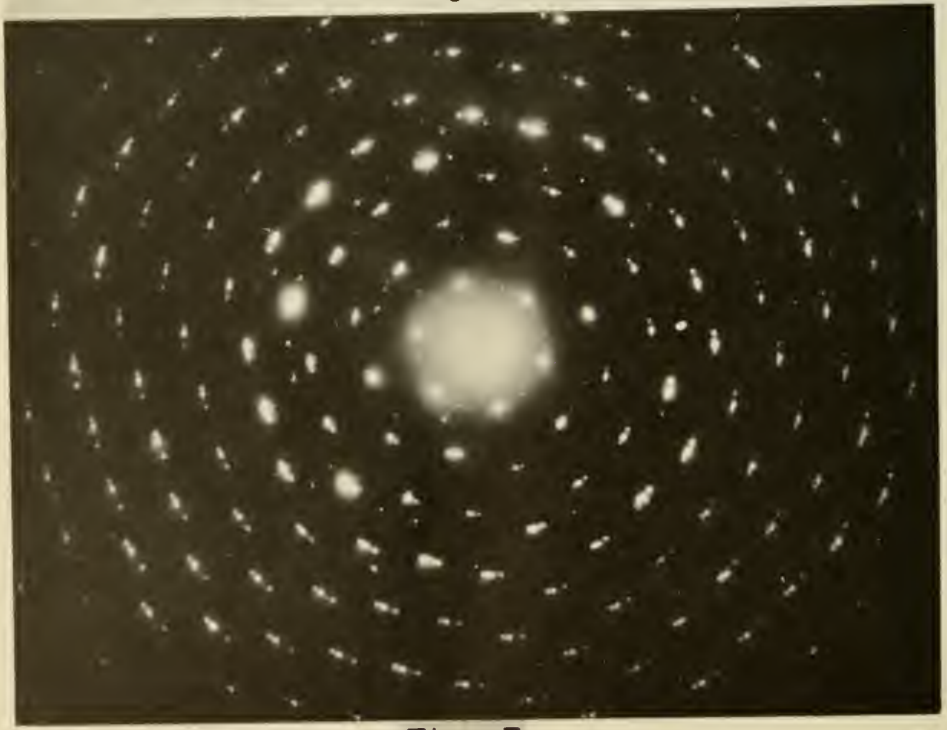


Fig.-3

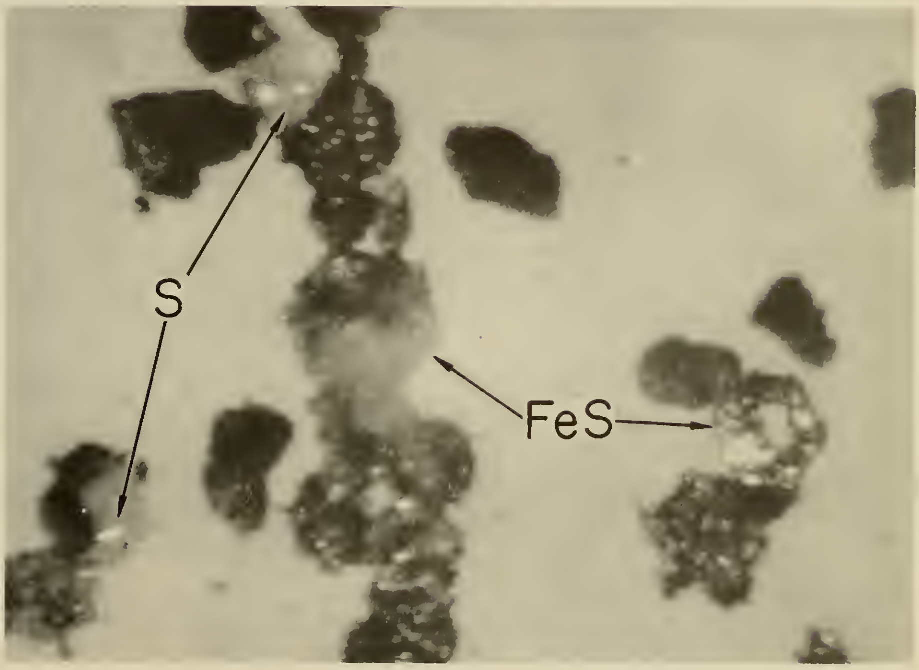


Fig. 4

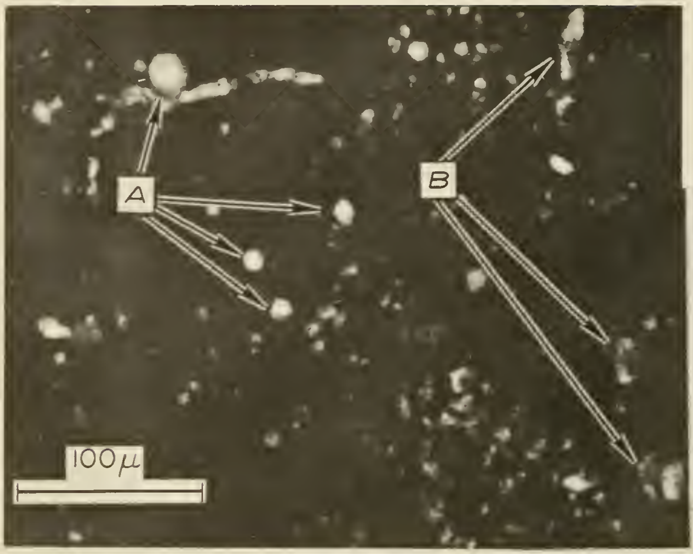


Fig.-5A

Fig.-6A

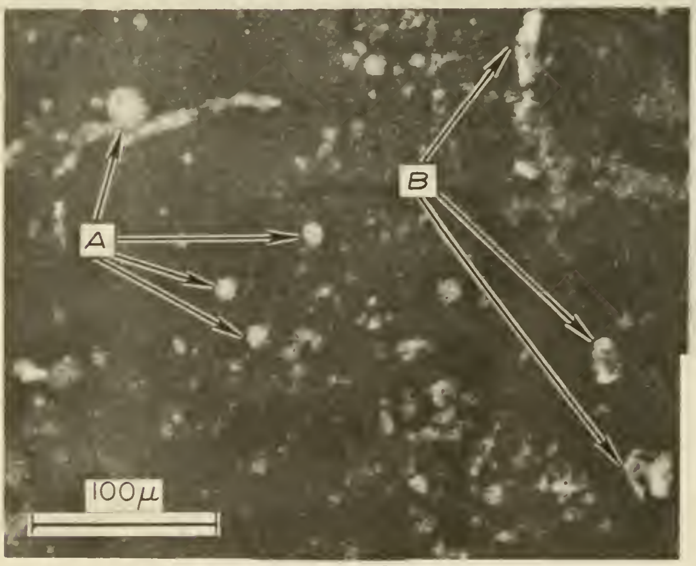


Fig.-5B

Fig.-6B

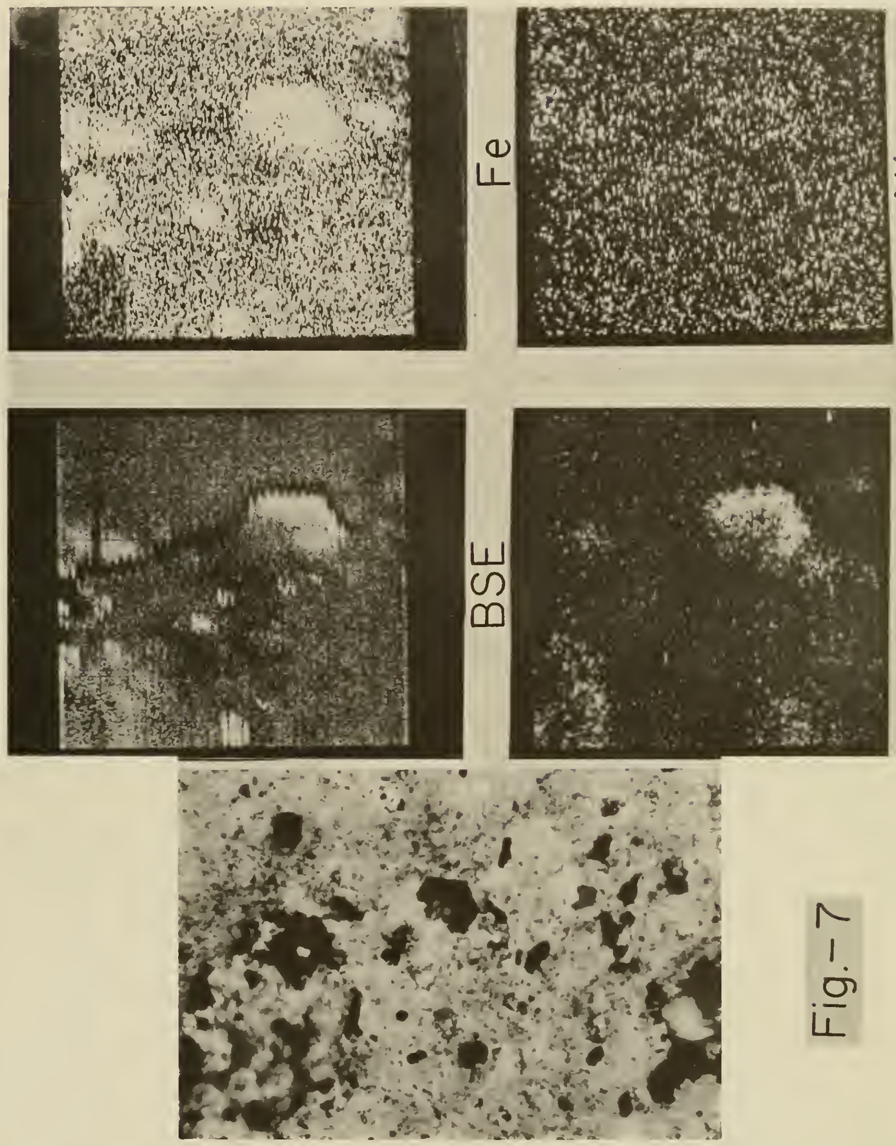


Fig.-7

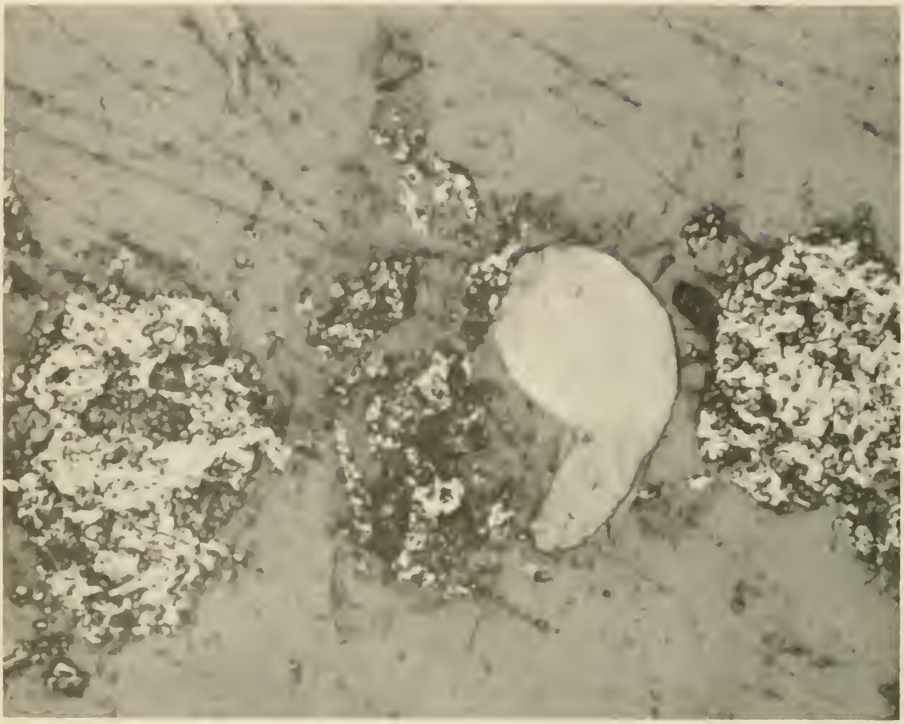
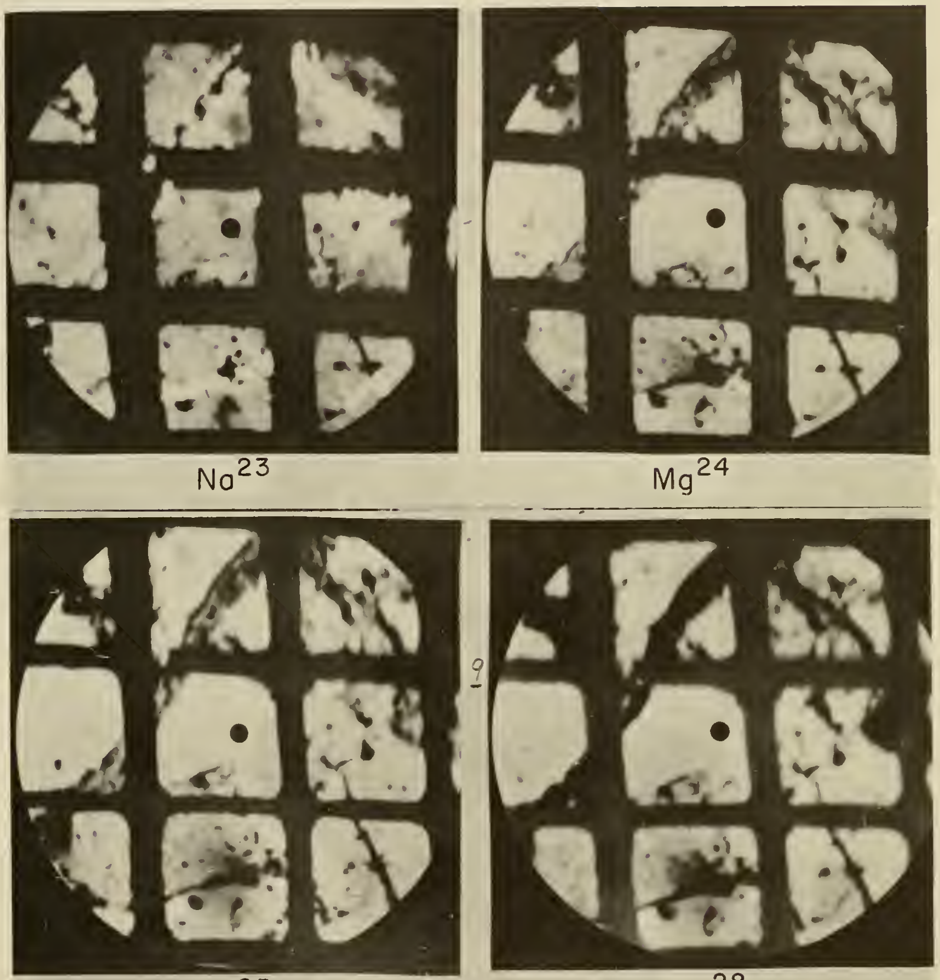


Fig.-8b

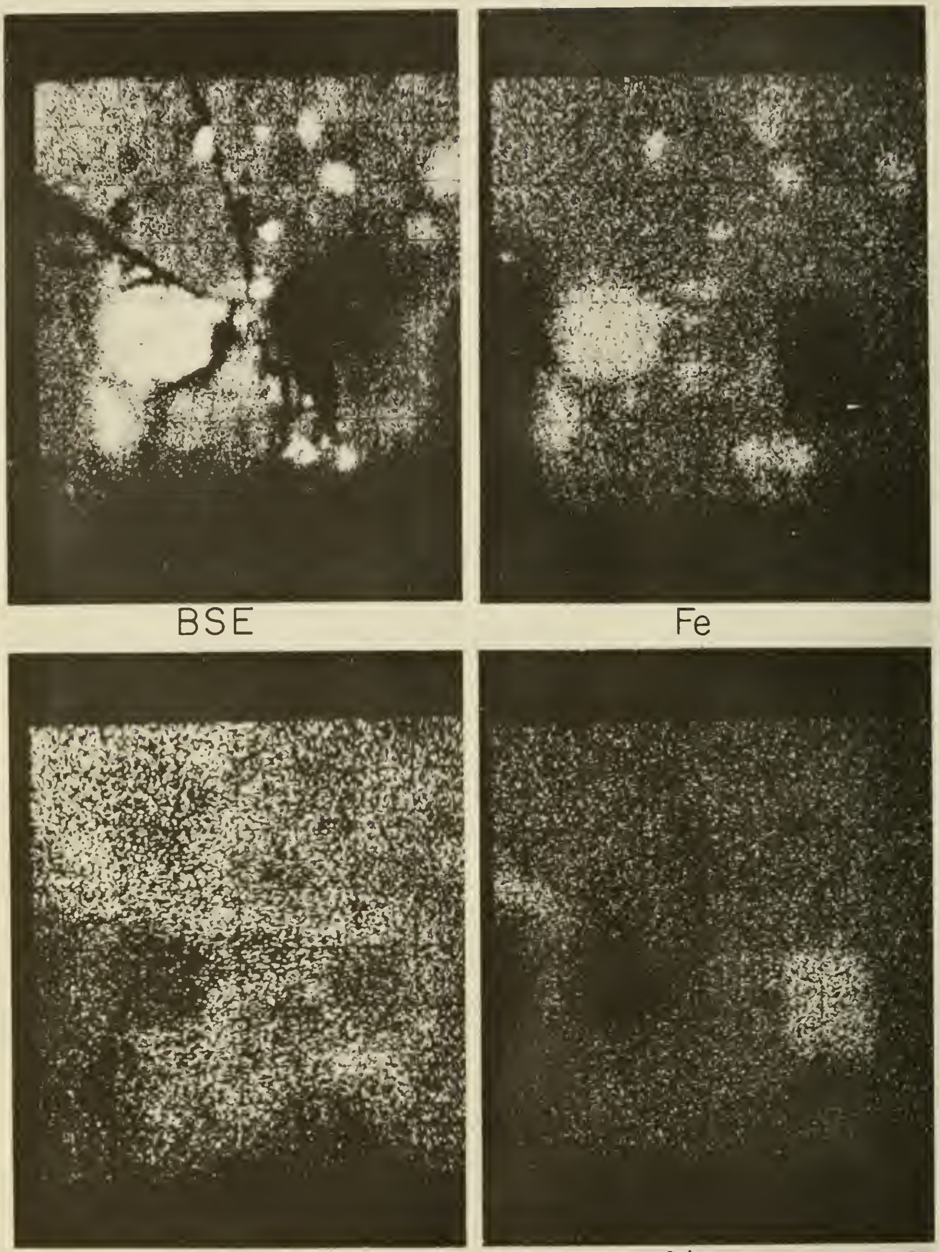
Fig.-8a



Na^{23} Mg^{24}

Mg^{25} Si^{28}

Fig.-9



BSE Fe

S Mg

Fig.-10

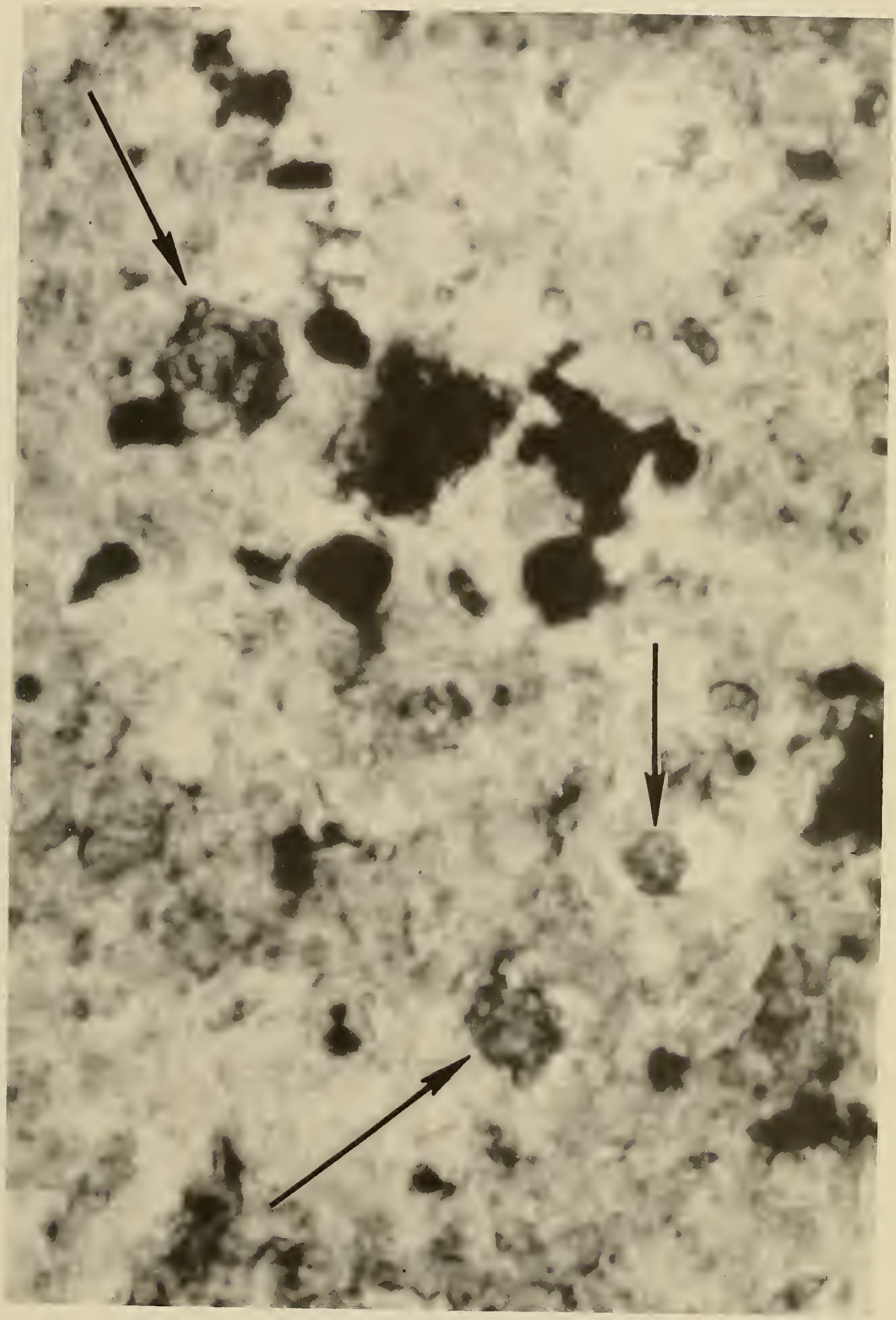


Fig -11

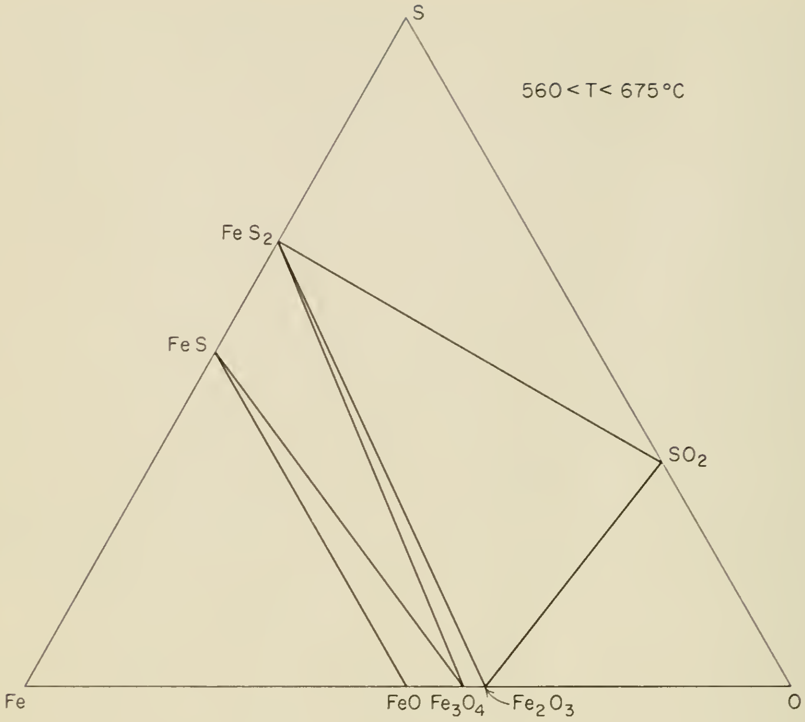
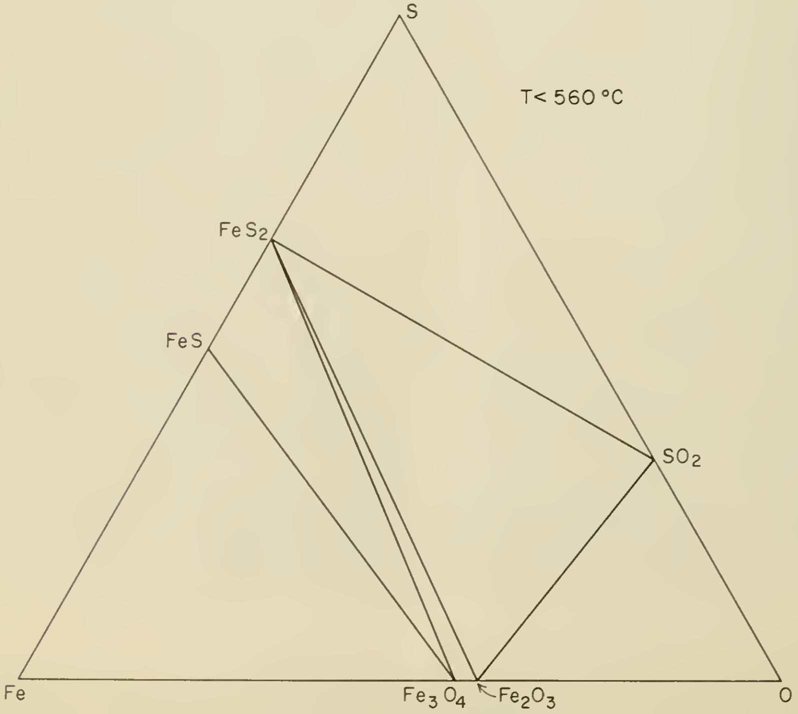

S
560 < T < 675 °C
Fe S$_2$
Fe S
SO$_2$
Fe
FeO
Fe$_3$O$_4$
Fe$_2$O$_3$
O

Fig-12


S
T < 560 °C
Fe S$_2$
Fe S
SO$_2$
Fe
Fe$_3$ O$_4$
Fe$_2$O$_3$
O

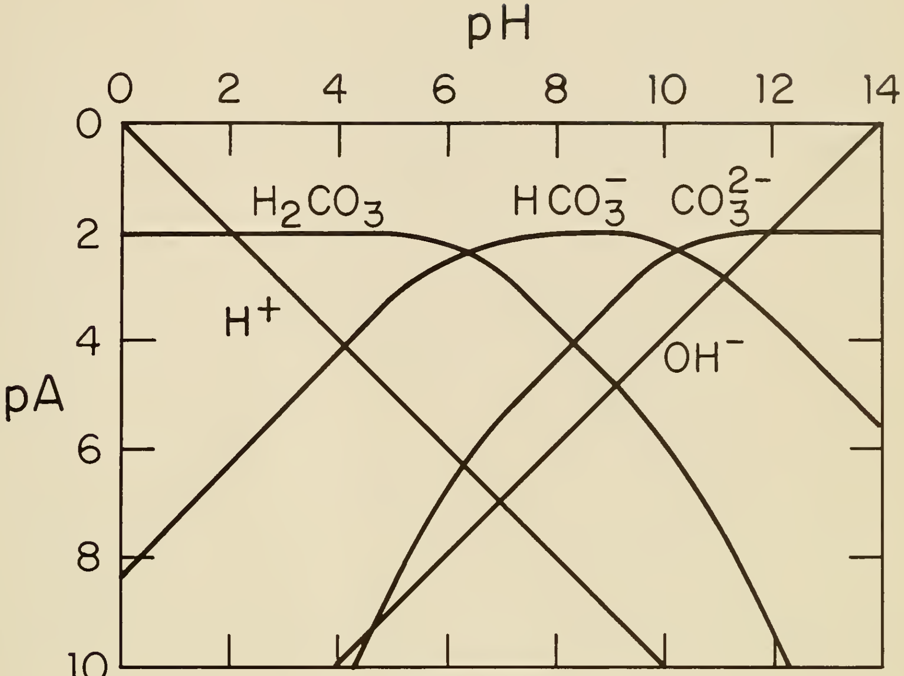


Fig.-14a

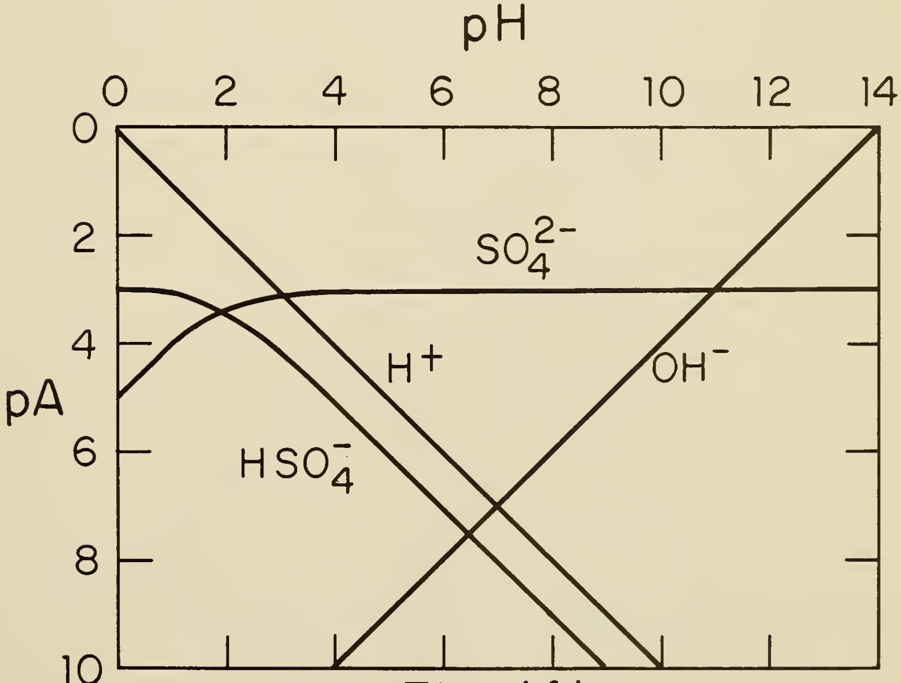


Fig.-14b

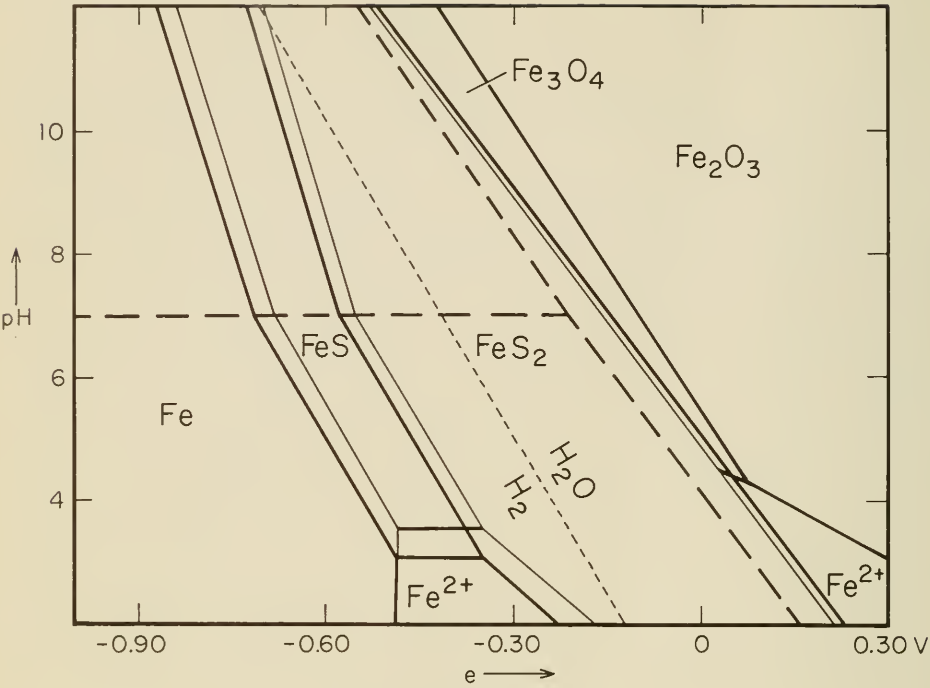


Fig.-15a

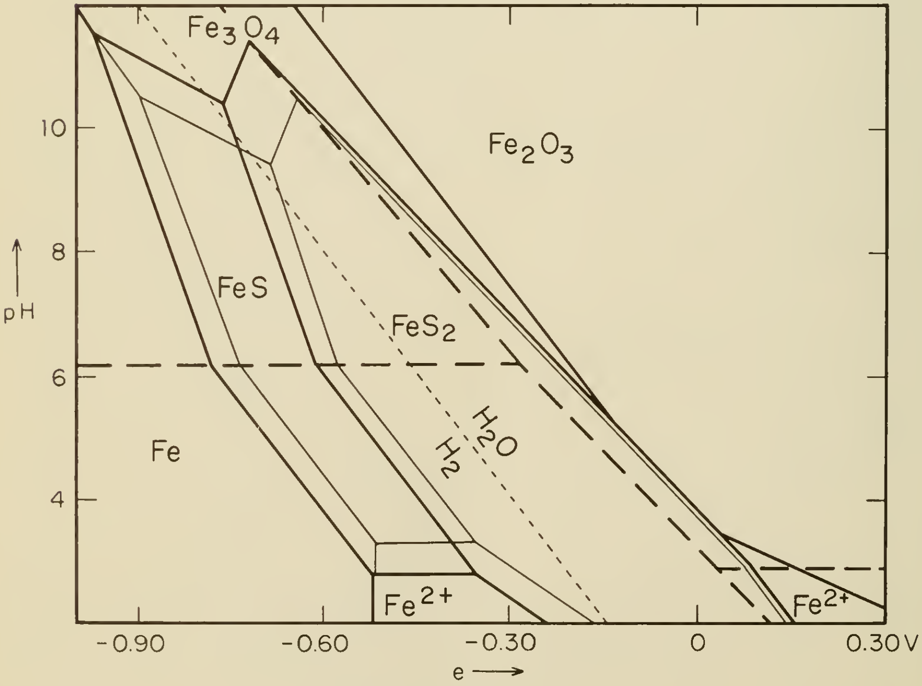


Fig.-15b

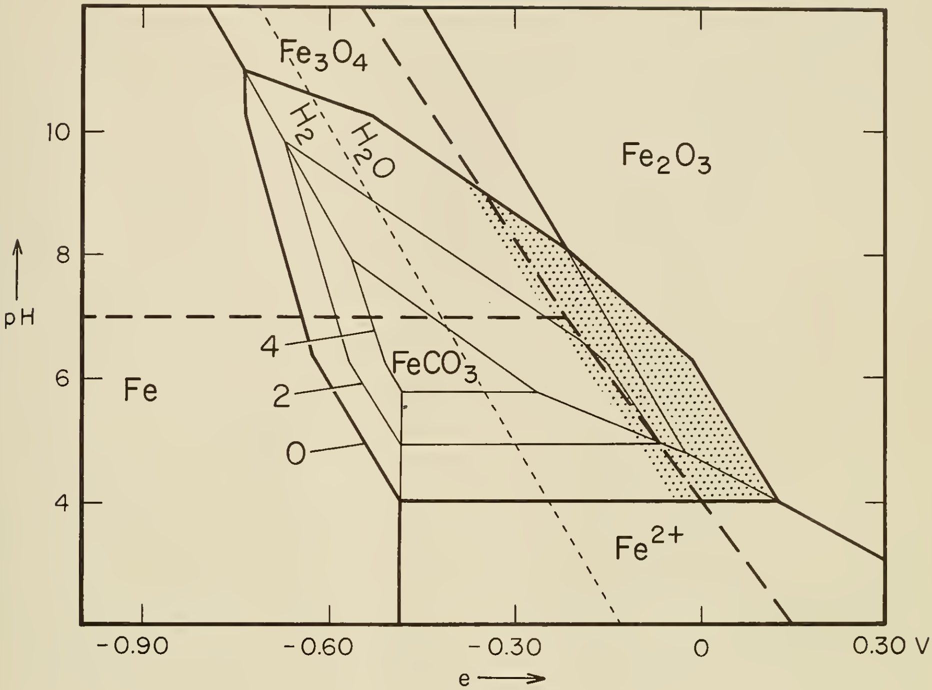


Fig.-16a

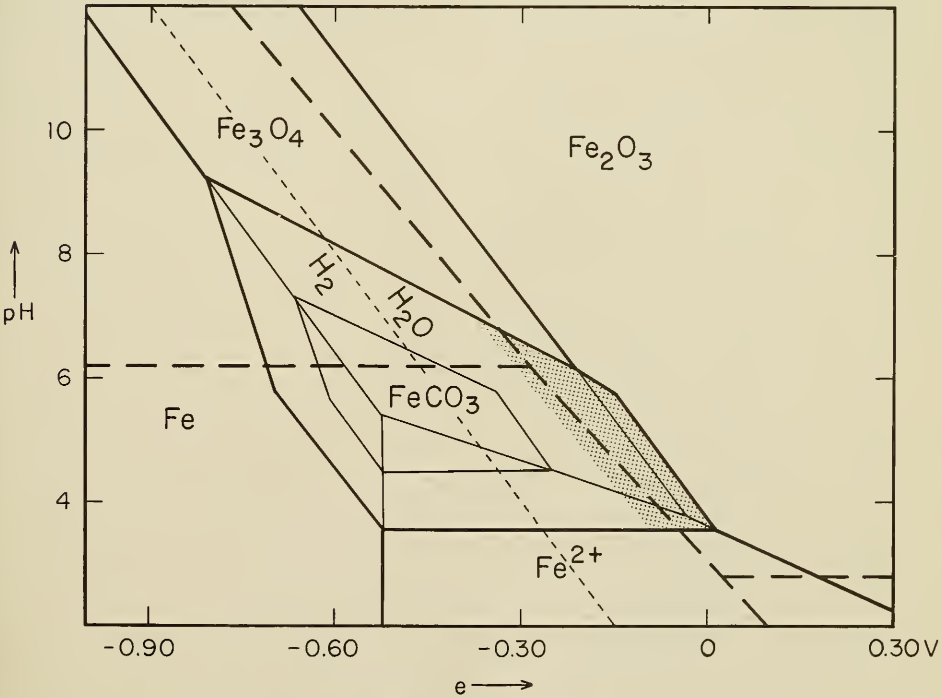


Fig.-16b

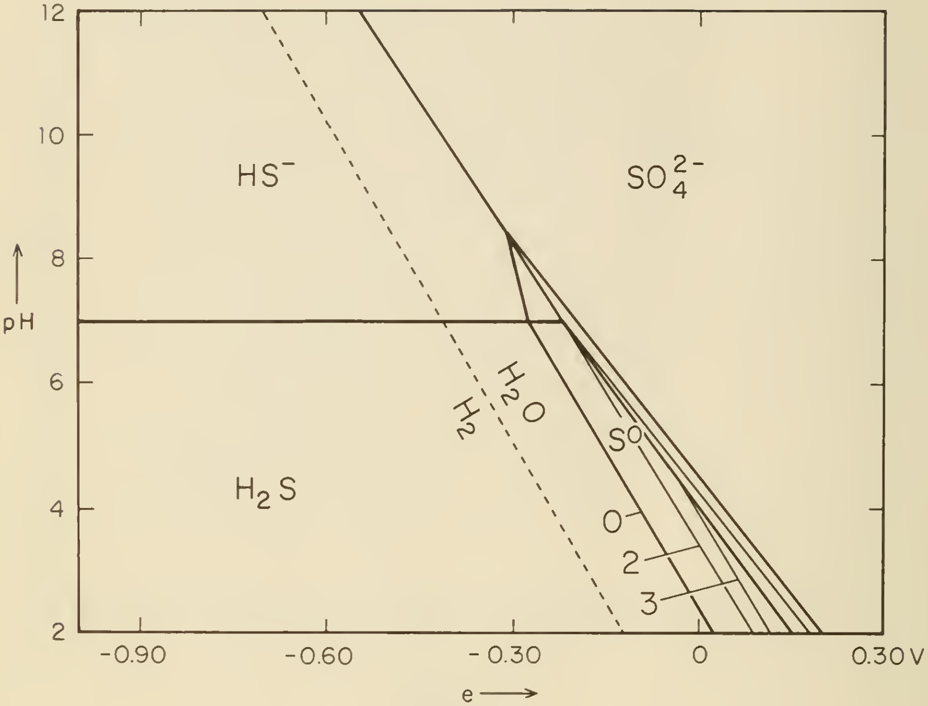

12
10
8
6
4
2
pH
HS$^-$
SO_4^{2-}
H_2S
H_2O
H_2
S^0
0
2
3
-0.90
-0.60
-0.30
0
0.30 V
e

Fig.-17

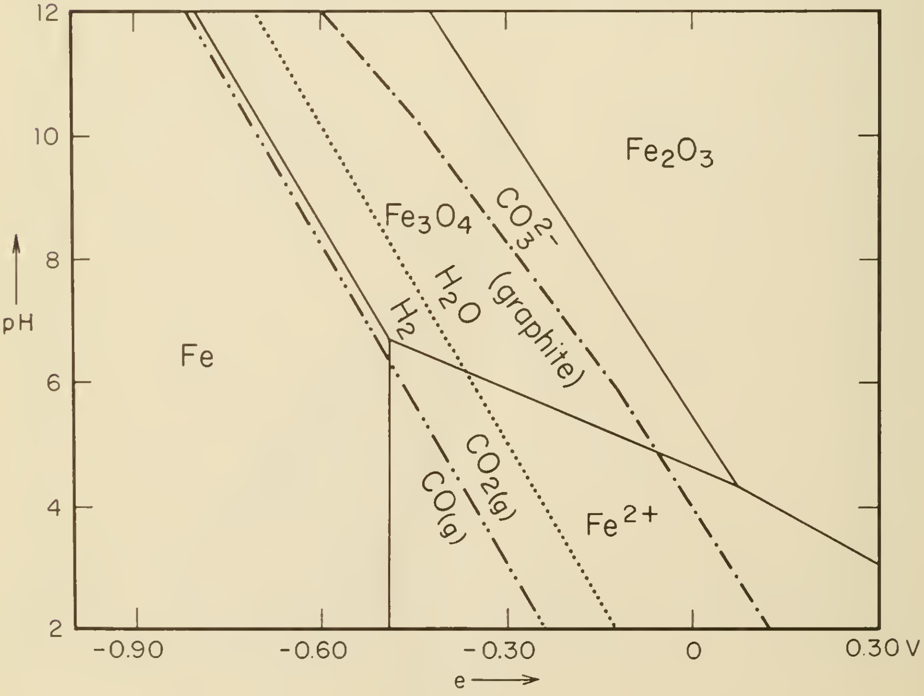

12
10
8
6
4
2
pH
Fe
Fe_3O_4
Fe_2O_3
Fe^{2+}
CO_3^{2-}
(graphite)
H_2O
H_2
$CO_2(g)$
CO(g)
-0.90
-0.60
-0.30
0
0.30 V
e

Fig.-18

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 151, NUMBER 4

PARAPERCIS KAMOHARAI (FAMILY MUGILOIDIDAE), A NEW FISH FROM JAPAN WITH NOTES ON OTHER SPECIES OF THE GENUS

(WITH ONE PLATE)

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(PUBLICATION 4669)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
MAY 18, 1966

PORT CITY PRESS, INC.
BALTIMORE, MD., U. S. A.

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(With One Plate)

ABSTRACT

Parapercis kamoharai, of the fish family Mugiloididae, was described as new from off Osaka Prefecture, Japan. Corrections are given for several species of *Parapercis* reported on by Cantwell (Pacific Sci., vol. 18, No. 3, pp. 239-280, 1964).

INTRODUCTION

A revision of the fish genus *Parapercis* Bleeker by Cantwell (Pacific Sci., vol. 18, No. 3, pp. 239-280, figs. 1-9, 1964) and a review of the fishes of the family Parapercidae found in the waters of Japan, by Kamohara (Repts. Usa Mar. Biol. Sta., vol. 7, No. 2, pp. 1-13, pls. 1-2, 1960) have enabled me to determine that two specimens sent to me by Chuichi Araga of Tokyo represent a new species. I appreciate very much Mr. Araga's permission to publish here a photograph which he took of the species when alive in his aquarium, plate I.

PARAPERCIS KAMOHARAI, new species

Plate I

Holotype.—USNM 196021, off Osaka Prefecture, Japan, collected by Chuichi Araga, standard length 145 mm., total length 175 mm.

Paratype.—USNM 199239, same data, standard length 181 mm., total length 205 mm.

Description.—The following data are expressed in thousandths of the standard length, first for the holotype, then for the paratype.

Length of head 280 and 263; length of snout 96 and 97; diameter of eye 57 and 50; least width of fleshy interorbital 34 and 34; distance from tip of snout to rear edge of maxillary 110 and 102; least depth of caudal peduncle 93 and 93; greatest depth of body 173 and 171; length of fourth dorsal spine 65 and 63; longest pectoral ray 190 and 171; longest pelvic ray 200 and 187; longest caudal ray 200 and 174; length of base of dorsal fin 638 and 635; anal fin base 480 and 450.

The following counts are recorded first for the holotype then the paratype: Outer enlarged teeth at front of lower jaw on both types, 3-3, totaling 6; dorsal fin rays V, 21 and V, 21; anal 16 and 18; pectoral (right-left) 17-17 and 17-18; oblique scale rows just above lateral line 66 and 72; scales from base of first soft dorsal ray to lateral line 7 and 7; scales from anal opening obliquely backwards to lateral line 16 and 15; zig-zag scales around caudal peduncle 30 and 32; gill rakers on first gill arch 6+11 and 6+10.

Vomerine teeth present, palatine teeth absent; enlarged caninelike teeth in outer row at front of lower jaw, 3 on each side; dorsal spines with third and fourth about same length and longest, and fifth spine is 5/9 length of fourth, with membrane attached opposite its tip to first soft dorsal ray; soft rays of dorsal and of anal fins all about the same length.

Color pattern in alcohol.—Back light brownish with 3 wavy darker streaks, the most ventral one along lateral line anteriorly, above lateral line posteriorly, and extending on caudal fin; side and belly very light tan, with 7 pale bars on side ending in 7 black ocellate spots on lower side, leaving the belly plain light tan; along midside a narrow dusky line crossing the bars and extending on the caudal fin rays as a black streak; side of head with 6 or 7 dark vertical bars ending on branchiostegal membranes; preorbital area with numerous very small brown specks; maxillary with 3 dark bars posteriorly and snout and premaxillary with large dark spots; head behind orbits with wavy dark streaks; breast with a pair of black spots in front of pelvic base; axil of pelvic black; a large black spot just below base of pectoral, and axil of pectoral black; black spot on basal half of first three dorsal spines; dorsal soft rays with a row of black spots basally on membranes, and another along middle of that fin; soft dorsal fin with a submarginal dusky band, with distal edge of fin white; a single row of black spots along middle of anal fin on membranes; submarginally anal fin has a dusky band, with distal edge of that fin white; caudal fin with a white band from midbase extending posteriorly on middle rays but broken distally with a dark bar; upper and lower edges of pale midcaudal band black; dark spots on upper and lower lobes of caudal fin. Underside of head pale, unspotted; pectoral and pelvic fins plain whitish.

DISCUSSION

This new species keys to *P. xanthozona* (Bleeker) in Kamohara (loc. cit., p. 2) and Cantwell (loc. cit., p. 248) and has the following characters in common with that species: Palatine teeth absent; 6 enlarged teeth in outer row of lower jaw at tip; membrane of spinous dorsal fin connected to first soft dorsal ray opposite tip of last spine; dorsal spines V; scales around caudal peduncle 30 to 32; and no ocellate spot behind or above rear of head.

However, *kamoharai* differs from *xanthozona* in having, respectively, 16 to 18 instead of 19 anal rays; oblique scale rows, 66 to 72 instead of 55 to 64; gill rakers on first gill arch 16 and 17 instead of 17 to 20. The color pattern of *kamoharai* differs from *xanthozona* as follows: 7 instead of 9 bars on side; 2 rows of spots on soft dorsal fin instead of 3; 7 ocellate black spots along lower side, instead of 9 indistinct ones (lacking entirely in USNM 109818). A pair of dark spots on breast, and preorbital with tiny brown spots, all absent in *xanthozona*.

I am pleased to name this new species, *kamoharai* in honor of Toshiji Kamohara, Kochi University, Japan.

During this study I have found certain errors in regard to Cantwell's recording of the data concerning specimens of *Parapercis* in the U.S. National Museum Collection. The following corrections are noted:

P. sexfasciata, p. 252, USNM 57516, Yokahama, 2 specimens; p. 254, USNM 26242, 7 specimens; USNM 152484, Kobe Market; USNM 76536, 3 specimens; USNM 50255, 5 specimens; USNM 50257, Onomichi Bingo, Japan. 142745 is UMMZ not USNM.

P. schauinslandi, p. 257, USNM 55301 to 55305, 8 specimens.

P. nebulosa, p. 261, USNM 147985, Tarut Bay, Zaal. I., 30 specimens; USNM 196492, Persian Gulf, Tarut Bay, 2 specimens.

P. haackei, p. 262, USNM 179832, Rottnest Island, 2 specimens.

P. cylindrica, p. 262, USNM 122477, 5 specimens; USNM 122544, 9 specimens; p. 264, USNM 177914, 2 specimens; USNM 179796 and 179802, Hayman I.; USNM 179795, Heron I., 2 specimens; USNM 177915, Green I.

P. ommatura, pp. 265-266, 59644 should be USNM 59642, Hamashima, 1 specimen; 3776 should be USNM 37776; left out is USNM 50258, Tsuruga, 3 specimens.

P. cephalopunctata, p. 267, USNM 140784, 140785, 140786, all Rongelap Atoll; USNM 166740, Arno Atoll; USNM 154584, 140783, Kwajalein Atoll; USNM 140781, 140782, Eniwetok Atoll; USNM 140778, 2 specimens, 140798, 4 specimens, 140800, 6 specimens, 140773, 14 specimens, 140774, 7 specimens, 140776, 8 specimens, 140779, 6 specimens, 140780, 1 specimen, 140799, 4 specimens, all Bikini Atoll. USNM 140794, 12 specimens, 140794, 1 specimen, 142280, 2 specimens, all Rongerick Atoll. USNM 177913, Bora Bora I., 6 specimens; USNM 52283, Apia; USNM 167387, Onotoa Atoll; USNM 177905, Netherland Indies; USNM 75502, Naha, Okinawa.

P. clathrata, p. 268, USNM 140787 to 140789, 8 specimens, all Rongelap Atoll. USNM 140796 and 140797, 2 specimens, Bikini Atoll; USNM 196492, 2 specimens from Persian Gulf are not *clathrata* but are *nebulosa.*

P. polyophthalma, p. 270, USNM 75862 should be 199161, 1 specimen, Riu Kiu I.?; USNM 75501, Naha, Okinawa, 4 specimens; USNM 122332 (not 12234), Luzon, 1 specimen; USNM 122333 (not 12233), Cebu Market, 1 specimen.

Parapercis kamoharai Schultz Types

SMITHSONIAN MISCELLANEOUS COLLECTIONS
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Roebling Fund

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PRECIPITATION IN FIVE CONTINENTS

By C. G. ABBOT, D.Sc.
Research Associate, Smithsonian Institution

TWENTY-FOUR YEARS AGO I reported a family of regular harmonic periods, both in solar variation and, with identical periods, also implicit in weather records.[1] Twenty-seven members of this family in weather are of sufficient amplitude to produce by their combined simultaneous influence at least 60 percent control of precipitation.

In 1960 the Smithsonian Institution published my paper *A Long-Range Forecast of United States Precipitation."* [2] That paper tabulated precipitation for 32 cities in monthly and 4-monthly intervals from 1950 through 1967. Besides its usual free distribution of 1,500 copies, the Smithsonian sold over 5,000 copies.

The purposes of the present paper are:

(a) To acquaint foreign meteorologists with our results on solar radiation and weather.

(b) To publish forecasts for 23 cities, 1965 through 1970, and also to compare the forecasts from 1950 through 1964 with observed precipitation. The forecasts will be based exclusively on the meteorological records, 1870-1949.

(c) To indicate to what extent such forecasts are devalued by the severe bombing of England, Germany, and Japan in 1944-1945, and by the far greater hydrogen bomb explosions by the United States and the U.S.S.R. around 1950 and about 1960.

HISTORICAL SUMMARY

A succinct history of the entire research, completely illustrated and documented,[3] was published by the Smithsonian (Publication 4545)

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[1] Published as Chapter VII, vol. 2, 2d edition, 1943, Smithsonian Scientific Series. Republished by Smithsonian Institution separately, 1962, as Publication 4505.

[2] Smithsonian Miscellaneous Collections, vol. 139, No. 9, Publication 4390, 1960.

[3] *Solar Variation and Weather,* Smithsonian Miscellaneous Collections, vol. 146, No. 3, Publication 4545, 1963.

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in 1963. References to the original sources are given in the Appendix to Publication 4545. The *Journal of Solar Energy and Engineering* in 1957 and 1958 published the essentials and details of procedure found necessary to make long-range weather predictions. (See "Supplementary References," Smithsonian Publication 4545, page 67). Certain modifications of these directions will be given below. Another paper worth attention is *Solar Variation, a Leading Weather Element.*[4] Finally, Publications 4656[5] and 4659,[6] 1966, are of special interest.

It is well nigh certain that a theoretical link connects periodic solar variation with weather. Because the harmonic family of 27 members related to 273 months occurs with identical periods in both. Thus far, no meteorologist, or mathematician skilled in hydrodynamics, has sought this link. I, indeed, have made a suggestion toward it. (Smithsonian Publication 4135, p. 3). Generally the principal features of changes which result from periodic solar variation occur *simultaneously* in graphs comparing forecasts with observation. Occasionally, however, large *shifts* of the order of 3 to 5 months occur between the dates predicted and effects observed.

To demonstrate that 27 regular weather periods exist, hitherto officially unrecognized, but of sufficient amplitude to mainly control precipitation and temperature, I will repeat below some proofs given in Smithsonian Publication 4545, and add new ones from the present studies. It will not be necessary in these weather studies to consider variations in solar radiation, because (apart from a recognition of the well-known sunspot cycle of $11\frac{1}{3}$ years) *all predictions of weather* to be given below are *exclusively* based on, and computed solely from, *World Weather Records,* volumes I, II, III, IV, published by the Smithsonian Institution and the U.S. Weather Bureau. The weather records to be used in predicting all lie within the interval 1870-1949. Records of 1950-1965, used below for comparison with predictions, have been furnished mainly by Dr. H. Landsberg, climatologist of the U.S. Weather Bureau, and partly by my own correspondence with friends in several countries.

The *phases,* but not the lengths, of the 27 weather periods used

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[4] Smithsonian Miscellaneous Collections, vol. 122, No. 4, Publication 4135, 1953.

[5] *An Account of the Astrophysical Observatory of the Smithsonian Institution, 1904-1953,* Smithsonian Miscellaneous Collections, vol. 148, No. 7, Publication 4656, 1966.

[6] *Forecasting from Harmonic Periods in Precipitation,* Smithsonian Miscellaneous Collections, vol. 148, No. 8, Publication 4659, 1966.

vary from place to place and from time to time because of atmospheric differences in transparency which alter timing. So each station must be treated separately, and atmospheric confusion eliminated. To accomplish the elimination of atmospheric confusion, I divide the year into seasons: January-April; May-August; September-December. I also treat in two separate groups intervals when Wolf sunspot numbers are $\gtrless 20$. Finally, I divide the basic interval, 1870-1949, approximately into halves, because forestry, manufacturing, and gas-propelled transportation, accompanying population increases, change the transparency of the air. See figure 1.

In official publications of monthly weather tabulations *all* available years are generally averaged into monthly normals. I found it necessary to distinguish in separate groups the months when Wolf numbers of sunspots are $\gtrless 20$. For there are important differences between these groups both in mean amplitude and in run through the year. So the monthly percentages of normal were computed by Mr. Jon. Wexler to suit two sets of monthly normals, with Wolf numbers $\gtrless 20$.

The elimination of the atmospheric confusion of phases, to which I have just referred, required electronic tabulations of no less than 222 independent groups of precipitation values for each of the 23 foreign stations listed below. My assistant, Mrs. Lena Hill, and I have received from Mr. Wexler for each station a packet of electronically printed paper 15 inches square and $\frac{3}{4}$-inch thick. It required us to work about 2 months to make the desired forecast for each station, after we received these sets of 222 tabulations made by Mr. Wexler. Some years earlier he also had prepared the records of precipitation for 32 United States cities forecasted in Smithsonian Publication 4390, and for the 10 temperature stations forecasted in Publication 4471.[7]

CLASSIFICATION

The following nomenclature is adopted (see figure 1):

Category 1, Wolf sunspot numbers <20. Category 2, Wolf numbers >20.

Division 1, years 1870-1909. Division 2, years 1910-1949.

Then for periods $\frac{273}{63}$ up to $\frac{273}{18}$ the year is subdivided as follows:

January to April; May to August; September to December.

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[7] *A Long-Range Temperature Forecast,* Smithsonian Miscellaneous Collections, vol. 143, No. 5, Publication 4471, 1961.

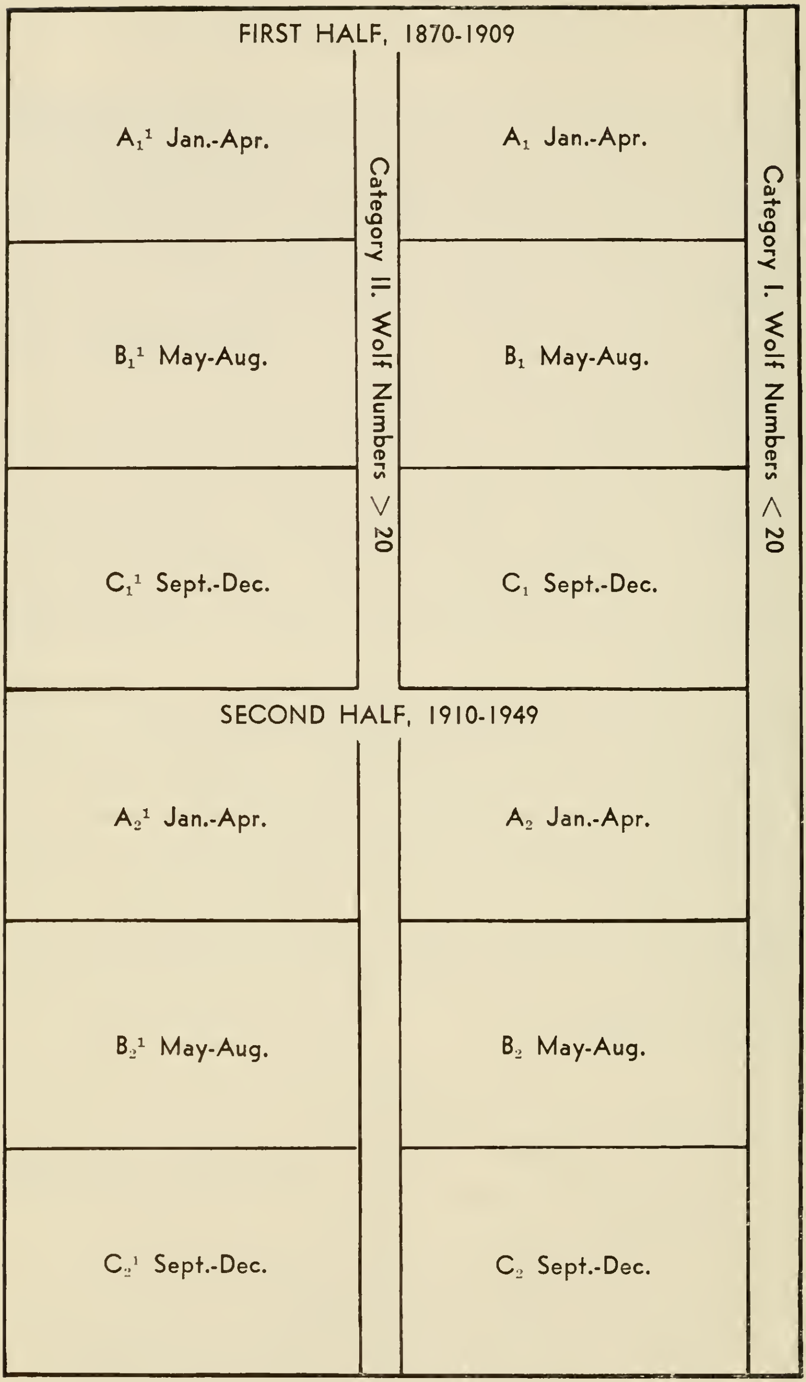

FIG. 1.—Groups of harmonic periods. Distribution of records for periods under 16 months.

This subdivision of the records requires electronic tabulation for each city to make 222 separate tables, as follows:

The 15 periods, $4\frac{1}{3}$ months to $15\frac{1}{6}$ months,	$3\times15\times2\times2$	$=180$
The 9 periods, $18\frac{1}{5}$ months to $45\frac{1}{2}$ months,	$9\times2\times2$	$=36$
The 3 periods, $54\frac{3}{5}$ months to 91 months,	3×2	$=6$
	Total	222

TABLE 1.—*Periods, harmonics of 273 months, used for forecasting*

Fraction	Months	Fraction	Months	Fraction	Months
$\frac{1}{3}$	91	$\frac{1}{12}$	$22\frac{3}{4}$	$\frac{1}{27}$	$10\frac{1}{9}$
$\frac{1}{4}$	$68\frac{1}{4}$	$\frac{1}{14}$	$19\frac{1}{2}$	$\frac{1}{28}$	$9\frac{3}{4}$
$\frac{1}{5}$	$54\frac{3}{5}$	$\frac{1}{15}$	$18\frac{1}{5}$	$\frac{1}{30}$	$9\frac{1}{10}$
$\frac{1}{6}$	$45\frac{1}{2}$	$\frac{1}{18}$	$15\frac{1}{6}$	$\frac{1}{33}$	$8\frac{3}{11}$
$\frac{1}{7}$	39	$\frac{1}{20}$	$13\frac{13}{20}$	$\frac{1}{36}$	$7\frac{7}{12}$
$\frac{1}{8}$	$34\frac{1}{8}$	$\frac{1}{21}$	13	$\frac{1}{39}$	7
$\frac{1}{9}$	$30\frac{1}{3}$	$\frac{1}{22}$	$12\frac{9}{22}$	$\frac{1}{45}$	$6\frac{1}{15}$
$\frac{1}{10}$	$27\frac{3}{10}$	$\frac{1}{24}$	$11\frac{3}{8}$	$\frac{1}{54}$	$5\frac{1}{18}$
$\frac{1}{11}$	$24\frac{9}{11}$	$\frac{1}{26}$	$10\frac{1}{2}$	$\frac{1}{63}$	$4\frac{1}{3}$

DATES

The dates given in table 2 may be used to separate ($SS>20$ and $SS<20$) groups of months.[8]

TABLE 2.—*Intervals for Wolf Sunspot Numbers* $\gtrless 20$

SS > 20	
July 1857—Aug. 1865	Mar. 1868—Apr. 1875
Jan. 1880—July 1886	May 1891—Nov. 1898
July 1903—Mar. 1910	Jan. 1915—July 1921
Apr. 1925—May 1931	Mar. 1935—May 1942
Mar. 1945—Jan. 1953	May 1955—(May 1962)
SS < 20	
Jan. 1854—June 1857	Sept. 1865—Feb. 1868
May 1875—Dec. 1879	Aug. 1886—Apr. 1891
Dec. 1898—June 1903	Apr. 1910—Dec. 1914
Aug. 1921—Mar. 1925	June 1931—Feb. 1935
June 1942—Feb. 1945	Feb. 1953—Apr. 1955

Supplementary dates.—In our use of tables of periods in weather for forecasting beyond 1957, it is necessary to make extrapolations

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[8] SS stands for sunspots.

for Wolf numbers beyond 1962 from the table of dates (table 2). Ths is done (of course with marginal uncertainty) by averaging the intervals (given above) in months of SS>20 and SS<20, and assuming that future sunspot intervals will be approximately the same as these averages. The uncertainty will not lead to important errors of forecasts, for generally the curves representing SS>20 and SS<20 for the periods are similar for a given period, and differ but a few months, or even not at all, in phases. I use for future intervals after 1962: for SS>20, 84 months; for SS<20, 54 months.

PLACES SELECTED FOR FORECAST STUDY

TABLE 3.—*Cities where precipitation is forecasted*

In EUROPE: Greenwich, Paris, Madrid, Uppsala, Copenhagen, Berlin, Vienna, Rome, Sibiu, Moscow, Kief, Athens, Orenburg

In ASIA: Nagpur, Tokyo

In AUSTRAL-ASIA: Adelaide, Wellington

In AFRICA: Tunis, Lagos, Johannesburg, Cape Town

In SOUTH AMERICA: Rio de Janeiro, Buenos Aires

NOTE.—Records for Rome were unavailable to Mr. Wexler after 1930. From 1950 onward the effects of the hydrogen bombing prevented any good forecasts for Rome up to 1962, and left no means of knowing what, if any, adjustments for scale and level should be made, 1963-1970. I will use one figure to show that before 1930 Rome reacted to the periodic impulses as well as other stations.

Records for Orenburg were so very irregular in amplitudes that no forecast was prepared.

INFLUENCE OF HARMONIC PERIODS

All of the 27 harmonics appeared implicitly in the records of precipitation in sufficient amplitudes to be of importance for controlling precipitation in all of 55 stations so far studied in the world. All of the 27 periods approximate in form to sine curves, when cleared of overriding subperiods and graphed. As stated above, their phases are different in different places, in different times, and suffer different displacements of phases, varying with length of period. This leads to the classification above shown in figure 1, and to another measure, as about to be explained.

Combinations among periods 4⅓ to $13^{13}/_{20}$.—In the eighty years from 1870 to 1949 there are 240 repetitions of the period of 4⅓ months and 26 repetitions of 91 months. The other periods lie between these limits as regards repetition. With the separations into groups shown in figure 1, periods where Wolf numbers are >20 include more entries than those where Wolf numbers are <20. For some periods, notably $13\frac{13}{20}$ months, but also for others, some groups have as few as 3, 2, or only 1 repetition. But even for the large groups the number of repetitions is in some cases so small that mean values obtained by electronic computation have little weight. To have stronger mean values for computing forecasts from the forms and amplitudes for all periods used, we combine the electronic mean values for periods $4\frac{1}{3}$ months up to $15\frac{1}{6}$ months in groups of 6 (or of 5) columns. Here I quote from Smithsonian Publication 4545, pp. 26, 27.

> The combination of 6 member columns into a general mean, as we do for periods less than $15\frac{1}{6}$ months, will best be understood by a numerical example. The letters a, b, c denote, respectively, data of January-April; May-August; September-December. Subscripts 1 and 2 with them mean first and second halves of the records. As expected, these columns are not in the same phase. The signs, ok, ↑, and ↓, show how much the columns must be moved up or down bodily to be brought into the best posture for uniform phases. When the mean percentage departures from normal in the final column of the table 5 are used in the summation for prediction, the columns marked "ok" are to be replaced by the general mean column *without shifting*. The general mean values are to be *lowered* 2 months at b_1, *lowered* 3 months at b_2 and *raised* 1 month at a_2, so as to be in proper phases in the summation.

Table 4—*Berlin. Period, 7.0 months. Wexler's table. Means.*[1]

Cat. 2, Div. 1.						Cat. 2, Div. 2					
a_1	↑3	b_1	↑2	c_1	ok	a_2	↓1	b_2	↑3	c_2	ok
94		96		93		114		94		100	
97		100		96		105		97		100	
99		99		96		103		105		101	
99		95		91		100		109		97	
99		99		94		105		109		97	
99		95		101		103		115		99	
98		91		95		109		112		98	

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[1] From Smithsonian Publication 4545, p. 26.

Table 5—*Berlin. Period, 7.0 months.*
Rearranged table with symbols unchanged.[1]

Cat. 2, Div. 1						Cat. 2, Div. 2						Sums	General mean
a_1	ok	b_1	↑2	c_1	ok	a_2	↑3	b_2	↓3	c_2	ok	Σ	÷6
99		99		93		109		109		100		+ 9	+1
99		95		96		114		115		100		+19	+3
99		99		96		105		112		101		+12	+2
98		95		91		103		94		97		—22	—4
94		91		94		100		97		97		—27	—4
97		96		101		105		105		99		+ 3	+0
99		100		95		103		109		98		+ 4	+1

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[1] From Smithsonian Publication 4545, p. 27.

Beyond 15⅙ months in period, practically every period, when plotted, betrays confusion, for shorter harmonic periods override the period sought. This requires what is by far the most arduous computation of all. After the electronically prepared tables are received from Mr. Wexler they must be treated to clear the overriding shorter harmonics away. It is sometimes difficult to decide which submultiples are present until after one or two futile trials. Such repeated trials with periods 54 to 91 months in length are very tedious.

I will refer to examples of this procedure from Smithsonian Publication 4545, pp. 22, 23, and 32, and cite the studies of Rome, Kief, and Cape Town of the present paper, figures 2, 3, and 4. It will be clear from these examples that stations in far separated regions of the world present harmonics of 273 months as approximately perfect sine curves, of large percentage amplitude, when confusing harmonic submultiples are removed. The foregoing must be convincing, I think, that our discovery is sound of important harmonic periods in weather related to the master period of exactly 273 months.

FORECASTS OF PRECIPITATION FOR 23 FOREIGN CITIES

Preceding pages have shown that 27 periods which are exact harmonics of 273 months may be so fully cleared of confusion as to display in all cases approximately sine curves in form. The basic interval for determination of forms and amplitudes of these harmonic periods in this paper covers records of precipitation of the 23 cities from about 1870 through 1949 or 80 years. See table 6. In this basic interval are 26 repetitions of 91 months, 240 of 4⅓ months. We have determined the percentage of normal monthly precipitation from 1870 to 1949 for 27 periods at 23 cities. Therefore, knowing the average form and amplitude of these 27 periods for 80 years preceding 1950, it was assumed that by adding the amplitudes of the 27 periods, as thus determined, throughout later years a fair monthly forecast can be extrapolated covering the interval 1950 through 1970. Favorable results had been obtained by such methods for 32 cities in the United States, as published by Smithsonian Publication 4390. Figure 5, as an example, graphs the forecast and observed values from 1938 through 1949 for Lagos, Nigeria. The years 1938 through 1949, though lying *within* the base period, 1870 through 1949, are, it must be conceded, as fair a test of the method as those following 1949. For no observation of a single year of the march of weather, 1938-1949, can affect the "forecast" for that year by more than $\frac{12}{80\times 12}$, or 1¼ percent.

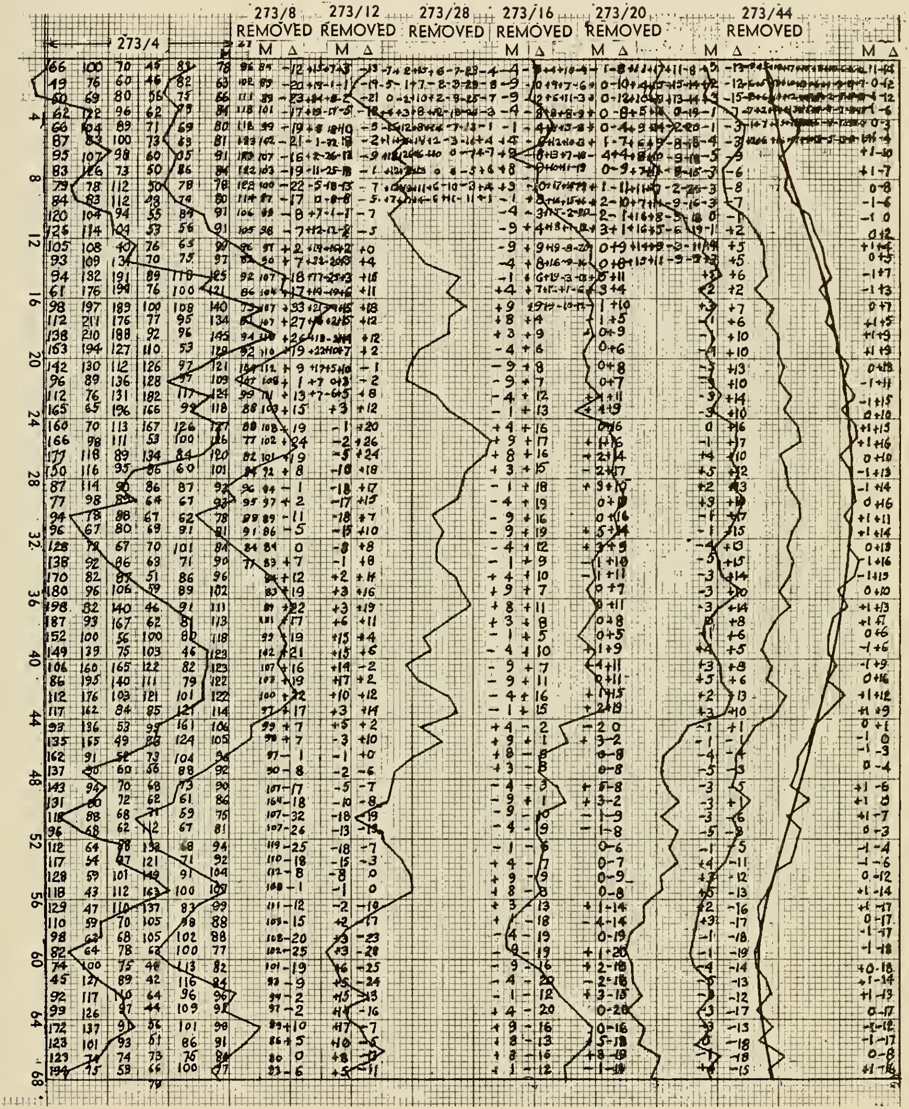

Fig. 2.—Rome, Italy. Precipitation. 68¼-month period cleared.

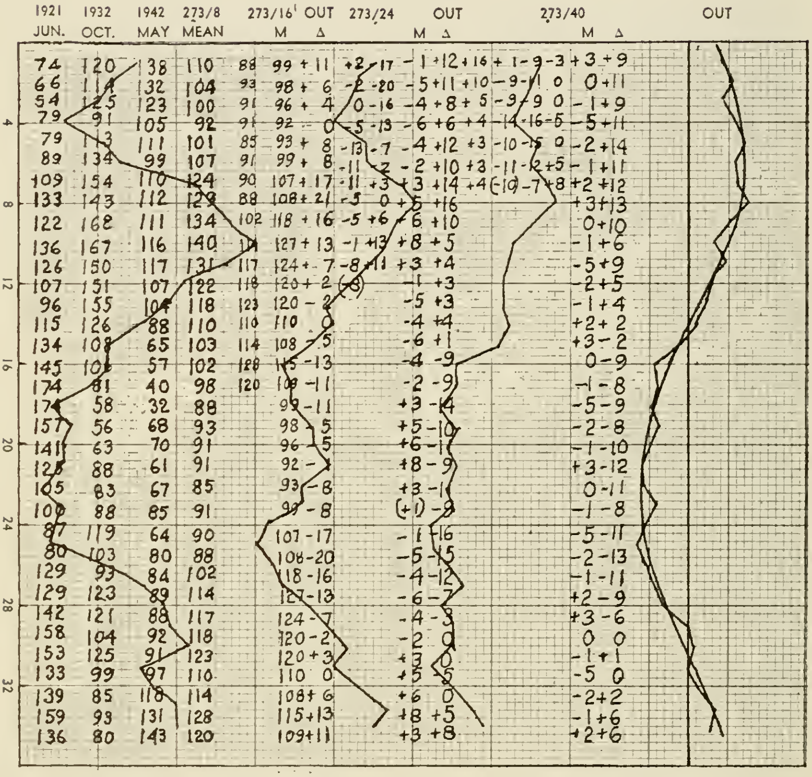

FIG. 3—Kiev, U.S.S.R. Precipitation. 34⅛-month period cleared.

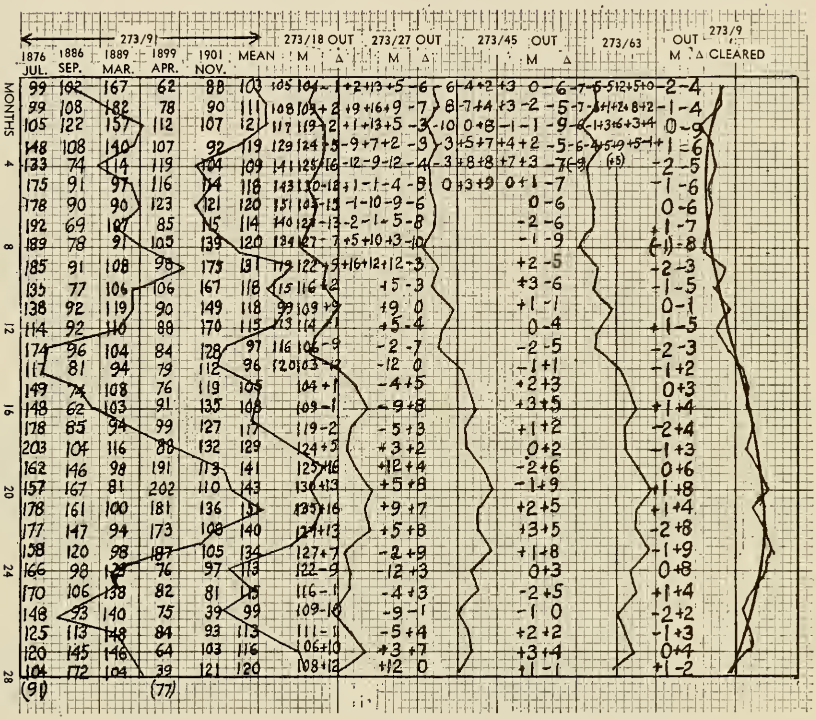

Fig. 4.—Cape Town, South Africa. Precipitation. 30⅓-month period cleared.

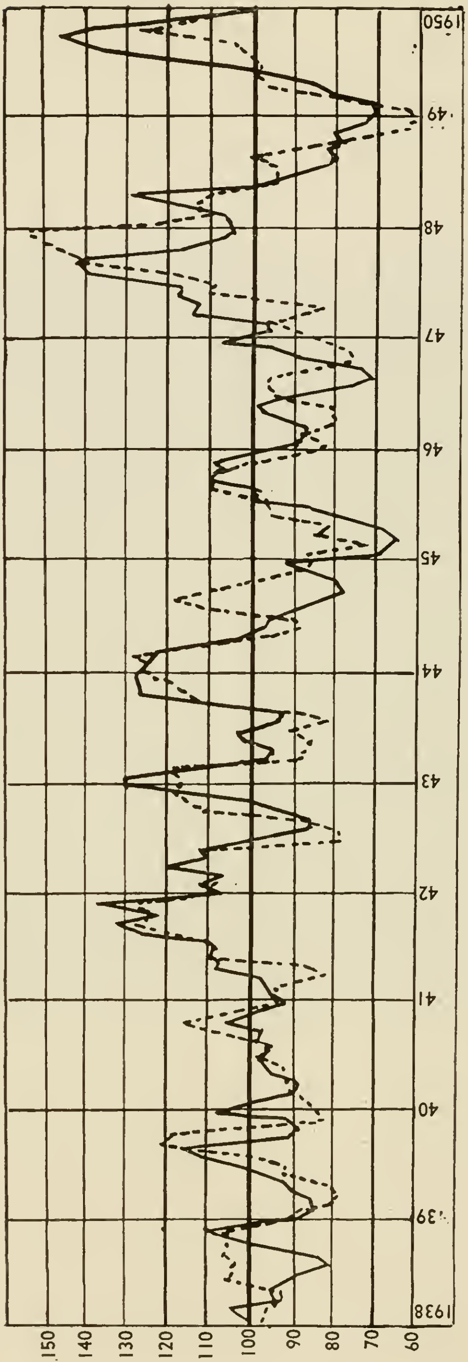

Fig. 5.—Lagos, Nigeria. Monthly precipitation. Forecast and observed values, 1938-1949.

Forecast: solid line —— Observed: dotted line . . . . . .

TABLE 6.—*Normal monthly precipitation, 1870 through 1949, expressed in tenths of an inch or in millimeters.*

A = Wolf number > 20. B = Wolf number < 20.

Month	ADELAIDE AUSTRALIA [In tenths of an inch]		ATHENS GREECE [In millimeters]		BERLIN GERMANY [In millimeters]		BUENOS AIRES ARGENTINA [In millimeters]		CAPE TOWN SOUTH AFRICA [In tenths of an inch]		COPENHAGEN DENMARK [In millimeters]	
	A	B	A	B	A	B	A	B	A	B	A	B
January	7.3	9.2	48.3	60.7	40.9	45.7	87.2	84.1	8.7	5.4	36.9	40.3
February	8.2	7.4	44.3	42.6	40.0	32.9	70.1	74.3	5.6	5.3	31.3	29.5
March	12.0	9.4	33.2	32.5	42.2	37.7	144.2	102.8	6.8	10.0	37.4	30.8
April	17.9	16.9	18.5	20.6	40.5	38.2	90.6	91.0	19.1	20.0	33.6	35.3
May	26.8	25.6	19.0	21.9	47.8	47.0	95.9	62.5	44.6	34.2	39.8	42.6
June	31.7	28.3	19.7	15.5	52.6	60.4	61.3	61.4	40.4	43.0	46.0	51.4
July	23.6	26.0	5.1	6.8	73.3	74.5	68.4	50.3	35.7	38.2	64.5	63.9
August	22.4	25.8	13.0	6.7	50.0	66.4	81.5	52.9	37.6	31.6	68.2	69.5
September	22.5	19.2	14.4	18.4	41.7	44.2	73.3	87.6	23.9	22.6	54.3	56.4
October	16.3	18.5	31.7	48.1	44.3	51.6	93.8	82.4	17.1	15.2	59.3	61.3
November	12.2	11.5	69.0	55.4	43.2	45.2	85.0	84.9	10.8	9.1	46.1	51.2
December	11.1	10.0	66.1	73.8	39.1	48.9	92.0	102.6	8.3	8.9	45.1	45.6
	GREENWICH ENGLAND [In millimeters]		JOHANNESBURG SOUTH AFRICA [In tenths of an inch]		KIEF U.S.S.R. [In millimeters]		LAGOS NIGERIA [In tenths of an inch]		MADRID SPAIN [In millimeters]		MOSCOW U.S.S.R. [In millimeters]	
	A	B	A	B	A	B	A	B	A	B	A	B
January	45.7	58.4	55.4	64.8	37.8	35.0	13.1	9.0	24.9	35.8	25.7	29.3
February	38.6	40.0	47.6	52.8	35.7	34.8	13.8	20.1	31.2	36.7	24.6	26.9
March	42.2	40.1	38.2	48.0	49.0	41.9	38.7	40.2	37.4	43.2	46.9	32.3
April	46.9	41.6	23.7	14.8	54.8	43.6	54.1	59.1	45.1	43.1	29.8	30.8
May	49.2	42.9	7.9	9.3	49.5	55.0	93.8	114.9	30.7	46.5	48.2	44.1
June	50.4	47.3	3.0	2.1	81.3	70.2	178.6	178.3	31.5	32.1	68.6	68.0
July	58.7	39.0	5.2	3.4	84.5	72.8	112.4	103.0	9.1	10.9	80.4	81.0
August	60.3	57.4	4.7	4.1	61.2	65.9	33.0	22.7	13.7	9.2	79.5	68.8
September	43.0	52.2	9.4	10.0	51.8	41.8	57.1	55.7	37.6	34.1	50.8	61.2
October	56.3	67.8	29.2	23.7	37.2	51.8	82.4	82.3	54.2	43.0	49.1	51.5
November	59.4	60.1	48.1	49.6	50.7	45.0	24.3	29.5	51.0	55.0	38.6	40.7
December	54.6	55.5	54.7	56.0	35.7	47.1	12.0	9.9	38.5	42.9	36.8	36.8

TABLE 6.—*Normal monthly precipitation, 1870 through 1949, expressed in tenths of an inch or in millimeters.—Continued.*

A = Wolf number > 20. B = Wolf number < 20.

Month	NAGPUR INDIA [In tenths of an inch]		ORENBURG U.S.S.R. [In millimeters]		PARIS FRANCE [In millimeters]		RIO DE JANEIRO SOUTH AMERICA [In millimeters]		ROME ITALY [In millimeters]		SIBIU ROUMANIA [In millimeters]	
	A	B	A	B	A	B	A	B	A	B	A	B
January	4.7	4.9	18.6	24.7	40.7	46.0	12.4	14.5	7.2	9.0	30.6	26.9
February	5.6	8.0	18.4	13.0	33.9	40.6	9.8	13.5	8.2	7.0	24.9	25.3
March	4.3	6.3	21.5	20.9	42.7	39.2	12.3	13.4	7.8	7.5	37.3	32.6
April	6.0	5.7	21.4	22.4	45.3	45.2	10.5	10.2	7.6	8.0	54.2	51.3
May	8.6	6.9	35.5	38.6	51.0	53.5	6.6	6.7	5.9	5.9	83.7	85.3
June	74.9	92.5	36.9	45.4	52.6	54.4	5.2	5.6	4.5	4.2	113.1	117.7
July	141.5	152.2	39.0	40.3	62.1	57.2	3.3	4.5	1.8	1.6	82.1	98.5
August	115.5	106.6	33.7	30.6	66.0	52.9	3.8	4.1	2.5	2.2	83.1	72.4
September	78.3	80.5	21.5	29.5	46.1	50.2	6.6	6.1	8.0	6.8	59.6	47.8
October	22.2	21.8	37.2	32.6	55.5	61.9	8.3	8.2	15.0	12.3	46.4	45.1
November	6.9	7.4	32.5	29.6	52.7	51.4	10.1	9.2	11.4	12.0	38.4	31.4
December	3.5	4.0	26.0	26.4	48.6	52.8	13.4	12.7	10.3	10.4	30.7	27.5

	TOKYO JAPAN [In millimeters]		TUNIS TUNISIA [In millimeters]		UPPSALA SWEDEN [In millimeters]		VIENNA AUSTRIA [In millimeters]		WELLINGTON NEW ZEALAND [In tenths of an inch]	
	A	B	A	B	A	B	A	B	A	B
January	53.7	47.6	51.5	63.3	33.6	34.8	40.3	39.4	27.3	32.9
February	71.2	78.5	50.3	52.8	29.2	25.9	41.2	36.9	34.6	30.6
March	110.2	105.5	39.6	40.5	31.4	27.9	48.3	44.7	26.1	34.8
April	128.1	131.8	35.2	34.2	30.1	30.4	55.8	53.0	33.9	41.1
May	148.0	144.0	17.1	23.1	41.1	39.0	71.2	73.0	52.6	43.6
June	157.4	177.6	12.5	8.8	46.0	49.8	67.9	73.1	42.5	49.0
July	129.7	144.6	2.5	2.7	65.3	69.3	69.8	85.9	55.4	52.8
August	144.6	148.9	6.5	5.8	65.0	77.7	58.4	75.2	42.0	50.6
September	231.2	227.6	21.9	33.0	53.1	52.4	56.1	46.2	38.1	39.0
October	216.7	197.0	38.8	47.3	52.5	50.9	55.2	55.7	41.3	41.1
November	94.6	102.8	48.5	68.4	45.8	42.3	47.5	48.3	35.1	33.2
December	57.9	53.0	71.8	65.3	45.3	39.7	47.5	49.3	37.5	32.1

SMOOTHING

In figure 5 the monthly "forecasted" values represent the *average* influence of from 26 to 240 repetitions of the harmonic periods. So they may be fairly regarded as "smoothed" values. To be fairly compared with them, the "observed" precipitation, 1938 through 1949, must also be "smoothed." Heretofore in my publications I have employed the "5-month consecutive" smoothing. But this frequently tends to displace maxima or minima by 1 or even 2 months. I now introduce in figure 5 a better formula. It still involves 5 months, but as follows: $\frac{1}{10}(a+2b+4c+2d+e)$. This gives the central month, c, two-thirds as much weight as the other 4 months combined, instead of one-fourth the weight of the other 4 months combined, as was the case in "5-month consecutive" smoothing.

EFFECT OF HYDROGEN BOMBS

I had intended to present the foreign city forecasts of precipitation after 1950 nearly as I had published forecasts for 32 American cities in Smithsonian Publication 4390. But when the United States and the U.S.S.R., about 1950, began exploding powerful hydrogen bombs, whose products rose to immense heights and remained long in the atmosphere, the new conditions might well invalidate my assumption that the average forms and amplitudes of 27 periods which prevailed 1870-1949 would indicate what precipitation would follow in succeeding years.

I found evidence to support the following conclusions:

(1) That my method of forecasting gave good worldwide results for the decade, 1940-1949.

(2) That it is less successful generally, 1950-1963, except for a few stations during 1953-1957.

(3) That there was enough probability that it would hold, 1965-1970, so that tabulation of forecasts for those years may be useful.

A brief method of demonstrating conclusions (1) and (2) lay in the presentation of spot graphs connecting predictions with observations. For if the summation of average forms and amplitudes of 27 periods, as they were from 1870 through 1949, *perfectly* represented the observed march of percentages of normal precipitation for those years, then the spot graph for 1940-1949 would be a 45° line with all spots lying upon it. A glance at *World Weather Records* shows, of course, that no such perfection can be expected. Take for example only the month of June at Athens:

Year observed:	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950
Precipitation (in mm.):	8.6	13.3	18.4	0.6	0.1	0.4	48.8	23.7	38.9	0.4

Normal: 15.3 millimeters.

Yet even for Athens the spots on graphs should clearly *tend to approach* the 45° line. They do in the decades preceding 1950, but scatter widely after 1950.

I now draw attention to figures 6, 7, 8, 9, 10, 11, which present spot graphs of forecasts and observed values smoothed by $\frac{1}{10}(a+2b+4c+2d+e)$. The figures show for Adelaide, Athens, Greenwich, Buenos Aires, Johannesburg, and Uppsala, precipitation in percentages of normal. The bombing, beginning about 1950 was discontinued for several years, but revived with monstrous power about 1958. My predictions, 1950-1964, seem much devalued, except for some stations during the quieter years 1955-1958. I have spot graphs for many other stations. Nearly all in some measure tell the same story as those here presented. It was noticed that at Tokyo the years 1943-1945 fell in the bombing group, for at that time occurred the bombing of Hiroshima and Nagasaki, though done with comparatively weak plutonium bombs. These caused only a moderate effect compared with that caused later by hydrogen bombs.

THE FORECAST FOR NAGPUR

Nagpur is the only one of the 23 foreign stations which has a purely monsoon precipitation. Nearly all of its yearly precipitation falls in the months June, July, August, and September. In the 9 years, 1941-1949, *World Weather Records* tabulate 447 inches, of which 385 inches, or 86 percent, falls in those 4 months. The forecast for Nagpur was prepared identically as for other stations. That is, Wexler computed the percentages of normal monthly precipitation for 80 years, tabulating 222 separate tables of departures from normal. We added the separate contributions of the 27 periods for each month 1938-1949. We also smoothed the *observed* monthly precipitation for these 12 years by the formula $\frac{1}{10}(a+2b+4c+2d+e)$. These monthly percentages of normal, forecasted, and smoothed-observed, were plotted for Nagpur for years 1944-1949, but they seemed meaningless because of the monsoon distribution. I omit them here.

I, therefore, reduced the monthly *departures* from *normal* to millimeters, forecasted and smoothed-observed, 1944-1949. This *actual* precipitation is plotted in figure 12. These forecasts are fully as

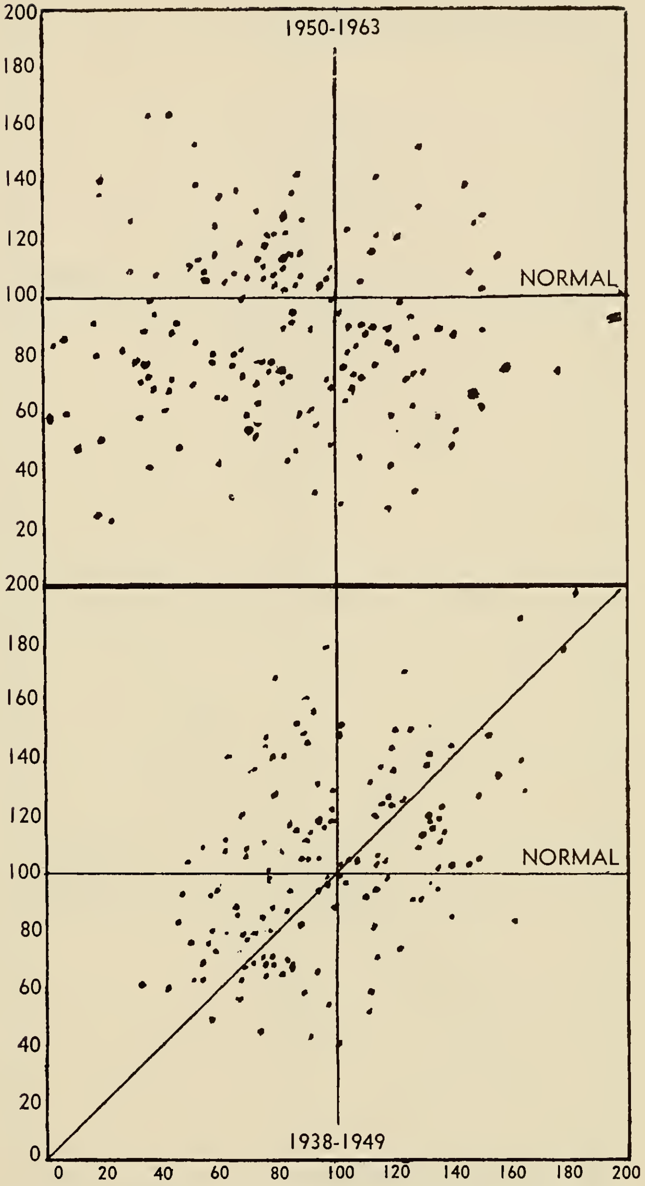

FIG. 6.—Adelaide, Australia. Precipitation, forecast and observed, 1938-1949 compared with 1950-1963, in percentages of normal, showing the effect of hydrogen bombs.

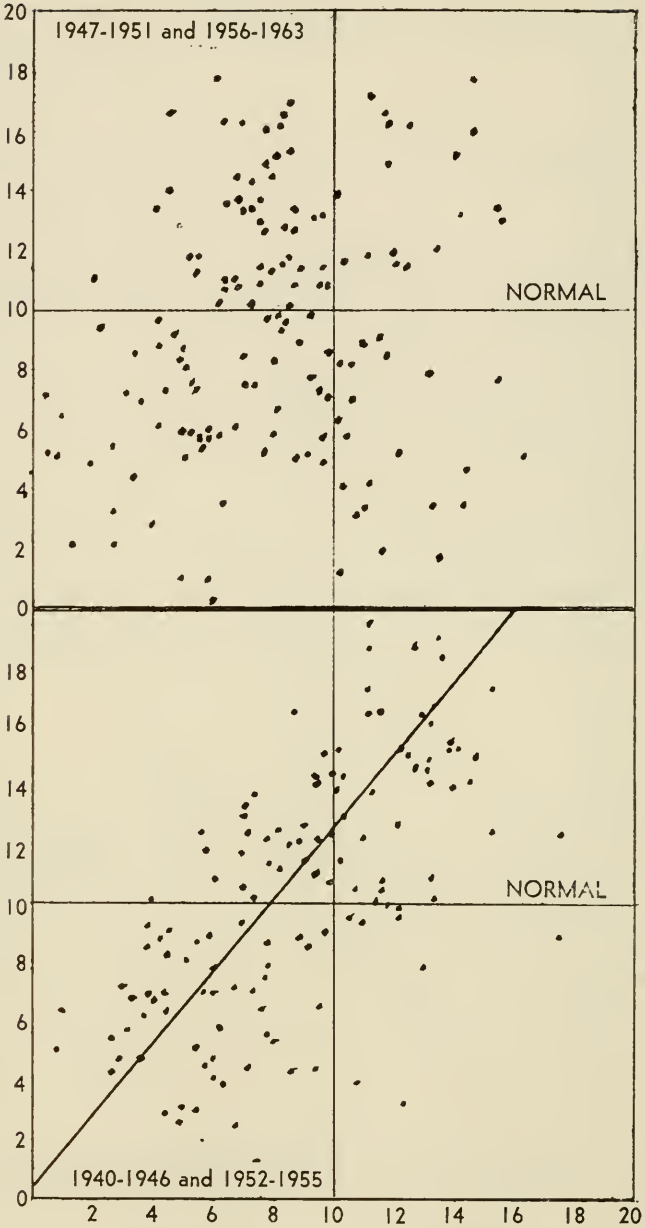

FIG. 7.—Athens, Greece. Precipitation, forecast and observed, 1940-1946, 1952-1955 compared with 1947-1951 and 1956-1963, in percentages of normal, showing the effect of hydrogen bombs.

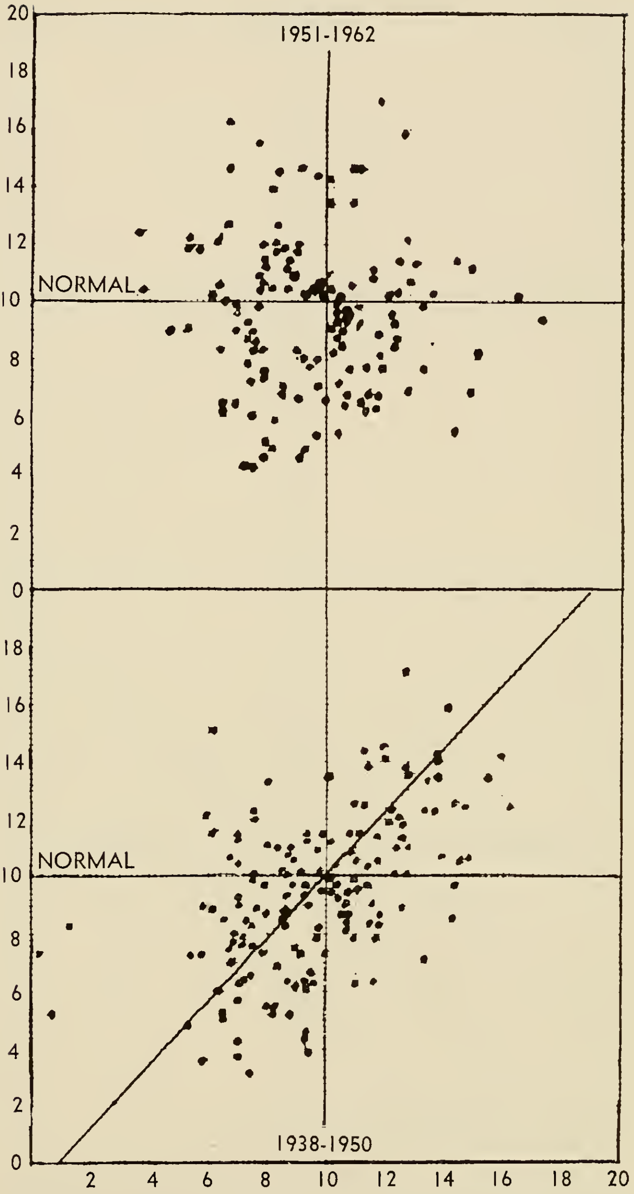

Fig. 8.—Greenwich, England. Precipitation, forecast and observed, 1938-1950 compared with 1951-1962, in percentages of normal, showing the effect of hydrogen bombs.

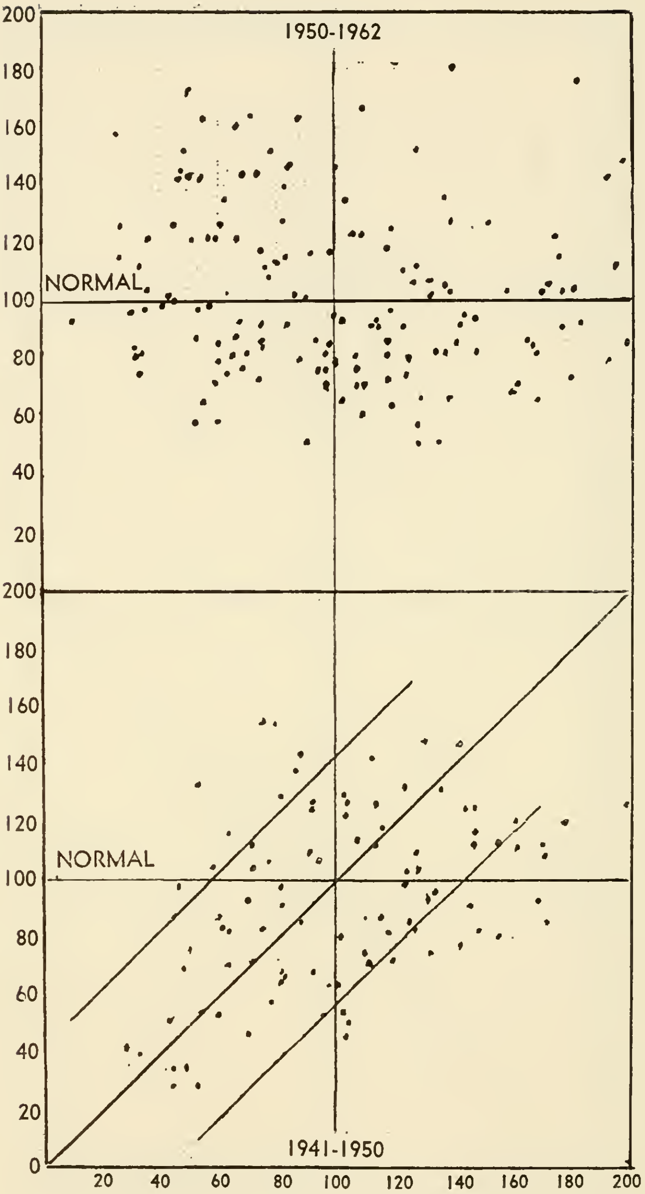

Fig. 9.—Buenos Aires, Argentina. Precipitation, forecast and observed, 1941-1950 compared with 1950-1962, in percentages of normal, showing the effect of hydrogen bombs.

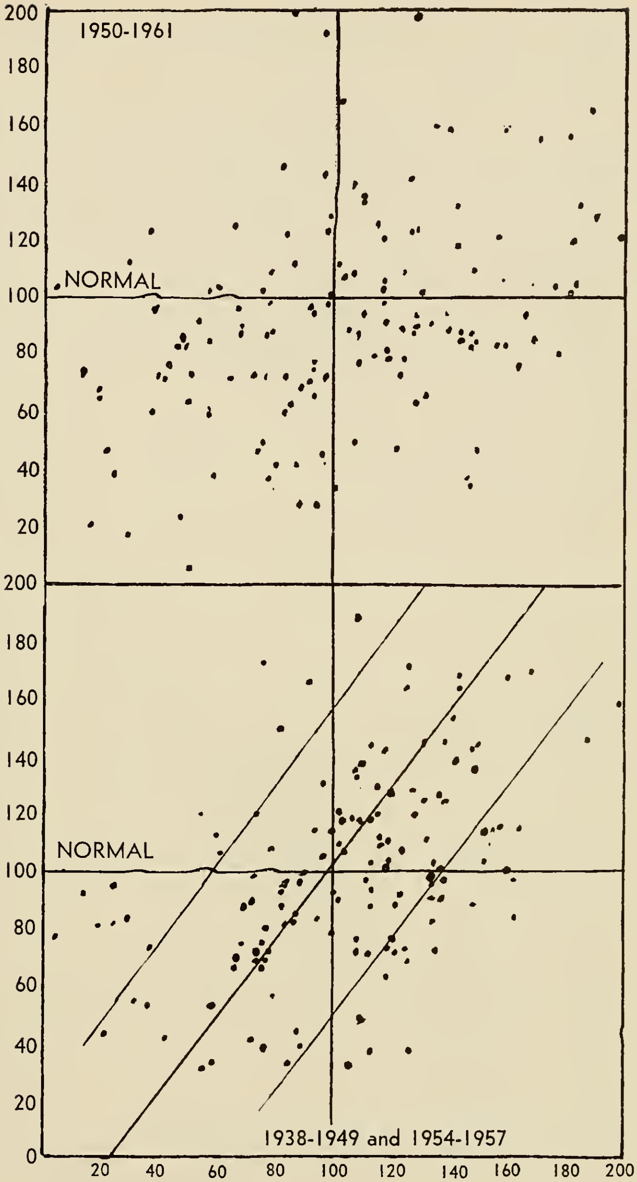

FIG. 10.—Johannesburg, South Africa. Precipitation, forecast and observed, 1938-1948 and 1954-1957 compared with 1950-1961, in percentages of normal, showing the effect of hydrogen bombs.

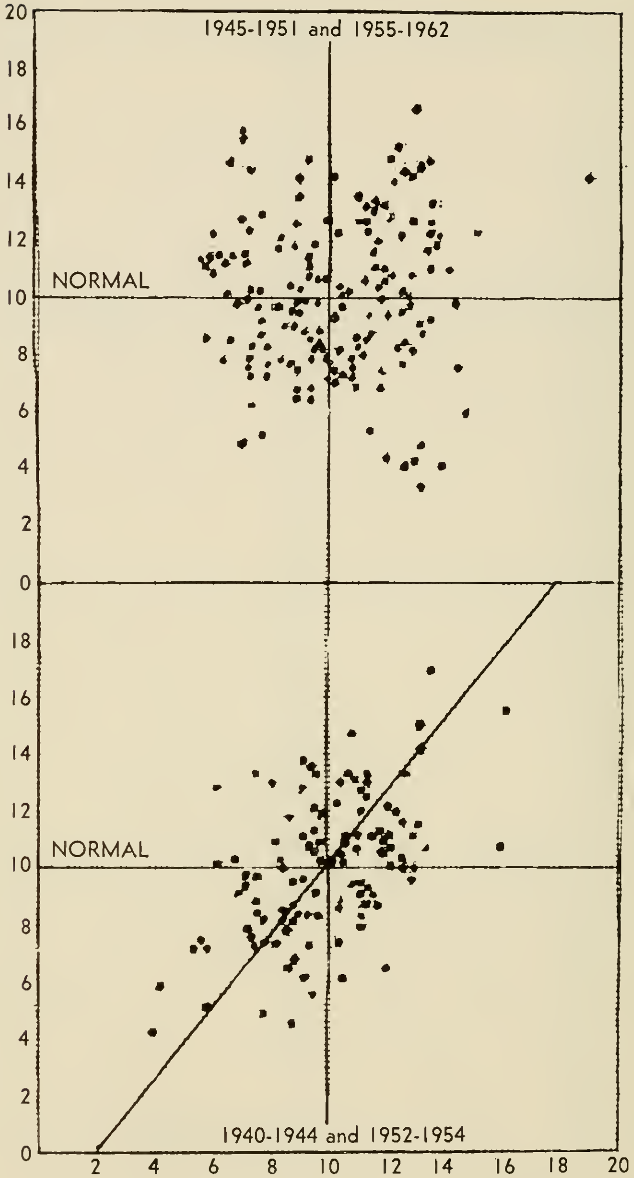

Fig. 11.—Uppsala, Sweden. Precipitation, forecast and observed, 1940-1944 and 1952-1954 compared with 1945-1951 and 1955-1962, in percentages of normal, showing the effect of hydrogen bombs.

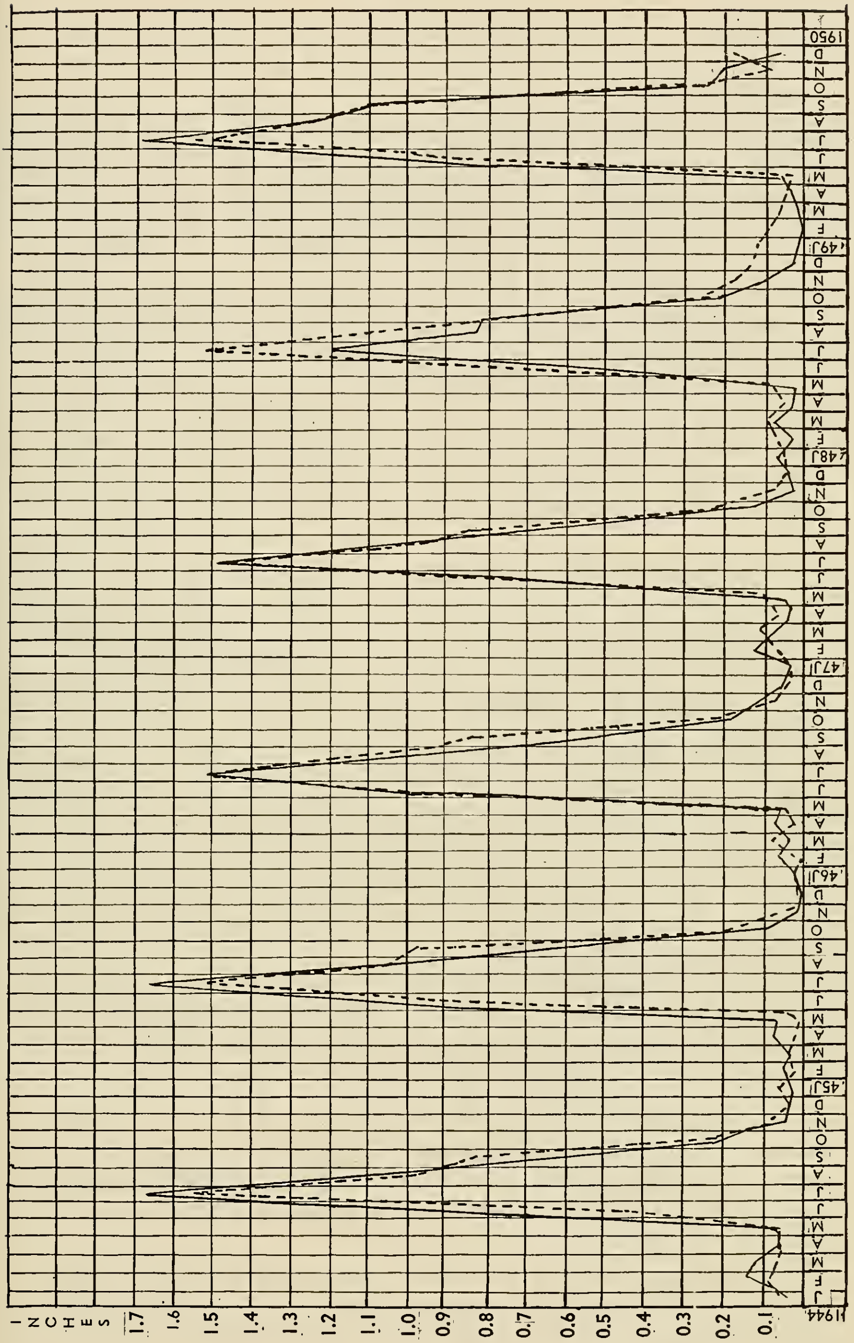

FIG. 12.—Nagpur, India, monthly precipitation (in millimeters), forecast and observed, 1944-1949.

Forecast: dotted line .... Observed: solid line ———

representative of the events through those 6 years as could reasonably be hoped for, both as to timing and quantity of precipitation. It may be noted that after February 1945 the short dotted line marks the change from Wolf sunspot numbers, *less*, to Wolf numbers *greater* than 20.

The *coefficient of correlation* at Nagpur between "forecasted-from-1870" and "smoothed-observed precipitation," 1944-1949, as observed in millimeters, has the astonishingly high percentage value +90.1 percent. Equally long-interval correlation coefficients between forecasts and smoothed-observed events for others of the 55 world stations, which we have forecasted, usually run between +50 and +70 percent. At Tokyo, 1938-1949, omitting bombing years 1944 and 1945, the coefficient of correlation indeed is higher. It reaches $+72.5 \pm 4$ percent.

The results of Tokyo precipitation are so instructive that I present in figure 13 the monthly forecast and smoothed observed precipitation, 1938-1943, with comments thereon.

COMMENTS ON FIGURE 13

This figure was prepared in long-hand by copying a section of the original computation, which was in pencil. I sent a photographic copy covering the 30 years 1933 to 1963 to Dr. Arakawa in Tokyo, about 4 years ago.

1. Figure 13 will testify that the preparation for computing long-range forecasts of weather from early records of forms and amplitudes of 27 harmonics is *very tedious*. Many of the signs and numbers copied for figure 13 were so dim in the original penciled computation that probably some errors occurred in copying them in ink. If so, such errors do not prejudice the curves of prediction and event. These are as originally drawn in ink.

2. I chose 6 years when prediction and event show large amplitudes of variation from the normal monthly values of figure 9. The extreme range of variation exceeds 130 percent of normal precipitation.

3. In the 4½ years, 1938 to June 1942, the dotted curve of observation averages about 25 percent of normal *above* the full curve of prediction. But from July 1942 through 1945 the observed curve (as sent to Dr. Arakawa) averages about 40 percent *lower* than the predicted. I attribute this to the plutonium bombing of Hiroshima and Nagasaki in 1943.

4. Even larger and more capricious discrepancies between prediction and event occurred for the years 1950 to 1953, and also for the years 1959 to 1963. This may well be due to the enormously powerful

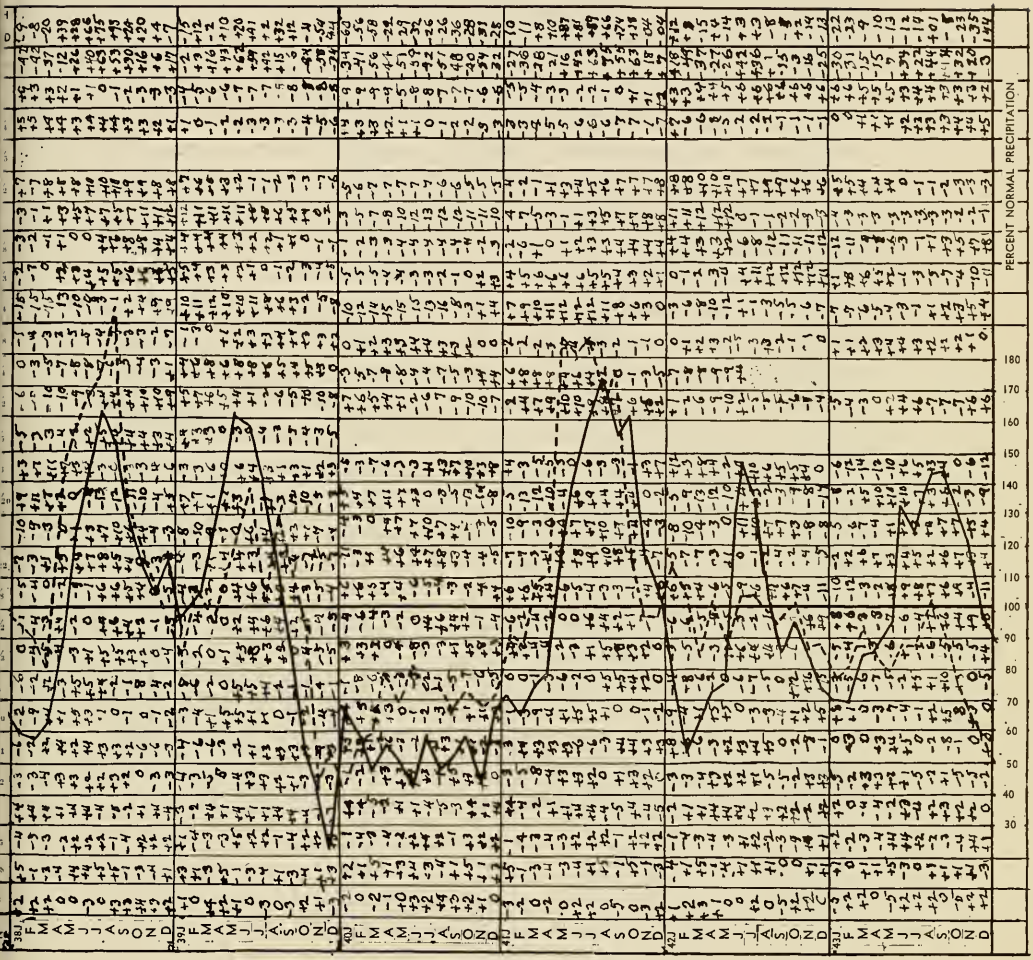

FIG. 13.—Tokyo, Japan. Monthly precipitation, forecast and observed, 1938-1943.

Forecast: solid line ——— Observed: dotted line ......

hydrogen bombs, released at high levels in the atmosphere by the U.S.S.R. and United States, about 1950 and 1958. My predictions indicate that these tremendous explosions, and their fallout, produced noticeable effects on precipitation in all continents. I have given illustrations to show this in figures 6-11.

YEARLY FORECASTS AND OBSERVATIONS

To support the value of long-range predictions made from harmonic periods found implicit in *World Weather Records,* 1870-1949, I give in figures 14-17 yearly values covering about 25 years each for four widely separated cities. The cities chosen are Buenos Aires, Copenhagen, Johannesburg, and Lagos. The yearly mean values are plotted in light lines, full and dotted, as departures from yearly normals. To make the comparison clear, both forecasted and observed yearly means are then smoothed by the formula $\frac{1}{10}(a+2b+4c+2d+e)$. It becomes fully apparent that the differences between prediction and event are much less than the average amplitudes of their common variations. Yet their agreement is disturbed after 1950 by the bombing effects considered above, and illustrated in figures 6-11, except at Johannesburg where the bombing effect is hardly noticeable. Some differences in phases occur in each illustration.

MONTHLY AND 4-MONTHLY FORECASTS

As stated above I had expected to compare monthly forecasts with observations 1950-1970, but found the bombing effect so noticeable from 1950 to 1964 at most cities that it seemed doubtful that such a comparison from 1950 would be useful. But for what it may prove, I give in table 7 forecasts monthly and 4-monthly, 1965-1970.

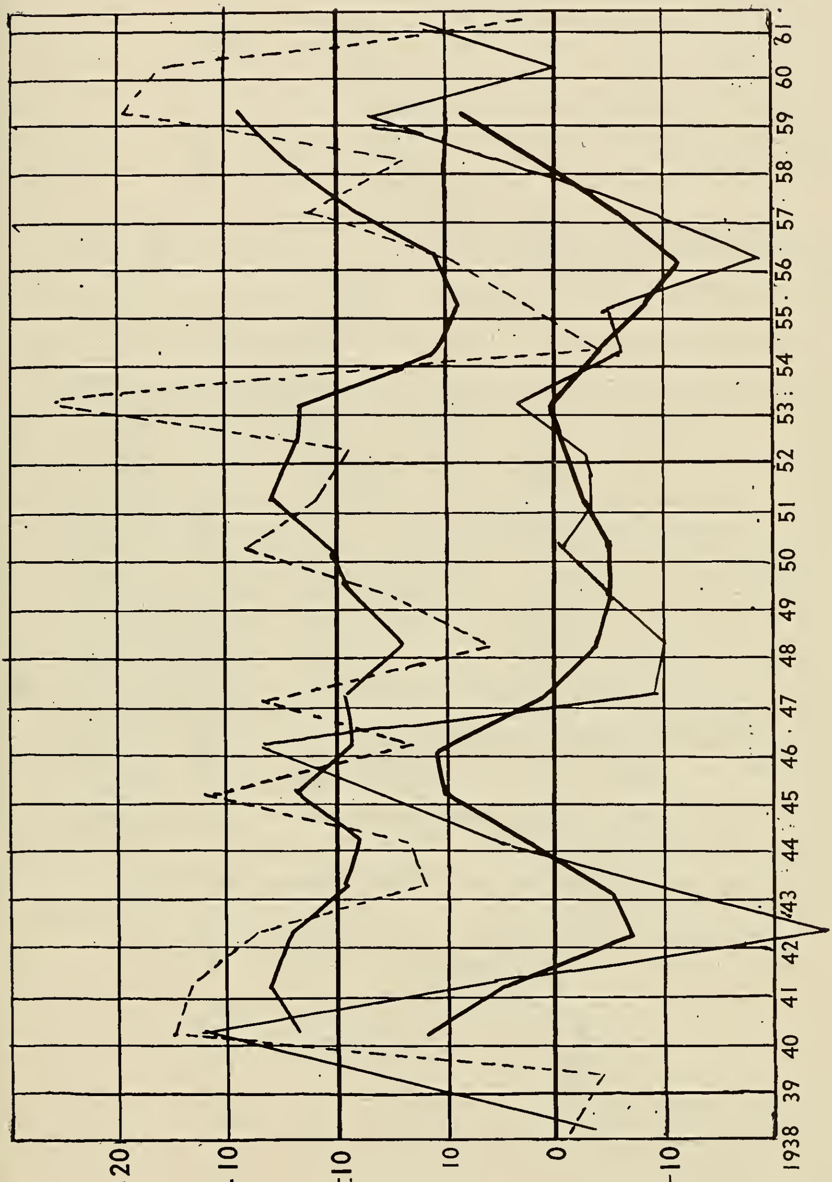

Fig. 14.—Buenos Aires, Argentina. Yearly precipitation, forecast and observed, 1938-1961.

Forecast: dotted line .... Observed: solid line ——

Smoothed: heavy solid line ——

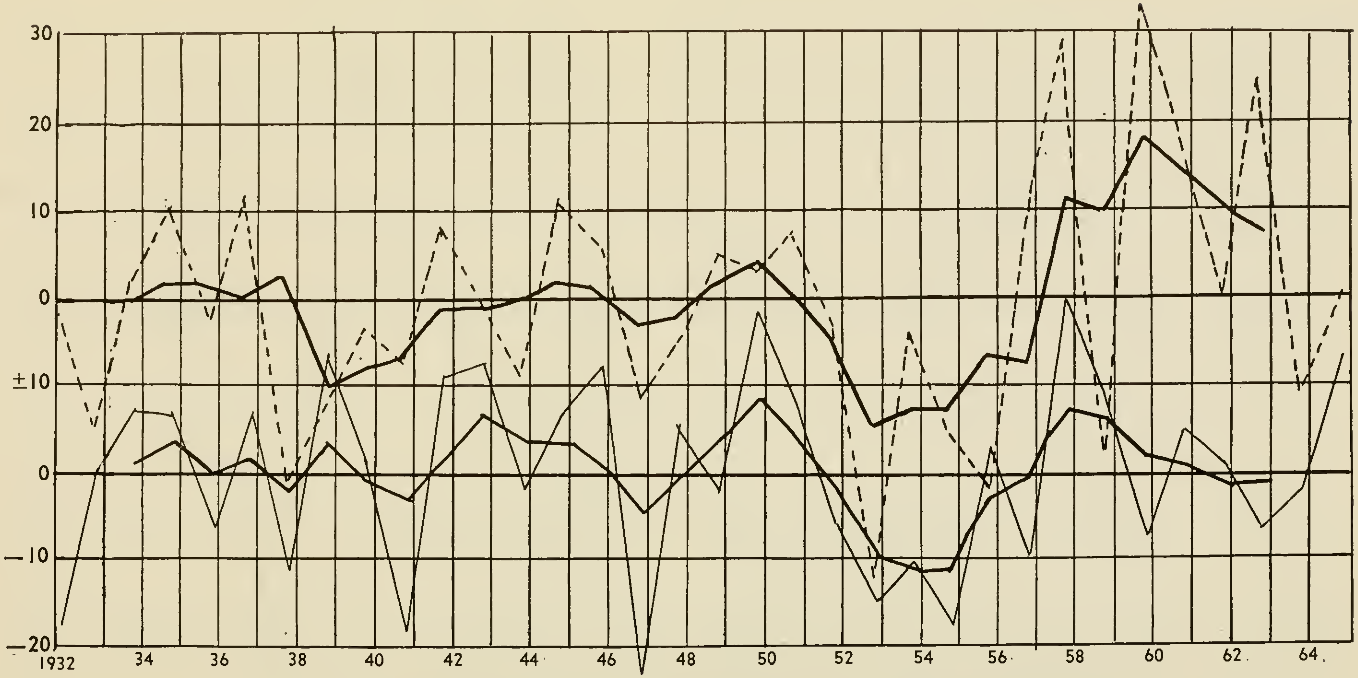

FIG. 15.—Copenhagen, Denmark. Yearly precipitation, forecast and observed, 1932-1964.

Forecast: solid line ——— Observed: dotted line ......

Smoothed: heavy solid line ———

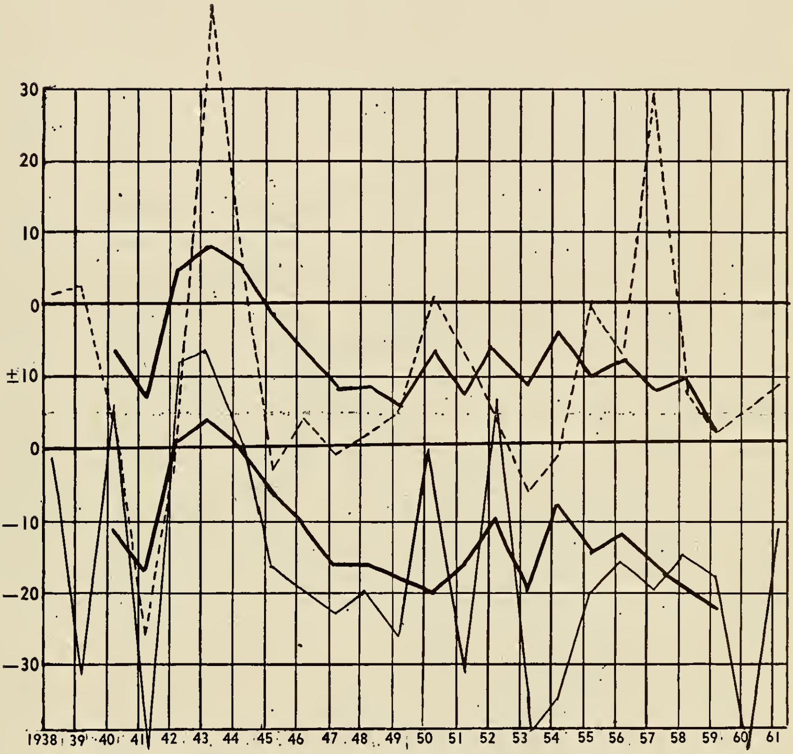

FIG. 16.—Johannesburg, South Africa. Yearly precipitation, forecast and observed, 1938-1961.

Forecast: solid line ——— Observed: dotted line ......

Smoothed: heavy solid line ———

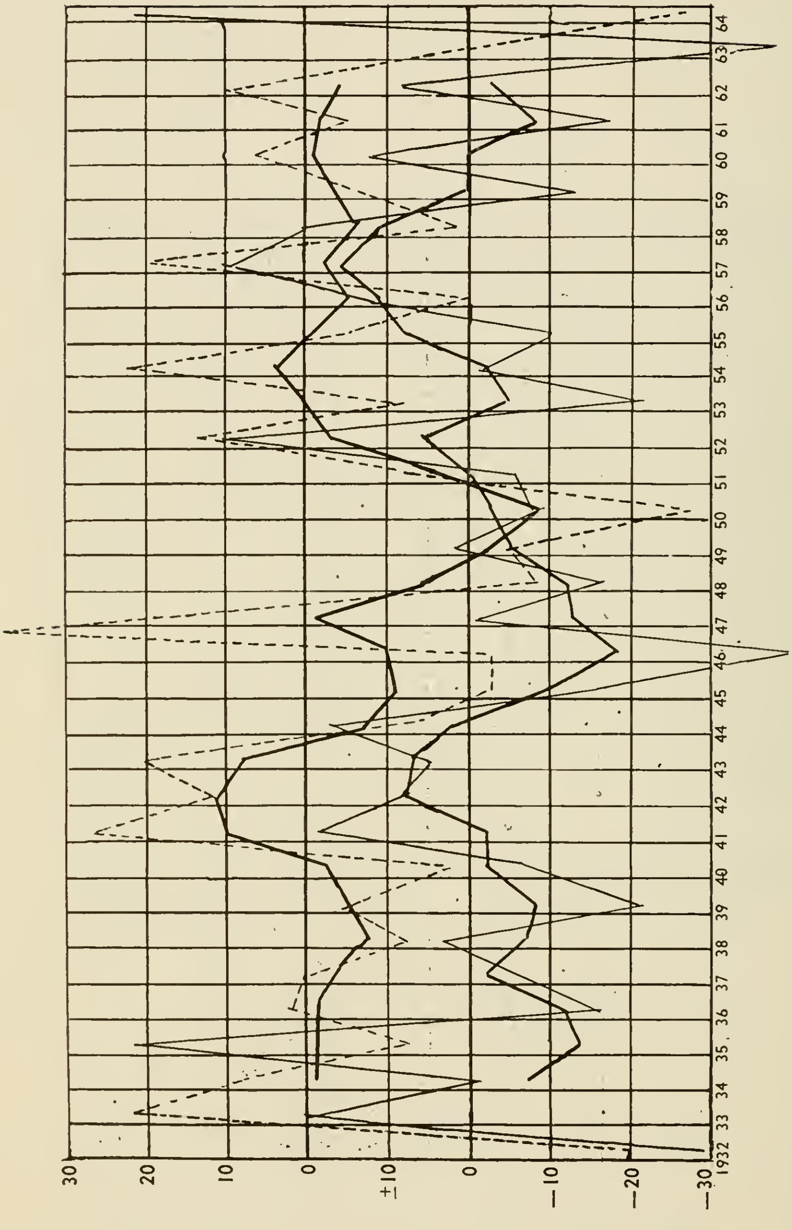

FIG. 17.—Lagos, Nigeria. Yearly precipitation, forecast and observed, 1932-1964.

Forecast: solid line ——— Observed: dotted line ......

Smoothed: heavy solid line ———

Table 7.—*Predicted departures from normal precipitation, 1965-1970.*

A = January-April. B = May-August. C = September-December.

Period	Adelaide	Athens	Berlin	Buenos Aires	Cape Town	Copenhagen	Greenwich	Johannesburg	Kiev	Lagos	Madrid	Moscow
1965												
A	+6	+27	—34	+1	+17	+2	—22	—106	+55	—29	—25	—16
B	—11	+30	0	—6	+55	—19	—15	—41	0	—35	+14	+70
C	+40	—89	+12	—21	—8	+58	+92	—61	—43	+73	+76	—57
1966												
A	—10	+1	—12	—51	+6	+4	—5	+20	+20	—34	+36	—62
B	—15	+27	—42	+8	—3	+1	—60	+62	—25	+32	+61	+12
C	+4	+6	+4	+37	—18	+2	—12	—17	—9	+36	—2	—53
1967												
A	+31	+42	+6	+15	—15	+1	—13	+4	+21	—55	+46	—21
B	—34	—34	+2	—23	—3	—20	—5	+89	0	+31	—36	+8
C	+3	+30	+29	+22	—8	+3	—5	+20	+17	+1	—14	—21
1968												
A	—12	+47	+22	+6	0	+10	+36	+46	+10	—27	+13	+20
B	—57	—66	—16	—16	+4	—7	—6	+13	+5	—40	—38	+84
C	+88	+14	+29	+59	—4	—13	—31	—21	+4	—25	—27	+13
1969												
A	+52	+42	+32	+69	+13	+49	+31	+17	+17	—51	+20	—18
B	—64	—73	—36	+13	+27	+22	+36	0	+10	—60	—61	+5
C	+32	—48	—37	—22	—11	—18	+13	—52	—13	+34	—45	+29
1970												
A	—40	+57	+16	+40	—22	+15	+25	+50	+28	+17	+82	—24
B	—16	—41	+13	—35	—3	+33	+10	+20	—2	+102	+32	+102
C	+92	+24	—6	+45	+22	+7	+1	—22	—16	+56	0	+15

Table 7.—*Predicted departures from normal precipitation, 1965-1970.—Continued*

A = January-April. B = May-August. C = September-December.

Period	Nagpur	Orenburg	Paris	Rio de Janeiro	Rome	Sibiu	Tokyo	Tunis	Uppsala	Vienna	Wellington
1965											
A	+5	—11	—90	+18	+20	+27	+30	+60	+9	—54	+16
B	—102	+106	+40	0	+3	+12	+18	—103	+10	+12	—11
C	—23	—33	+46	+4	+88	—16	+11	+34	+18	+14	—50
1966											
A	—33	—130	—18	+21	+24	—27	—10	+52	—40	0	—26
B	—26	+6	—21	+30	—19	—26	+34	—102	—4	+29	+44
C	+38	—72	—28	+54	—26	+12	—14	+4	+13	+6	+1
1967											
A	+80	—57	—14	—8	—14	—4	—26	+10	0	—26	+12
B	+32	+10	—38	—29	—36	—10	+22	+39	+6	—8	+11
C	+24	+2	+22	+4	—43	+7	+31	+16	+33	+33	+13
1968											
A	+3	—16	+34	+32	—8	—18	—8	—17	+23	+2	+21
B	—48	+114	+8	—18	+4	—13	+17	—7	—8	—28	—30
C	—57	+44	0	—10	—18	+41	+21	+22	+30	+49	—2
1969											
A	+47	—58	+22	—1	+83	—4	—22	—77	+30	+25	+30
B	+11	+56	+5	+7	—24	—14	+11	—71	—25	—1	—13
C	—3	+27	+3	+39	—6	+39	—6	+36	+12	—1	+6
1970											
A	+40	—57	+19	+10	+61	—6	—17	—71	+22	+12	—27
B	—59	+80	+9	—10	—16	—21	+11	—64	+45	—17	+1
C	+5	—25	+11	—15	+2	+11	+13	+20	+36	+6	+36

SMITHSONIAN MISCELLANEOUS COLLECTIONS
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THE EARLY HISTORY OF THE SUN*

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The early history of the sun is related to many aspects of astrophysics and in particular to the origin of the solar system. Ideas about its origin have been many, and these have been extensively debated for a little more than three centuries, going back to the time of Descartes. But the subject is still wrapped in mystery. The sun's role in problems of the origin of the solar system seems somewhat less complicated than those played by the planets, yet it seems safe to say that not until we understand how the sun was formed will we understand the formation of the planets.

There have been two general classes of theories concerning the origin of the solar system. One involves the theory that there was a close passage of another star near the sun during which an enormous amount of gas, from which the planets subsequently condensed, was torn from the sun. This idea, first put forward by Buffon about two centuries ago, has generally fallen into discard. Among the reasons for this is that the gas torn out of the sun would be much more likely to disperse in space than to condense and form planets, and it would contain no deuterium of the sort that we find in the heavy water mixed into the oceans. Worth noting in passing is that in this type of theory the early history of the sun would be unrelated to the formation of the planets.

In the other class the theory is that there was a condensation of interstellar gas and dust out of space, and both the sun and planets are formed from this. The conservation of angular momentum during the condensation process may be expected to flatten the condensed system into a disc with general dimensions of the order of

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* The 30th annual James Arthur Lecture on the sun, delivered at the Smithsonian Institution on March 10, 1965.

those of the solar system. Some version of this general class of theory is generally believed by astrophysicists working on the problem today.

It is very instructive to look at a color photograph of a distant spiral galaxy of the general sort that is thought to resemble our own galaxy. Such a picture will show many dark absorption lanes in the general plane of the galaxy produced by dust in the space between the stars which is mixed with great quantities of interstellar gas. In addition to this dust and gas, the light coming from the central portions of the galaxy will tend to be rather yellowish or even reddish, with a large central bulge above and below the plane of the galaxy, indicative of the general class of stars that astronomers call red giants. The starlight coming from farther out in the vicinity of the gaseous galactic disc tends to be much bluer. Astronomers describe the stars producing this light as young blue giants. The red giant stars which cluster toward the center are in fact very old stars which were formed many billions of years ago. They are not much, if any, more massive than the sun. However, the young blue giants are much more massive and also enormously more luminous. They radiate energy at such a prodigious rate that they will exhaust their hydrogen nuclear fuel in periods of only a few million years. This is why we are certain that they were formed very recently in the past.

Astronomers use a variety of techniques in trying to discover how old our galaxy may be. Most of these techniques are associated with attempts to determine how long ago the oldest stars in the galaxy were formed. Such methods depend upon a variety of theoretical and empirical methods. While they cannot be trusted too closely, they indicate that the oldest stars in our galaxy seem to have been formed at least 10 billion years ago, and perhaps as much as 25 billion years ago.

The sun lies in the central plane of our galaxy, in the neighborhood of the gas and dust and newly formed blue giant stars. If we assume that the sun was formed at the same time as the remainder of the planetary system, it is then possible to determine the age of the sun by standard radioactive dating techniques. Such techniques measure the relative abundances of radioactive isotopes and their decay daughters in meteorites and in rocks derived from the mantle of the earth. The greater the amount of the radioactive daughter which has accumulated in the vicinity of its parent, the older is the age of the material. Measurements of this kind indicate that the solar system is 4.5 billion years old, thus much younger than the galaxy.

Most attempts to reconstruct the history of our galaxy tend to indicate that star formation rates were probably much higher during the early history of our galaxy than they are today. Hence it seems likely that the general physical conditions in our galaxy at the time the solar system was formed were rather similar to those we see in the galaxy today. This conclusion is very important in attempts to unravel the early history of the solar system, since it gives us a definite set of physical conditions that we can logically postulate for pre-solar-system history. Without such definite assumptions it would be difficult to know where to start.

There are regions in the interstellar gas in our own galaxy where the gas density has become quite high. We see such a region—the Orion Nebula is one—as a shining nebulosity because the gas is illuminated by nearby hot stars. It is possible to use very simple physical arguments to determine whether gas is likely to form stars in regions such as this.

Star formation will require any cloud of gas in space which is to participate to become unstable against collapse to very much higher densities. The forces which tend to bring about this collapse are gravitational in nature. The denser is the given amount of mass, the greater are the self gravitational forces on that mass. Alternatively, if we consider gas of a given density in space, then the larger the cloud containing that gas density, the greater will be the self-gravitational forces tending to pull that matter together.

There are also forces which tend to expand a cloud of gas in space. The heat energy contained by the gas which is absorbed from nearby stars is sufficient to bring about expansion. In the ultraviolet region of the spectrum which is emitted from such a star, the radiation will ionize all of the hydrogen in the vicinity of the star. (Hydrogen constitutes about three fourths of the mass of the interstellar gas.) The absorption of ultraviolet radiation will heat it to a temperature of about 10,000°K., and it would tend to expand very violently. However, the ultraviolet radiation beyond the ionization energy of the hydrogen is used up in this ionization after traveling some distance away from its parent star. Beyond this distance the hydrogen is not ionized, and starlight is sharply cut off at the hydrogen ionization limit. This starlight is still energetic enough to ionize certain other atoms, such as carbon, silicon, and iron, and this ionization process still imparts some heat to the gas. It is sufficient to maintain the temperature of the neutral hydrogen regions somewhere in the vicinity of 100°K.

In order to determine when star formation is likely, we must determine when the gravitational forces that tend to pull the gas together will overcome the thermal forces that tend to expand it. Most of the time the thermal forces predominate and the bulk of the interstellar gas clouds are stable against collapse. Occasionally, in a gas cloud which is dense enough or sufficiently massive, the gravitational forces predominate, and hence we expect such a cloud to collapse. However, we learn from precise physical analysis of the situation that the minimum mass of interstellar gas required to make the gravitational forces predominate is at least a few hundred times the mass of the sun, and it may be as high as 100,000 or more times. Thus the gas which starts to condense in space is much more massive than a star of the order of mass of the observed star clusters, and typical stars would have to be obtained from such a cloud after a fragmentation process.

When we look at a detailed picture of the interstellar gas clouds, we see what appear to be many fine small irregularities in them. These irregularities are likely to represent both density and velocity fluctuations in the gas. It is these irregularities which are likely to cause the gas cloud to break up into many small pieces when it collapses in space. We would identify such pieces as stars which will form and presumably become like our sun.

Figure 1 indicates schematically what is likely to happen to one of these fragments as it contracts. At the beginning of the sequence the fragment is shown to be nearly spherical, but it is collapsing at the center. We also suppose the fragment to be rotating to some extent. Such rotation will be a consequence of the conservation of angular momentum in the fragment from the time that it was a part of the original interstellar gas cloud, which is likely to be rotating at least as much as would be required to complete one rotation per revolution around the center of the galaxy. The interstellar gas clouds appear to be permeated by magnetic fields which connect one piece of gas to its neighbor and thus tend to make the different parts of matter move together on a large scale. If there is turbulence in the gas, this can easily increase the amount of angular momentum in any small part of the mass. The later stages of the collapse indicated schematically in figure 1 will show that as the collapse continues, the rotation will cause the fragment to become a flat disc. This is because the gas near the edge of the disc is spinning rapidly enough so that the centrifugal forces associated with the spin are sufficient to

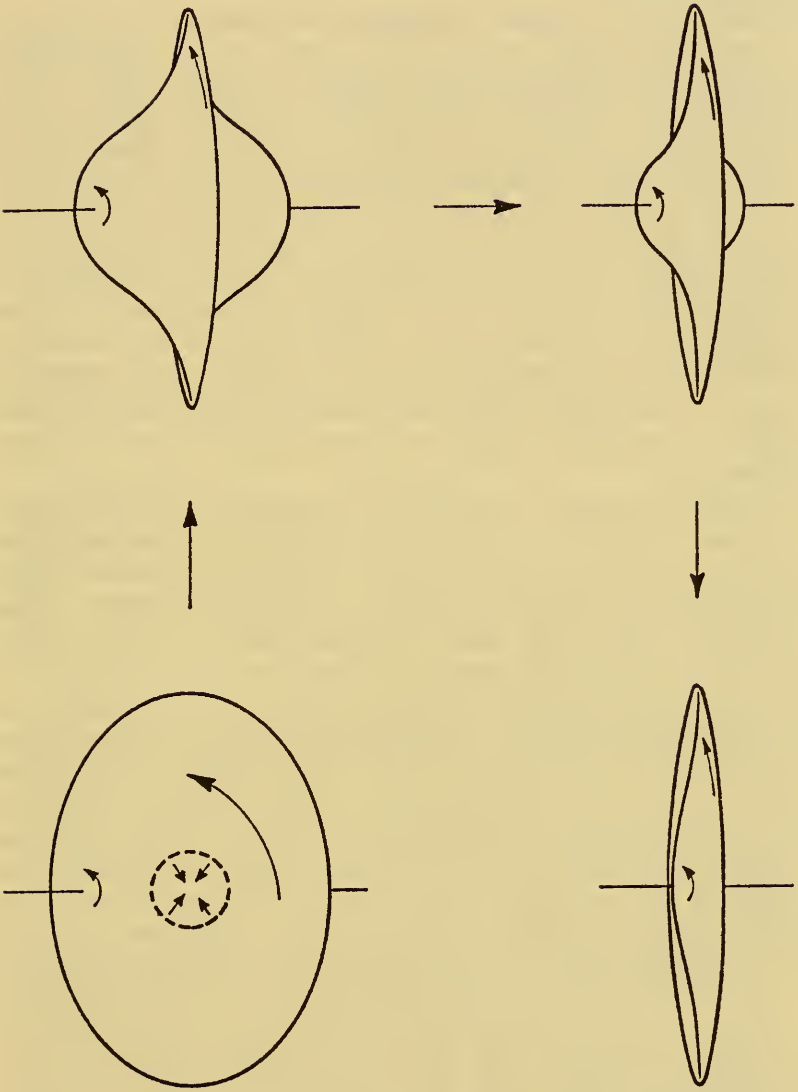

FIG. 1.—Schematic sequence of shapes as a fragment of an interstellar gas cloud collapses and flattens to a disc.

balance the gas against the gravitational forces which tend to pull it inward.

Much of the discussion and argument concerning the early history of the solar system centers on the question of how much angular momentum the primordial disc of gases is likely to contain. This discussion is concerned not only with how much initial angular momentum the gas would have when it starts to collapse, but also with the ability of the magnetic fields passing through the gas to transfer angular momentum away from the collapsing fragments to the surrounding interstellar matter that does not participate in the collapse. Perhaps the foremost advocate of an efficient transfer of angular momentum away from collapsing gas clouds has been Fred Hoyle. He has suggested that so much angular momentum can be transferred from a collapsing fragment of solar mass that this fragment does not begin to shed mass from its rapidly rotating equator until the radius has dropped below that of the orbit of the planet Mercury.

On the other hand, I have been an advocate of the opposite point of view: that if a gas cloud were rotating just once per revolution around the galaxy, the conservation of angular momentum during its collapse would require the primordial gas disc to have a radius at least as large as the orbit of the planet Pluto. In fact it would probably be considerably larger than that.

Furthermore, when this primordial disc is formed with dimensions comparable to the present solar system, there will not be a sun at the center. The disc will indeed be densest in the center, but the amount of gas there will be much too small to form a body in hydrostatic equilibrium which we could identify with a star. Thus it would be necessary to determine what processes might be responsible for gathering material toward the center in order to form the sun. Probably the most important of these processes is turbulence in the gas.

A discussion of the role played by turbulence in astrophysics started in the 1940's when the German astrophysicist, von Weizsäcker, pointed out that a large scale disc of gas of this sort would tend to be highly turbulent. He assumed that the largest organized motions in the gas, the turbulent eddies, would have dimensions comparable to the distances between the planets. Basing his calculations upon von Weizsäcker's ideas, ter Haar calculated that it might take only about 1,000 years to dissipate the primordial solar nebula and form the sun. Dissipation tends to bring matter inward in the disc because turbulence tends to make the gas in the disc rotate as a rigid body. The disc can only dissipate providing mass flows inward and angular momentum flows outward and becomes concentrated in smaller and smaller amounts of gas near the edge of the disc, which itself expands outward.

However, all these early calculations overlooked a rather important point having to do with the dimensions of the largest turbulent eddies. The eddy motion, which in part requires a large departure of the gas motions from being purely circular about the center of the disc, becomes subject to restoring forces which tend to prevent very large displacements in the radial distance. Hence ter Haar's calculation undoubtedly gives too small a time for the dissipation of the disc. Nevertheless, in view of the discussion we shall presently make about the time scale of contraction of the sun once it is formed, it seems unlikely that ter Haar's estimate of the dissipation time is too small by very many orders of magnitude.

I will turn now to the question of the details of solar evolution. The calculations which I will describe were carried out at our Institute for Space Studies in New York, in collaboration with Mrs. Dilhan Ezer, a theoretical astronomer.

The layman may find it strange that a theoretical astrophysicist can determine what goes on in the interior of a star like the sun. We cannot peer into the interior of the sun to determine the conditions which are present there. However, from the point of view of the basic physics which is involved, this is not a great problem, for it is probable that we understand the interior of the sun much better than we understand the interior of the earth. The basic reason for this is that the interior of the sun is extremely hot, so that the atoms in the interior are stripped of their electrons, and the basic physics of these particles is very simple. On the other hand, in the interior of the earth the temperature is not so hot, the atoms retain their electrons, and a wide variety of extremely complicated chemical processes can take place. Inside the sun we describe the gas composed of the atomic nuclei and the electrons as constituting a "perfect" gas which obeys extremely simple physical laws.

The equations which we need for the purpose of constructing a model of the solar interior are also very simple in principle. The equation of hydrostatic equilibrium tells us that the pressure at a given level in the solar interior must be just that amount which is necessary to hold up the layers that lie farther out. It must also be so arranged that there is a steady and continuous energy flow out of the interior of the sun. The temperature must fall off in such a way that the energy generated in the deep interior of the sun flows to the surface in a smooth and steady fashion.

There are basically three different ways in which heat can flow in the interior of the body. These are conduction, convection, and radiation of heat. In the interior of a star like the sun conduction is not important, but both radiative and convective transfer of heat are. Ordinarily, if the temperature does not change very rapidly from one point to another, only radiative heat transfer takes place, in which heat is radiated in one place and reabsorbed in another place, with a small tendency for a net flow of radiation in the direction of decreasing temperature. However, if the temperature does vary greatly between two points, transport of heat can take place by convective transfer, in which there is a bulk motion of the gas between the two points.

What one has to do in order to construct the model of the sun is to put these various physical ideas together and to determine a solution which satisfies the basic mathematical equations. Several years ago one used to sit down at a desk calculator and grind away on its handle until, after many trial and error calculations, a satisfactory run of physical variables through different parts of the star could be found which produced a fairly satisfactory model. Now we have electronic computers to do all this drudgery, and hence we make the drudgery much greater by trying to improve the physics that is put into the problem by making it as realistic as possible.

One of the critical points in the construction of models for the early evolution of the sun is the opacity of the surface layers. The opacity is a measure of the ability of the material to absorb the radiation that is trying to stream through it. Figure 2 shows some opacities which are relevant to the problem. Each one of the lines shows the opacity for material of given density as a function of temperature. Note that the opacity tends to be very high for temperatures between 10^4 and 10^5 degrees. At lower temperatures the opacity falls off greatly.

This is the key to an argument which was given four years ago by a Japanese astronomer, C. Hayashi. He pointed out that when a star like the sun was very big just after it had formed by contraction of interstellar gases, it could not have too low a temperature on the surface. This argument can be supported by the following kind of reasoning. Suppose the surface temperature to be very low, close to 1,000 degrees. The opacity of the surface layers would then be extremely small and we would be able to see very deep into the star.

As we looked into the deeper layers, we would see material of increasingly higher temperature, and also of increasingly higher opacity. When the opacity became high enough, several thousand degrees, we would be unable to see into still deeper layers. Consequently, the layers that we would see would be those which emitted light into space. They would constitute the true photosphere of the star. The energy streaming outward from the interior would heat the outermost layers, raising their temperature and opacity, and we would then no longer be able to see so deeply into the star. This process would

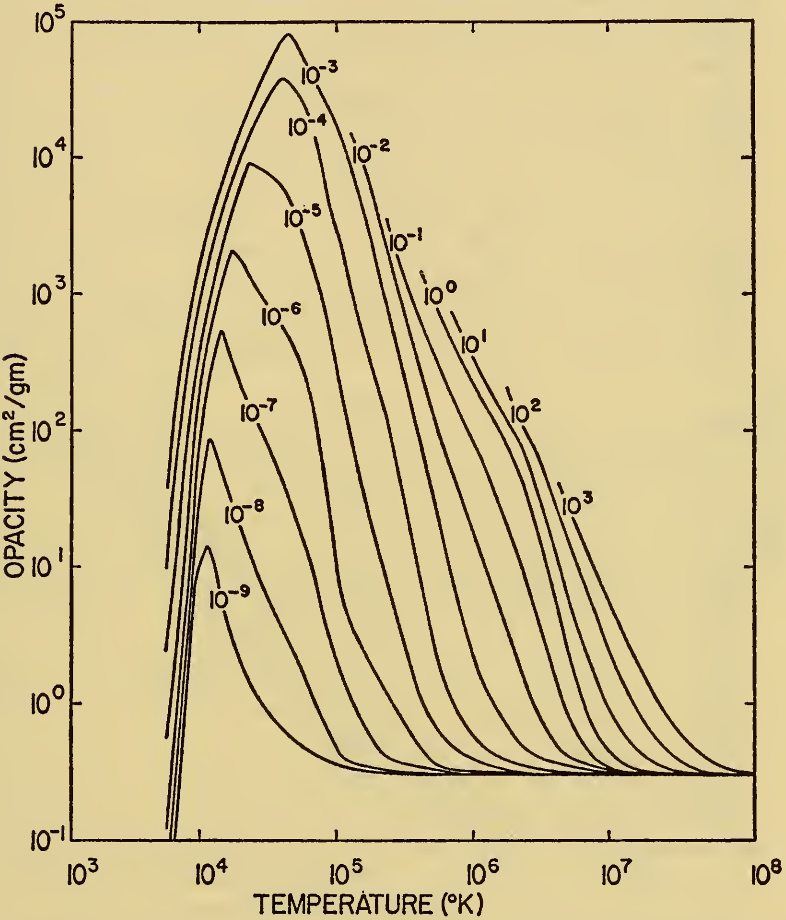

FIG. 2.—Opacity of solar material plotted as a function of temperature for lines of constant density (in gm/cm³).

continue until the temperature of several thousand degrees had worked its way up to a very shallow surface layer. This would then constitute the true photosphere of the sun. Consequently, it is not

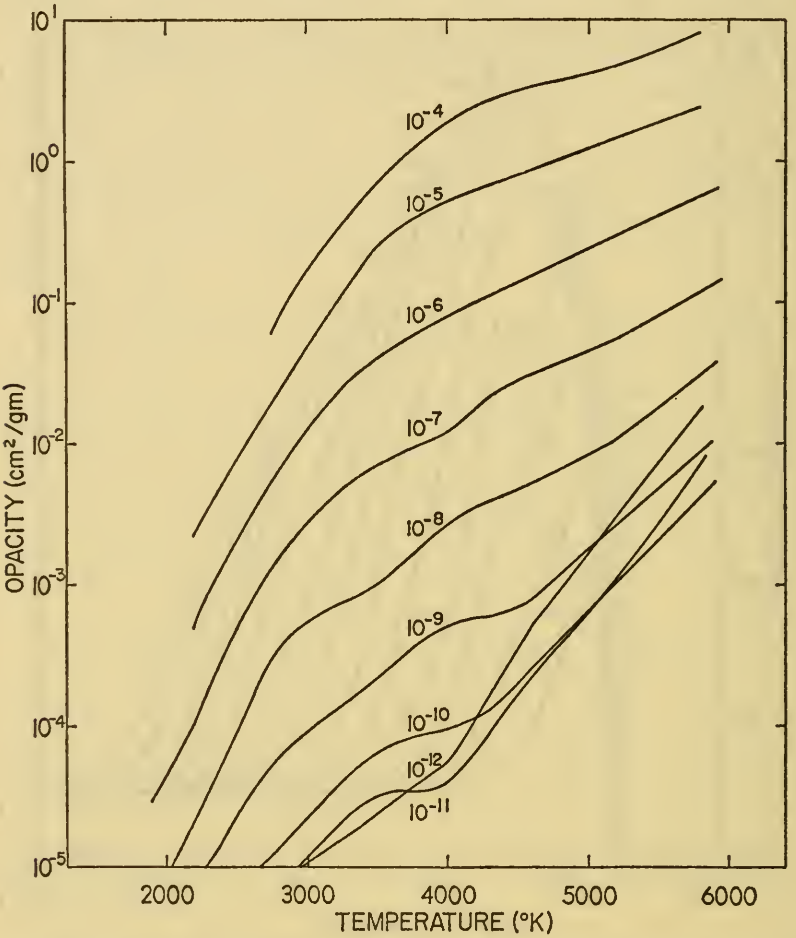

Fig. 3.—Opacity of solar material at lower temperatures, for lines of constant density (in gm/cm^3).

possible to have a satisfactory model of the outer layers of the sun at too low a temperature.

Figure 3 shows the low temperature end of the opacity curve in more detail. The curves have very steep slopes in this region of a few thousand degrees. Somewhere in this region of high opacity one would be able to find satisfactory conditions for the surface temperatures of the sun in its early stages of contraction.

However, Hayashi's contribution to this problem went far beyond the observation that the surface temperature of a giant star must be high. If the surface temperature of the star is high and its radius is very great, the total amount of energy emitted per second from such a star is enormous. This means that there must be a rapid rate of transportation of energy up to the surface layers in order to satisfy our condition on the smoothness of flow of energy. Radiative transport processes are not nearly efficient enough for this. The only way in which this can happen is for the entire interior of the star to be set into convective motion so that mass transport of energy can take place from the interior up to the surface. This requirement, that the interior of the star be fully convective, in turn makes certain demands on the interior distribution of mass; in particular, the central density cannot be too high relative to the mean density under such circumstances.

Figure 4 is a Hertzsprung-Russell diagram (or HR diagram) showing some early calculations that Mrs. Ezer and I made on the subject. In such a diagram one plots the light output or luminosity of the star versus the surface temperature, and at any given time a star can be represented by a point on this diagram. During the course of evolution of the star, the point will move about through various regions of the diagram. It is one of the duties of the theoretical astrophysicist to try to explain the characteristic motion of this point in the HR diagram. Correspondingly, the observational astrophysicist tries to determine how the stars are distributed in a diagram like this and to indicate just which facts the theorist must try to explain. In figure 4 is plotted the luminosity of the sun, in units of the total energy output that the sun now has, versus the temperature on the surface in thousands of degrees. Most stars lie along the line in the HR diagram which is designated the main sequence.

The models calculated by Mrs. Ezer and me, which were intended to represent an evolutionary sequence on the HR diagram, were computed according to a very simple assumption. The energy sources were taken to be not nuclear but gravitational in origin. As the matter in a star shrinks in its own gravitational field, it releases gravitational potential energy in the interior. This leads to the heating of the interior layers of the star. Now there is a fundamental theorem, called the virial theorem, which tells us that, under normal circumstances, half the energy that is released by gravitational contraction is stored in the interior and increases the temperature as the shrinking takes place. The other half is radiated away from the surface of the star. However, in order for this other half to be radiated away, it has to be transported to the surface. Hence the rate of shrinkage of the star will be just that rate at which half of the gravitational potential energy that the star releases upon contraction can be transported to the surface and there radiated away. We assumed, in making these models, that the relative density distribu-

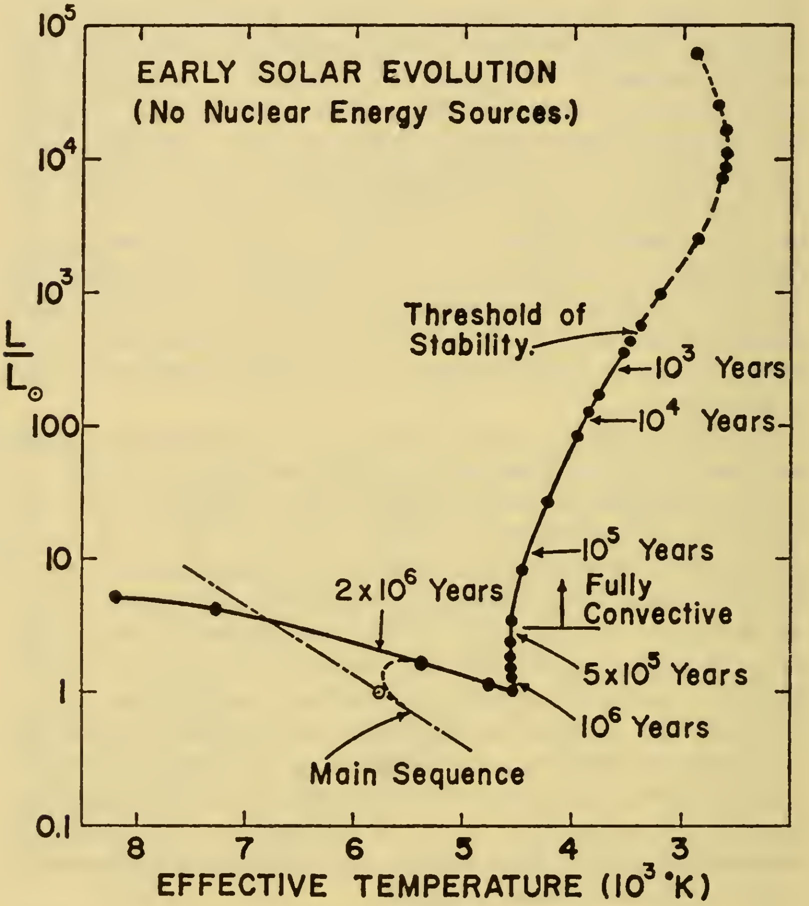

FIG. 4.—Hertzsprung-Russell diagram for the early evolution of the sun. Points show discrete models calculated with the assumption of homologous contraction. Indicated times are ages commencing from the threshold of stability.

tion in the interior of the sun would not be changed during the contraction, or, technically, that the sun was contracting homologously. This was obviously not an exceptionally good assumption, since the various models along our track had somewhat different density distributions in the interior; nevertheless, it sufficed to indicate the general way in which the evolution would go.

One can obtain a formal sequence of models along the line indicated in this diagram. However, all those models lying above the point indicated as the threshold of stability cannot exist in nature. At the beginning of the indicated sequence the sun would have a radius of about 1,000 times its present radius and would be much larger than the solar system. At the threshold of stability, which occurs at about 60 times the present radius of the sun, the released gravitational potential energy due to the contraction up to that point is just sufficient to supply the internal thermal energy of the model, plus the energy needed to dissociate hydrogen molecules, and ionize the hydrogen and helium in the interior to the extent called for by the model. In the models corresponding to a larger radius than the threshold of stability, the released gravitational potential energy is not sufficient to supply these energy demands. Hence the threshold of stability denotes the maximum radius the sun could ever have on purely energetic grounds. Any larger object would be dynamically unstable and collapse immediately. Beyond the threshold of stability the sun supports itself in hydrostatic equilibrium and slowly shrinks as it gets rid of its gravitational potential energy of contraction.

The initial shrinkage beyond the threshold of stability is very rapid. The track denoting solar evolution falls almost vertically in the HR diagram. This means that the surface temperature is remaining nearly constant while the radius rapidly shrinks. When the sun becomes small enough, in the vicinity of twice its present radius, the center of the sun ceases to be completely convective. The region of convection after that gradually recedes from the center toward the surface, and in the central region of the sun energy transport becomes primarily by radiative transfer.

When the central half of the mass of the sun becomes radiative, the track representing the evolution of the sun in the HR diagram ceases to fall rapidly; it turns around and starts increasing toward the upper left. This occurs because the bulk of the energy deposition by gravitational contraction now takes place in the inner layers of the sun where energy transport is by radiation. Under these circumstances it becomes the opacity of the deep interior rather than the opacity of the surface that principally governs the luminosity of the sun.

As the sun continues to contract, it becomes rather easy for the energy to flow out to the surface from the interior radiative portion, and hence the luminosity can now start gradually to increase. Since the radius is continuing to decrease, the surface temperature now increases at a regular rate, and the track of the sun lies toward the upper left.

At the time we made these calculations we were principally interested in testing Hayashi's ideas on the high luminosity and completely convective nature of the contracting sun. Consequently, we did not make allowance for thermonuclear reactions to produce energy in the interior of the sun as it contracted. However, we put in a dashed line in figure 4 to indicate the probable track the sun would follow when thermonuclear reactions became important. Because of their high temperature sensitivity, thermonuclear reactions generate energy much closer to the center of the sun than corresponds to the energy deposition by gravitational contraction. As a result there is a greater amount of mass for the energy to flow through before it reaches the surface, and the increased opacity thus cuts down the luminosity of the sun somewhat.

After this preliminary look at the situation we tried to carry out these calculations a little more seriously, paying more attention to the details of all the physical conditions that would be involved in the interior.

Whereas we used traditional methods of computation in constructing the models shown in figure 4, in which one integrates the differential equations of the structure both inward from the surface and outward from the center to a fitting point, to obtain the models shown in figure 5 we used a much more modern method of computation developed by Henyey for use with computers. We calculated two evolutionary tracks which corresponded to two different assumptions about the efficiency of the energy transport by turbulent convection inside the sun.

Consider what is involved in turbulent convection of gases. Imagine a blob of gas at some point in the interior of the sun. Let us raise this blob of gas slightly, not letting radiation flow across its surface, but keeping it in pressure equilibrium with its surroundings. At the higher level there will be a smaller pressure, so the blob of gas will be cooled by its expansion. The subsequent motion of the blob depends entirely on whether its temperature in its displaced position is higher or lower than the temperature of the surrounding medium. If the temperature is higher, the blob of gas will be less dense than its surroundings, and buoyancy forces will come into operation, causing it to be thrust upward. This is the condition in which convective energy transport takes place and turbulent mixing of the gases occurs. If the temperature of a blob is cooler than its surroundings, negative buoyancy forces will come into effect and the blob will be thrust back toward its starting position. Under such conditions the medium is

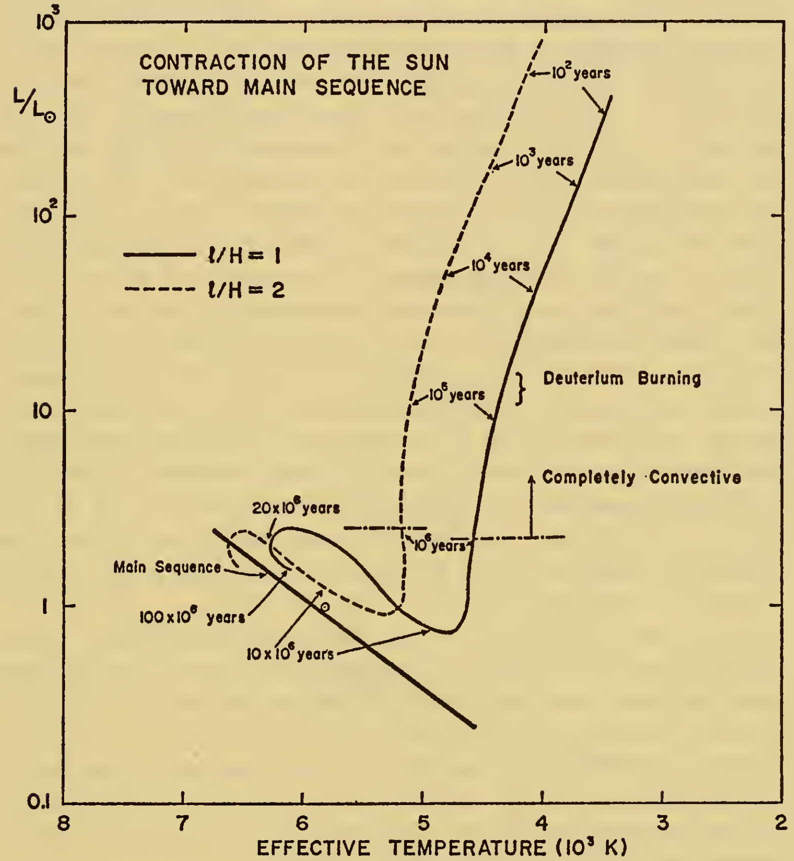

FIG. 5.—Hertzsprung-Russell diagram for the early evolution of the sun, with the evolutionary model sequences calculated by the Henyey method. The two evolutionary sequences correspond to two values of the ratio of turbulent mixing length to pressure scale height, 1/h. The composition contains about one-third helium by mass.

stable against convection and the only energy transport which is possible is radiative transfer.

The most efficient transport takes place for the largest blob that we can imagine to be formed and to rise through the interior of medium. Under such circumstances there are many modes of turbulent instability likely to be present in the blob that will fairly rapidly disrupt it into many small pieces, which will then dissolve into the surroundings. We are interested in the distance through which the blob can be accelerated before this dissipation by mixing into the surroundings takes place. The distance through which the acceleration takes place is called the mixing length that must be used in the convection theory. This is a number which must be assumed in the theory. Actually, one is best advised to assume several values of this mixing length and to see which one gives agreement with the observation. That was the purpose of the two tracks calculated for figure 5. It was hoped that the tracks would fall on either side of the present position of the sun at a suitable evolutionary age of 4.5 billion years, and one would then be able to interpolate and find what value should have been the correct mixing length for solar evolution. These two tracks correspond to a mixing length assumed to be one or two pressure scale heights. In a pressure scale height the pressure decreases by a factor of 2.7; in two pressure scale heights the pressure falls off by a factor of 7.

It may be seen in figure 5 that the two tracks descend almost vertically from the threshold of stability downward in the HR diagram; they pass from the condition of full convection to the condition of partial radiative transfer in the interior, they evolve toward the upper left of the HR diagram, and when nuclear reactions become important they turn downward. However, at no time do they bracket the present luminosity of the sun. The luminosity of the models always remains much higher than that of the sun.

Under such circumstances we must conclude that the opacity in the interior of these models of the sun is too small. This suggests, in turn, that we were using the wrong composition for the solar interior. The composition chosen for the models in figure 5 consisted of the relative abundances of the elements as deduced from solar spectroscopic analyses, plus chemical analyses of meteorites, plus spectroscopic analyses of certain other stars, particularly for the helium-to-hydrogen ratio. The helium assumed for the models was about one-third of the mass of the sun, corresponding to the amounts analyzed to be present in massive O and B stars recently formed in space. It is evident from figure 5 that improved fits to the solar luminosity would be obtained if the opacity in the interior could be increased, which, in turn, would correspond to raising the hydrogen content of the interior.

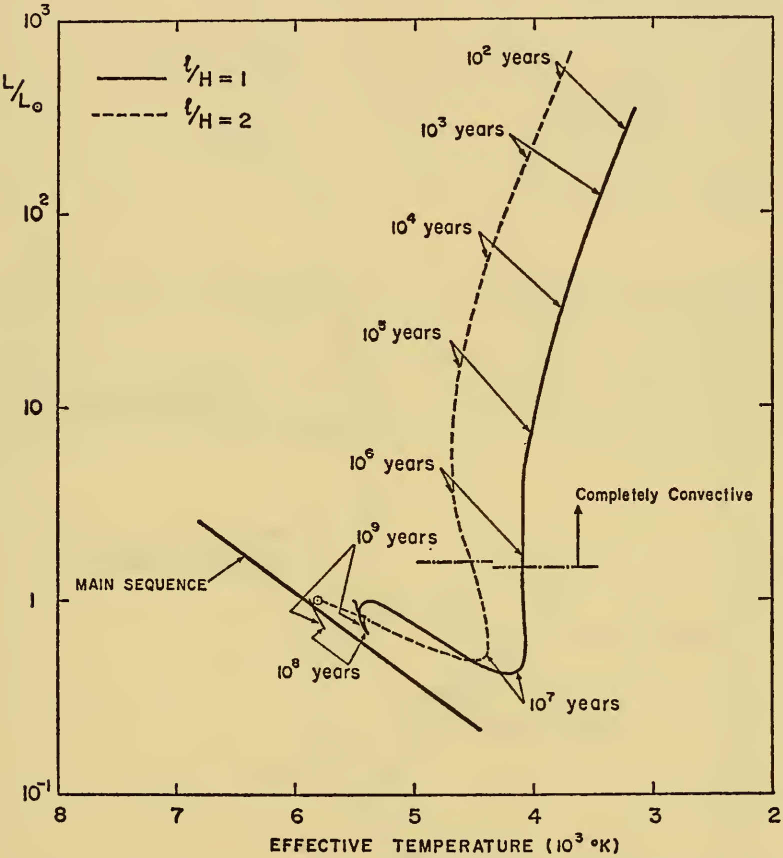

FIG. 6.—Hertzsprung-Russell diagram for the early evolution of the sun. This is similar to figure 5, but the helium content has been reduced to 24 percent by mass.

Just at this time our attention was brought to an indirect way of determining what the probable helium content of the sun is. A rocket flight flown by a group of experimenters at the Goddard Space Flight Center had measured the relative abundances of heavy ions in the solar cosmic rays. These established the relative abundances of helium and oxygen nuclei in the solar cosmic rays. When the solar composi-

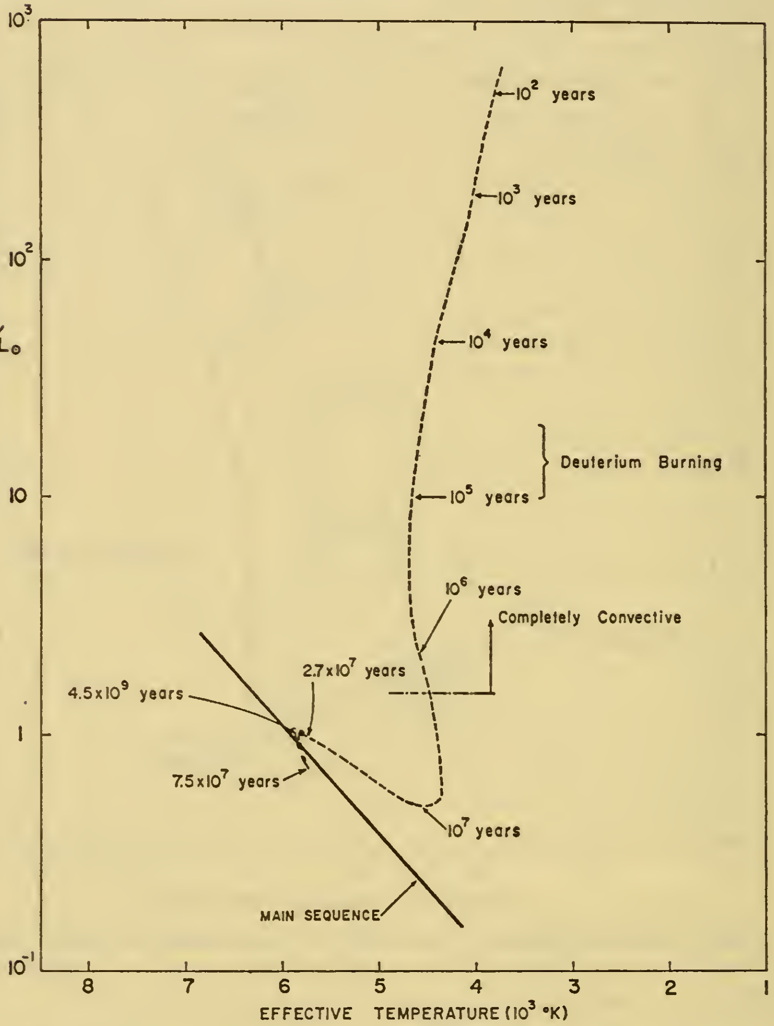

Fig. 7.—The adopted Hertzsprung-Russell diagram for the early evolution of the sun.

tion of helium is recomputed on this basis, the helium comes out at 24 percent of the mass. Consequently the calculations shown in figure 5 were repeated with the new composition for the solar interior deduced from solar cosmic rays.

The results of this recomputation are shown in figure 6. Again we have two tracks for the evolution of the sun, corresponding to the mixing lengths in the convection theory. Each of these tracks has almost exactly the right luminosity for a solar evolution age of 4.5 billion years. The track calculated for a mixing length equal to two pressure scale heights also goes almost exactly through the correct surface temperature of the sun at this age. We have therefore not felt it necessary to interpolate a mixing length between the two values shown.

Figure 7 shows the track which was finally adopted for the sun. We arrive at the conclusion that the sun went through a high-luminosity fully convective stage during its early contraction history, but we should not necessarily expect that the sun will start its evolutionary track at the threshold of stability. The manner in which the sun moves onto the Hayashi track remains to be worked out.

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 151, NO. 7

THE BIRDS OF SOCOTRA AND ABD-EL-KURI

(With 8 Plates)

By
S. DILLON RIPLEY
Secretary
Smithsonian Institution
AND
GORMAN M. BOND
Research Assistant

CITY OF WASHINGTON
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PORT CITY PRESS, INC.
BALTIMORE, MD., U. S. A.

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INTRODUCTION

Socotra (locally spelled "Soqotra") is the largest island in an archipelago lying 120 miles east of the "Great Horn of Africa" and about 300 miles south of the Arabian coast. Not until the latter part of the nineteenth century did exploring parties visit these islands with the special purpose of investigating their fauna.

The earliest expeditions, conducted by Professor I. B. Balfour of Glasgow University in 1879-80 and by two German scientists, Dr. Riebeck and Dr. Schweinfurth, in 1881, made extensive natural history surveys and collections on Socotra. These explorations were the first to direct attention to the unusual avifauna of this island. An annotated list of the birds collected by Balfour was published by Sclater and Hartlaub (1881) and a similar list covering the birds collected by Riebeck was published by Hartlaub (1881).

In 1888, the archeologist Theodore Bent visited Socotra. One of the members of his party, E. N. Bennett, made collections in several groups of zoology, including birds. During the winter of 1898-99, Henry O. Forbes of the British Museum and W. R. Ogilvie-Grant of the Liverpool Museums undertook a joint expedition to study the natural history of Socotra and Abd-el-Kuri. Later, Forbes (1903) compiled and edited a report upon this expedition. Ornithological notes and specimen records of the Bent expedition are included in Forbes' report. (Reference will be made in the present paper to the specimens collected by Ogilvie-Grant and Forbes and to the endemic species and subspecies which they described.) Since the publication of Forbes' monograph on the natural history of the islands, there have been no major contributions to the ornithology of Socotra and many aspects of the life history, ecology, and distribution of its avifauna have remained unknown.

SMITHSONIAN MISCELLANEOUS COLLECTIONS, VOL. 151, NO. 7

In 1964, the Smithsonian Institution commissioned Alec D. Forbes-Watson of Nairobi, Kenya, to undertake an ornithological survey of this interesting and little-known archipelago. This expedition, consisting of Forbes-Watson and two Turkana bird-skinners from Kenya, left Aden in early March and returned in mid-June of that year. During the 15 weeks spent on Socotra and on several of its neighboring islands, the party collected over 500 bird specimens, representing a total of 42 species. Forbes-Watson also collected a small number of reptiles and mammals but, unfortunately, the reptile specimens and all but a few mammal skins were stolen before the expedition returned to Aden.

This paper is a report by the authors on the bird specimens collected by Forbes-Watson during this expedition. Direct quotes attributed to him are taken from his field notes. All photographs also were taken by Forbes-Watson.

ACKNOWLEDGMENTS

Forbes-Watson received permission for the expedition to enter Socotra through the gracious kindness of His Highness the Sultan of Quishn and Soqotra, Issa Ali el Afreer. In many practical matters, his Chief Wazir, Sheik Ibrahim Khalid, provided helpful services and offered his friendly cooperation to the party on a number of occasions.

The relative inaccessibility of Socotra presented a major difficulty in arranging transportation for the expedition to and from the island. The party received much needed assistance in this critical matter through the generous cooperation of Air Vice Marshall Johnson, Air Officer Commanding, R.A.F., Aden, who provided them with air transport to and from the Hadibu airstrip.

Many other arrangements and plans associated with the undertaking were fraught with vicissitudes of the most trying nature. Without the help of a number of persons, the expedition could not have achieved success. In this regard, Forbes-Watson wishes to express his deep appreciation to the following: *In Kenya*: Mr. and Mrs. Nat Kolfsky, Anna Kolfsky, Myles North, John Williams, and the taxidermists Abilahi Loriu Lokiru and Loriu Lokiru. *In Aden:* Major and Mrs. Rose, Brian Doe, Arthur Watts. *In Socotra:* Whitney Straight and members of the Desert/Mountain Rescue Team. The present authors wish to express their deep appreciation to the authorities of the British Museum (Natural History), the American Museum of Natural History, the Peabody Museum of

Natural History, and the Field Museum of Natural History (Chicago), through whose cooperation comparative material was made available for study.

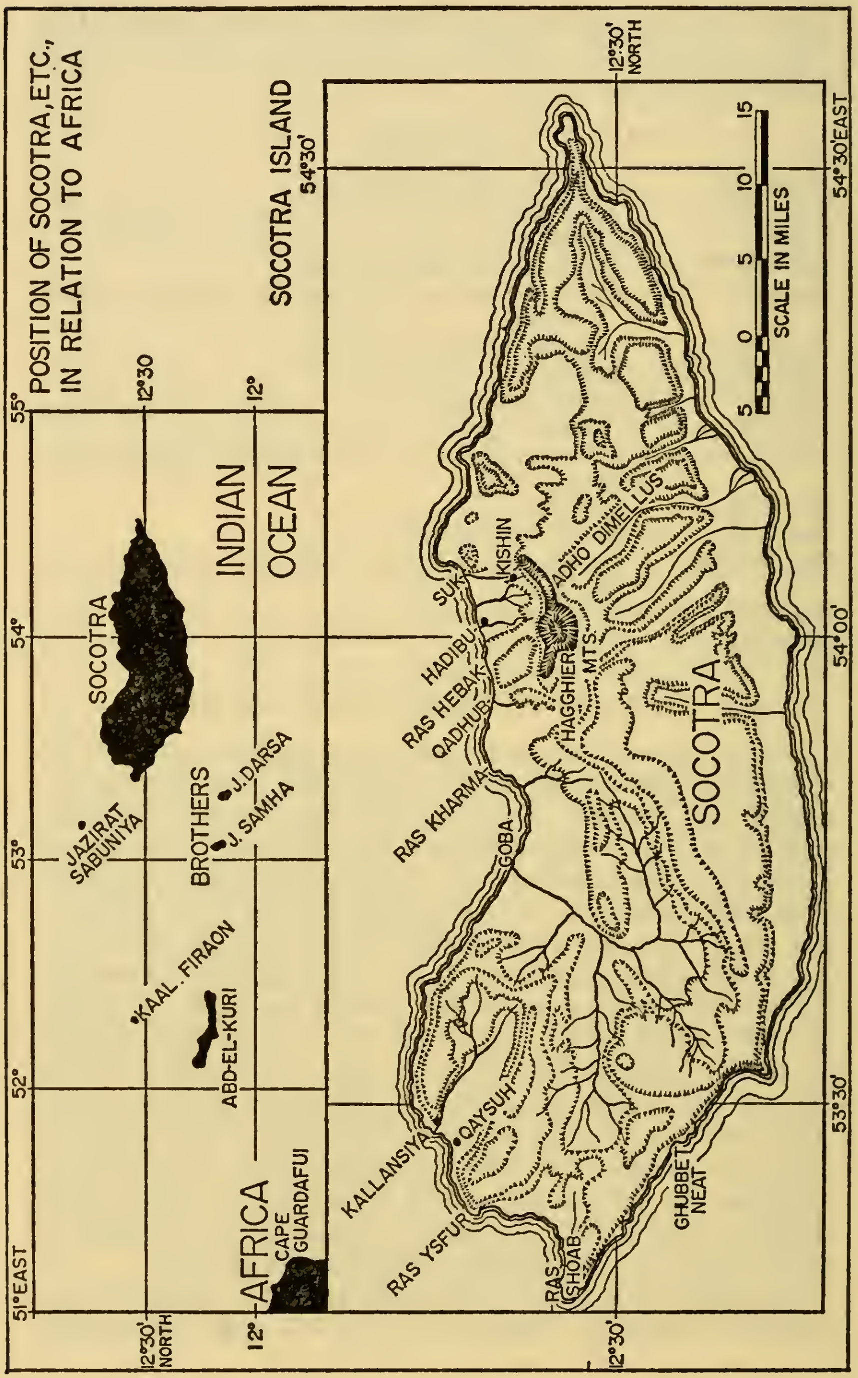
ITINERARY

March 7–15	Set up base camp at Hadibu Town
March 16–18	Traveled by dhow along coast eastward from Hadibu
March 19	Kallansiya
March 20–22	Traveled to Abd-el-Kuri by dhow
March 23	Visited the outlying islands of Kaal Firaon and Jazirat Sabuniya
March 24–25	To Hadibu via Kallansiya by dhow
March 26–April 1	Hadibu
April 2–3	Reconnaissance to Kishin
April 4–9	Hadibu
April 10–May 13	Kishin—base camp from which study of Hagghier Mountains was made
May 16–22	Hadibu
May 23–30	To Kallansiya by camel
May 31–June 7	Qaysuh—base camp set up here while studying west end of island
June 8–11	To Hadibu by camel
June 12–14	Hadibu

GEOLOGY AND PALEOGEOGRAPHY

Socotra, Abd-el-Kuri, and several of the islets between are formed of granite capped with limestone. Along much of the coastline, the granitic base rock rises sheer from the sea, but here and there, particularly at the mouths of rivers, it is indented by extensive coastal plains. On Socotra, the limestone plateau is interrupted by the Hagghier massif, which rises on the northeastern coast to an altitude of just under 5000 feet. The limestone plateau extends east, south, and west from the main peaks at an average altitude of 1500 feet. Geologically, Socotra resembles the Somali Plateau; thus, it appears to be a remnant of the land bridge that connected the mainland of Africa to southwestern Arabia from the Late Cretaceous to Early Miocene times. Later submergence is indicated by deposits of limestone that have been determined to be Eocene on the basis of a number of molluscs and echinoids identified from this formation. Collections of volcanic rocks have been made on Socotra, and Gregory (1903, p. 580) postulates the island has been involved in the same volcanic movement that formed the Gulf of Aden.

Regarding the emergence and submergence of the land during successive periods of alteration in sea level in past ages, Gregory


POSITION OF SOCOTRA, ETC., IN RELATION TO AFRICA
51° EAST
52°
53°
54°
55°
12°30' NORTH
12°30
12°
SOCOTRA
JAZIRAT SABUNIYA
BROTHERS
J. DARSA
J. SAMHA
KAAL. FIRAON
ABD-EL-KURI
INDIAN OCEAN
AFRICA
CAPE GUARDAFUI
SOCOTRA ISLAND
54°30'
12°30' NORTH
12°30'
53°30'
54°00'
54°30' EAST
SUK
KISHIN
HADIBU
RAS HEBAK
QADHUB
RAS KHARMA
GOBA
KALLANSIYA
QAYSUH
RAS YSFUR
RAS SHOAB
GHUBBET NEAT
ADHO DIMELLUS
HAGGHIER MTS.
SOCOTRA
5 0 5 10 15
SCALE IN MILES

(1903, p. 578) quotes T. G. Bonney: ". . . the topmost peaks of the Hagghier Mountains were at no time wholly submerged. . . . in the Hagghier Hills, we have probably a fragment of a continental area of great antiquity and of a land surface which may have been an 'arc of refuge' to a terrestrial fauna and flora from one of the very earliest periods in the world's history."

GEOGRAPHY AND CLIMATE

The archipelago of which Socotra is the largest island is situated in the Indian Ocean and is located between latitudes 12° and 13°N and longitudes 52° and 55°E. Latitude 53°55′E and longitude 12°30′N intersect near the center of the main island. Socotra is 85 miles from east to west and 25 miles across at its widest point. Although within sight of two main shipping lanes, Socotra is seldom visited by ships and there is no regular means of transportation to the island. This is due partly to the fact that there is no harbor, but mainly to the fact that, because very strong winds blow for about half the year, ships are warned to keep at least 40 miles away.

Most of the island is harsh, dry, and scrubby, relieved only here and there by oases near the infrequent water holes. Hadibu, located on the north coast, is the capital. It has a population of about 8000 Arabs in addition to Africans of slave descent. The chief occupation of the inhabitants, with the exception of the ruling Arab classes, is stock-raising, fishing, and pearling. The interior is populated chiefly by Bedu herdsmen.

The expedition performed a considerable amount of its work at or near Hadibu. Forbes-Watson gives a graphic description of the surrounding plain in his field notes:

> The Hadibu Plain is about six miles long and up to three wide. The sea-shore is mostly very pebbly, although there is a sandy beach near Suk, and some worn coral reefs are exposed at low tide especially as continuations of the minor promontories. These reefs are particularly attractive to migrant waders. The coast to the west of Hadibu is steeper and consists of earth cliffs about 20 feet high rising immediately behind the pebbly beach. Inland the plain consists of pebbles or gravel covered with a more-or-less thick boxwood scrub, this being thicker and taller the nearer it is to the foothills. There are one or two small hills, notably Hasun, south of Hadibu, where there are the remains of an Arab fort. Three main watercourses cross the plain, at Suk, Hadibu, and halfway between. These do not normally reach the sea, and in each case there is a sand-bar which prevents the fresh and salt-water from meeting (the fresh water is a few feet higher than the sea). The courses and lagoons are bordered by extensive date plantations, and the drier parts of the watercourses often have small rocky cliffs a few feet in height, otherwise the plain is rather flat and unbroken. To the west of the central river, and lying behind the beach, parallel

> to the sea, is a flat depression, which is periodically flooded by rains. Inland from this is an extensive bare plain, which, further inland, becomes better covered by small twiggy bushes a foot or two in height.

Immediately behind and south of the Hadibu Plain rise the pink granite cliffs of the Hagghier Mountains, which provide an impressive backdrop to Hadibu Town. Jebel Hajr, the tallest pinnacle, has an elevation of 4931 feet.

The second largest island is Abd-el-Kuri, which lies about midway between Socotra and the African coast. Less than 3 miles across at its widest point, it stretches about 20 miles from east to west. There is no surface water but there are a few brackish wells. This island supports a small population of pearlers.

Several other rocks and islets complete the archipelago. The Brothers are both flat topped with sheer sides. Jazirat Samha rises to 2557 feet and Jazirat Darsa to 1285 feet. Jazirat Sabuniya is a guano-whitened islet consisting of three peaks. It lies about 11 miles northwest of Socotra. Kaal Firaon consists of two bare guano-covered rocks separated by a narrow water-gap of surging current. Both islets are about 280 feet high.

Socotra falls within the Semiarid Tropical type climate of Thornthwaite (1933, p. 440). It is tempered by the northeast and southwest monsoon and is less torrid than the adjacent mainland. The dry southwest monsoon begins toward the end of May and the rainy season commences with the northeast monsoon in September. Highest precipitation is in November and December. Heat and humidity rise during the period of calm between monsoons. (Popov, 1957, p. 709).

Forbes-Watson describes his experience at the approach of the dry, summer monsoon:

> . . . there were heavy rain showers in each month, but each was of a very short duration. Even the Turkana skinners, who came from one of the hottest parts of Kenya, complained about the heat at mid-day. By the end of May the monsoon had started, and was strongest in the west, so much so that the tent had to be pitched in a pit or it would have blown away. Even so, it was ripped across, though the tent was new.

FLORISTIC AND FAUNAL RELATIONSHIPS

According to Good (1947, p. 38), Socotra belongs floristically to the Northeast African Highland and Steppe Region. In addition to a considerable element of tropical African affinity, it also contains a number of types more characteristic of the Northern Temperate Region. The vegetation of Socotra is considered by Pichi-Sermolli *et al* (1958) to belong to the Subdesert Steppe-Tropical type.

After studying a collection of plants from Socotra, Balfour (1903, p. 450) observed:

> It will be seen then that the new evidence brought by the expedition bearing upon the character and relationships of the Sokotran flora bears out the conclusions that have been based upon the plants previously brought from the island. The African—especially Abyssinian and Somaliland—connection is supported, the bonds with the opposite Asiatic mainland are strengthened, and most interestingly, the remarkable East Indian relationship receives a further illustration.

Harrison (1964, vol. 1, p. 5), in his study of the mammals of that area, places eastern Socotra in the Saharo-Sindian Zoogeographic Zone and western Socotra in the Tropical Ethiopian.

From the standpoint of bird distribution, Chapin (1932, p. 90) places Socotra in the Ethiopian Zone, Somali Arid District.

CHARACTERISTICS OF ISLAND BIRDS

Speciation in *Fringillaria* and *Onychognathus*

The genus *Fringillaria* is represented on Socotra by two species, *F. socotrana* and *F. tahapisi.* The presence of these two closely related species occurring together as residents of the same island may be accounted for in the following manner: Assuming that both *F. socotrana* and *F. tahapisi* evolved from a common progenitor on the African mainland, it must follow that both of these species were separated from one another by geographic barriers for a considerable length of time. The island originally may have been colonized by a wave of *Fringillaria* from the mainland. At a later date, a second wave of migrants arrived—but not before certain biological isolating mechanisms had become fixed in the pioneer species. The endemic, *F. socotrana,* is a monotypic species and has no representatives on the mainland. We may assume therefore that it arrived first (following the reasoning of Ripley, 1949, p. 154, in parallel cases among Indian birds). At a much later date, the island was colonized by another wave of migrants—the more widespread and adaptable species *F. tahapisi.*

It seems reasonable to assume that the sympatric distribution of *Onychognathus* may be accounted for in a similar manner. The fact that *O. frater* is an endemic species with no relatives on the mainland suggests that it also was a pioneer species. The monotypic species *O. blythii* is represented by populations on Socotra as well as on the mainland but, unlike *Fringillaria tahapisi,* it is not phenotypically separable.

A variety of isolating factors such as differences in habit, voice, and feeding niche requirements serve with varying degrees of significance to restrict random mating between closely allied forms. In this connection, Forbes-Watson has made the following observations which illustrate some of the factors that limit competition on an inter-specific level in both *Fringillaria* and *Onychognathus.*

Fringillaria species.—The commoner bird, *F. tahapisi,* is found from sea-level to at least 3000 feet, wherever an outcrop of rock forms a small scarp—such as along the edge of a dry gully—and in other areas, where the right combination of rock and feeding-grounds occur. In such situations it is found near thickets, but it has never been seen in them, whereas *F. socotrana* does occur in thickets, and also has been seen feeding on narrow ledges on rock-faces where *tahapisi* was not found. It appears that nonbreeding flocks of *socotrana* descend from the heights and forage socially at a much lower altitude than *tahapisi,* which was uncommon here. The two species were not seen together, but it is unlikely that *tahapisi* would favor the open slopes where the rarer bird was found. When *tahapisi* was seen feeding in flocks, it was invariably found in gullies, dry water-courses, and on more thickly covered hillsides, and, when disturbed, it flew fairly far away; the rarer bird was tamer and, when flushed, flew only a short distance before settling.

The calls of the two birds differ, that of *socotrana* being noted down as a high thin whistle (sometimes repeated two or three times), followed by a soft gurgle: "tseep . . . . guruguruguru." This first note is higher and thinner than the "seeoo" call of *Zosterops* and does not fall as does that call. The call of *tahapisi* is a soft metallic "jingling" song of quite different character.

On the ground, *socotrana* stands higher than *tahapisi,* which usually squats rather flat on the ground; also *socotrana* perches rather more freely than the other bird. The preference of *socotrana* for thickets and scrub points to a relict ecological tolerance for greater density of vegetation perhaps correlated with slightly increased moisture and more ample vegetation—in the view of the present authors.

Onychognathus species.—The two starlings were often seen together, but, except when feeding on ripening figs, have different feeding-habits, *O. frater* acting more like a thrush. The call of *frater* is softer and more whistled than that of *blythii,* though the alarm calls of both are similar, the typical harsh grating calls of the genus.

O. frater appears to be a shyer, quieter bird, and is less conspicuous. It was seen to obtain its insect food rather more from within a bush than on it and was never seen on the ground in the open nor associating with stock, whereas *blythii* is a bolder more obvious bird, more prone to flock, and is often associated with stock—cattle, donkeys, goats, and sheep—often perching on their backs but not actually feeding on them, apparently merely using them as beaters.

Here again, as in *Fringillaria socotrana,* the presumed earlier invader, *O. frater,* displays a relict ecological tolerance for slightly less arid conditions, a moister phase with more ample vegetation.

Plumage

Four monotypic species of passerine birds are endemic to Socotra. With two exceptions, the general aspect of these species is one of paleness, greyness, or general drabness of plumage. The two strongly colored endemic species, *F. socotrana* and *O. frater,* have a sympatric distribution on the island with their closely related, nonendemic cogeners, *O. blythii* and *F. tahapisi.* Even in this instance, the strong coloring and bold wing pattern of the endemics are reduced in intensity when compared with the nonendemic species. In addition to this, the sexual dimorphism exhibited by *O. blythii* (the females have grey heads) does not occur in the endemic *O. frater.* One polytypic species, *Passer insularis,* is found only on Socotra and Abd-el-Kuri and is represented on these islands by the geographical races *socotranus* and *insularis.* (In *P. insularis,* the Abd-el-Kuri form is paler than the race on the main island.)

Eleven species of Socotran birds, which differ in coloration from their mainland counterparts, are considered to be endemic subspecies. Again, with accountable exceptions, the Socotran forms are characterized by paleness or a reduction of color in the plumage. Only *Apus pallidus berliozi* is darker than the adjacent mainland subspecies *A. p. somalicus.* It is, however, considerably paler than the North African form *brehmorum* and may, indeed, have arisen from this stock rather than from the Somaliland population.

Another resident, *Rhynchostruthus socotranus socotranus,* is more boldly patterned about the head and neck than either of the other races in Somaliland or southwestern Arabia. This species is, however, a puzzling one and presents other problems as well. There is nothing in Africa or Europe that resembles it and its affinities are thought to be closest to some of the Himalayan cardueline finches (see also page 33).

In a recent study on the plumage of passerine birds on the Tres Marias Islands, Mexico, Grant (1965, p. 52) suggests that drabness originates as a by-product of the genetic reorganization of a population in the early stages of island colonization and, although there is no intrinsic value in this feature, its significance lies in the fact that islands have a small number of species; hence, the need for specific distinctiveness in that environment is, in many cases, reduced.

Size

Apus pallidus berliozi has a longer wing than its nearest counterpart on the mainland. *Lanius elegans unicinatus* has a longer and thinner bill than *archeri* of Arabia. Wing measurements of the remaining endemic subspecies on Socotra all fall within the range of their closest allies on the mainland, although wing measurements of Socotran birds fall off in the upper ranges, thus reducing their averages somewhat. (This also applies to *Passer insularis hemileucus* of Abd-el-Kuri in relation to the nominate race on Socotra.)

Based on this evidence, it may be said that most Socotran races average smaller than their mainland counterparts although the difference is slight and the trend is not without exception.

Family PROCELLARIIDAE: Petrels, Shearwaters

***Puffinus leucomelas* (Temminck): White-faced Shearwater**

"Recorded in April from seas just east of Socotra"—Macworth-Praed and Grant (1952, ser. 1, vol. 1, p. 13).

***Bulweria fallax* Jouanin: Jouanin's Gadfly Petrel**

The type of Jouanin's gadfly petrel was taken near Socotra (12°30′N,55°E) by G. Cherbonnier on June 20, 1954. This species is found commonly throughout the year in the Arabian Sea and the Gulf of Aden. It probably breeds in burrows on Socotra, Abd-el-Kuri, and the Kuria Muria islands off eastern Aden, possibly from October to March. While at sea, it feeds alone, often far from land. It is described as a lightly built, small, brownish-black gadfly petrel with a long, wedge-shaped tail and a short, thick bill. The feet are flesh colored with black outer edges to the legs and toes. Forbes-Watson saw a number of petrels as he was traveling by dhow from Socotra to Abd-el-Kuri but was unable to collect any of these birds.

Family PHAETHONTIDAE: Tropic-birds

Phaethon aetheureus indicus **Hume: Red-billed Tropic-bird**

Three or four were seen flying near Jazirat Sabuniya. One was heard screaming near the top of the islet and was caught by hand. It proved to be such a strong flyer that it escaped and flew out to sea. It is likely they were about to start breeding.—A. D. Forbes-Watson.

Family SULIDAE: Boobies, Gannets

Sula dactylatra melanops **Heuglin: Masked Booby**

PLATE 3 (top)

This species was seen on Socotra only in the vicinity of Kallansiya and was not common there. It was commoner along the north coast of Abd-el-Kuri, but most were seen on, and in the water near, Kaal Firaon and Jazirat Sabuniya, where they were nesting in March. There were possibly 100 pairs altogether, and breeding was in all stages. Several clutches of eggs were seen and four slightly-incubated sets were collected. There were also young of various ages, mostly one per pair of adults, but in several cases two very young birds occupied the same nest. No attempt at building was made, the eggs being laid in a depression in the rock. Sometimes a few gravel chips were present. About twenty percent of the flying birds near the islets were in dark immature dress, a much lower proportion than at sea or near Abd-el-Kuri, where it was around fifty percent.

Half-digested fish remains were seen at a nest containing two eggs, over which one of the parents was standing. A small gecko was seen on one of the eggs just below the belly of the booby. It was observed taking mouthfuls of the rotting fish. The booby did not seem to mind the intruder.—A. D. Forbes-Watson.

Sula sula sula **(Linnaeus): Red-footed Booby**

Ogilvie-Grant and Forbes (1903, pp. 50, 62) reported large flocks from the seas around Socotra and Abd-el-Kuri.

Sula leucogaster leucogaster **(Boddaert): Brown Booby**

Ogilvie-Grant and Forbes (1903, p. 62) obtained several specimens on Abd-el-Kuri.

Family PHALACROCORACIDAE: Cormorants

Phalacrocorax nigrogularis **Ogilvie-Grant and Forbes: Socotra Cormorant**

Of this species, previously unrepresented in the National Museum Collection, two specimens were taken by Forbes-Watson at Kallansiya, west end of Socotra, June 2. A female adult, in rather fresh sooty plumage has a wing measurement of 284 mm.; an immature bird of undetermined sex, 290 mm. Soft parts: iris dark emerald green; eyelid blackish with yellowish warty excrescences; bare facial skin blackish with grey ridges; bill black with yellowish sides, base dull grey green. Gular skin brown to grey-tinged green. Feet black, pinkish on joints; webs black; toes pink. Immature: iris dull greyish; eyelid yellowish pink; facial skin yellowish tinged green. Bill grey green, yellowish at base and sides; gular pouch pinkish, yellowish near base of bill. Feet dull greyish, paler on sides; webs dusky shading to pinkish near the toes. Stomach contents: fish.

This species was seen on all of the four islands visited by Forbes-Watson, but on Socotra it was recorded only from Ras Hebak and westward to Ras Bidu, where Ogilvie-Grant and Forbes (1903, p. 50) noted it also. Neither the two specimens collected in June nor the seven collected near Ras Bidu in March (which, unfortunately, could not be preserved) had enlarged gonads. Surprisingly, Forbes-Watson found little or no evidence of breeding activity by this species on Socotra or the outlying islands during his stay.

The following comments are taken from his field notes:

> They were also seen along the north coast of Abd-el-Kuri and on Kaal Firaon and Jazirat Sabuniya. It seems unlikely that any actually bred on the islands—if any do breed there, probably only a few do so. Those pale-bellied young birds seen on Jazirat Sabuniya were probably not bred locally. No adults were seen after March, all the birds seen subsequently near Kallansiya and Qadhub being in immature dress. Presumably the rest had left for Arabia.

Hartlaub (1881, p. 957) lists a specimen of *P. carbo* collected by Reibeck near Hadibu. There is a possibility that this was a misidentification based on the fact that young birds of both *nigrogularis* and *carbo* have the underparts extensively whitish.

Family ARDEIDAE: Herons

Ardea cinerea cinerea Linnaeus: Grey Heron

Herons were seen singly and in pairs near Hadibu, Qadhub, Goba, and the sand expanse north of Kallansiya. No sign of breeding was seen, although birds were seen in all months (March–June).

Ardea purpurea purpurea Linnaeus: Purple Heron

One pair was seen fishing among the mangroves at Goba in May. A single immature specimen was collected by Ogilvie-Grant and Forbes (1903, p. 53) near Hadibu.

Butorides striatus **subspecies?: Green-backed Heron**

These birds were seen on two or three occasions in March on the rivers near Hadibu. Green-backed herons have not been recorded previously on Socotra.

Bubulcus ibis ibis **(Linnaeus): Cattle Egret**

This widespread species may be added to the Socotra list on the basis of a single bird seen by Forbes-Watson near Kallansiya in early June.

Egretta garzetta garzetta **(Linnaeus): Little Egret**

Forbes-Watson recorded a single bird seen on two occasions on Kallansiya lagoon in early June. This is the first record for Socotra.

Egretta gularis schistacea **(Hemprich and Ehrenberg): Reef Heron**

Four or five reef herons, in both white and dark phases, were noted on the exposed reefs near Hadibu in March. All had left by April. Sclater and Hartlaub (1881, p. 173) list this species for Socotra, based on a pair of wings brought back by Balfour.

Family THRESKIORNITHIDAE: Spoonbills

Platalea leucorodia **subspecies?: Spoonbill**

Sclater and Hartlaub (1881, p. 173) mention spoonbills having been seen by Balfour on the margins of stagnant pools near the villages on the north coast. Mackworth-Praed and Grant (1952, ser. 1, vol. 1, pp. 78, 79) say both *P. l. leucorodia* and *P. l. archeri* Neumann occur but do not say who obtained them.

Family PHOENICOPTERIDAE: Flamingos

Phoenicopterus roseus **Pallas: Flamingo**

The Bent expedition of 1888 obtained one specimen and recorded "quantities of Flamingos on the beach" (Ogilvie-Grant and Forbes, 1903, p. 52). Forbes-Watson saw 12 birds, presumably of this species, near Qadhub at the end of May, 5 on the sandflats near Kallansiya on several occasions in June, and 1 was seen flying eastward from Hadibu in mid-June.

Family ANATIDAE: Ducks

Anas crecca crecca **Linnaeus: Common Teal**

Balfour reports these birds to be "specially prevalent on the Debeni River and Khorfariah" (Sclater and Hartlaub, 1881, p. 173).

Anas platyrhynchos Linnaeus: Mallard

Ogilvie-Grant and Forbes (1903, p. 51) report that Bennett collected a mallard on Socotra, but neither they nor Forbes-Watson met with it there.

Anas strepera strepera Linnaeus: Gadwall

Ogilvie-Grant and Forbes (1903, p. 51) list this species as being fairly common on the brackish estuaries of the rivers traversing the Hadibu Plain and in the swamps near Khor Garieh.

Anas penelops Linnaeus: Wigeon

The 1898-99 expedition found the wigeon fairly common about the mouths of the rivers near Hadibu and met with large flocks in a patch of marshy ground bordering the Dimichiro River near its entrance into Khor Garieh (Ogilvie-Grant and Forbes, 1903, p. 52).

Anas querquedula Linnaeus: Garganey

A female was taken on a lagoon 2 miles east of Hadibu on March 10 by Forbes-Watson. Weight 100 gms. This species has not been recorded previously in passage on Socotra.

Aythya nyroca (Güldenstädt): White-eyed Pochard

Riebeck shot a female at Kallansiya (Hartlaub, 1881, p. 956). The Forbes' party encountered a small flock swimming in a brackish estuary of the Wadi Dinehan, but none were collected (Ogilvie-Grant and Forbes, 1903, p. 52).

Family ACCIPITRIDAE: Hawks, Vultures

Buteo buteo subspecies?: Buzzard

Plate 3 (bottom)

Ogilvie-Grant and Forbes (1903, p. 48) found this species nesting on Socotra and secured several specimens. Forbes-Watson noted these birds occasionally on the Hadibu Plain, the cliffs near the sea, and in the limestone country to the east of Kallansiya. In the Hagghiers, he observed a pair carrying sticks to a nest on a cliff opposite Kishin camp. The nearest population of breeding *Buteo buteo* occurs in northern Iran, where *menetriesi* Bogdanov is the resident form. In an attempt to determine the racial affinities of the Socotran population, four specimens of *Buteo buteo* from Socotra were borrowed from the British Museum. With one exception, mensural differences fell within the range of *vulpinus* (Gloger), a race which occurs generally to the north of *menetriesi,* but individual variation in color was so pronounced in the small series that a positive racial allocation could not be made. It appears likely from the variation in bill measurements among those specimens measured that northern migrant buzzards may have been included in our series. The single specimen with an exceptionally large bill (adult male, Sept. 3, 1934, culmen from cere 26.5 mm.) could perhaps have been a resident specimen indicating the presence of a large, island form.

***Neophron percnopterus percnopterus* (Linnaeus): Egyptian Vulture**

PLATE 4 (top)

One of the most obvious birds on Socotra, but not seen on Abd-el-Kuri, although birds were seen on the extreme western point of Socotra at the nearest point to that island. They were quite bold and common—as many as 24 were seen at one time at Hadibu. One pair had a nest below Kishin camp at about 1,500 feet altitude, which was placed in a horizontal crack in a smallish block of granite. There was evidently at least one young, as the parents collected skinned-out bird bodies at Kishin and took them off down the valley in their bills. About half of the birds seen were in brown non-adult plumage.—A. D. Forbes-Watson.

***Circus aeruginosus* subspecies?: Marsh Harrier**

Forbes-Watson saw a single individual on two or three occasions in March flying over the lagoon at Hadibu.

***Pandion haliaetus haliaetus* (Linnaeus): Osprey**

Forbes-Watson found ospreys to be common on Socotra and Abd-el-Kuri, but no nests were seen. A dead osprey was found on Kaal Firaon. Ogilvie-Grant and Forbes (1903, p. 61) collected a pair on Abd-el-Kuri.

Family FALCONIDAE: Falcons

***Falco biarmicus* subspecies?: Lanner Falcon**

Regarding the occurrence of this species on Socotra, Forbes has this to say: "I saw a pair of Falcons, apparently Lanners, on the slopes of Dimimi, a mountain in the Hagghier range to the southward of our camp at Dahamis . . . . A second pair were seen on the wing in the Dimichiro Valley, but these kept at a safe distance" (Ogilvie-Grant and Forbes, 1903, p. 47).

Falco peregrinus subspecies?: Peregrine Falcon

Balfour obtained one specimen near Hadibu (Sclater and Hartlaub, 1881, p. 172). Forbes-Watson recorded a peregrine on two occasions near Hadibu. In early May, a pair was seen at 4000 feet in the Hagghiers. They were calling to each other as they circled and may have been nesting.

Falco tinnunculus archeri Hartert and Neumann: Kestrel

Three males and four females were collected near Hadibu from March 9 to May 20. A male and female were taken in the Hagghier Mountains on April 17. Both males and females averaged about 100 gms. in weight. Soft parts: iris brown; eye-ring yellow; bill blue grey, base yellowish; feet yellow; cere yellow; claws black. Stomach contents: grasshoppers in all except one, which contained a lizard. Gonads were small or undeveloped except for one male collected March 9, which had testes slightly enlarged. No nesting was noted although the birds seem to be resident. In both size and color, the Socotran population is inseparable from the Somali race *archeri*.

Family PHASIANIDAE: Quails

Coturnix coturnix coturnix (Linnaeus): European Quail

Forbes-Watson saw only one *Coturnix* near Suk at the end of March. Ogilvie-Grant and Forbes (1903, pp. 57, 63) report only a few from Socotra and Abd-el-Kuri. There was no evidence of breeding.

Coturnix delegorguei delegorguei Delegorgue: Harlequin Quail

Mackworth-Praed and Grant (1952, ser. 1, vol. 1, p. 266) list the harlequin quail as occurring on Socotra.

Family RALLIDAE: Rails, Coots

Porzana porzana (Linnaeus): Spotted Moorhen

Ogilvie-Grant and Forbes (1903, p. 56) list a specimen collected by Bennett on Socotra.

Gallinula chloropus chloropus (Linnaeus): European Moorhen

Riebeck (Hartlaub, 1881, p. 957) obtained five adult specimens of this species but did not indicate the exact locality.

Family CHARADRIIDAE: Plovers, Sandpipers, Snipe

Subfamily CHARADRIINAE: Plovers

Pluvialis squatarola (Linnaeus): Grey Plover

One female in winter plumage collected near Hadibu on March 13 has the iris brown, bill black, and feet black. Stomach contents: small snails and grit. Weight 100 gms. This species has not been reported previously from Socotra.

Pluvialis dominica fulva (Gmelin): Eastern Golden Plover

One specimen, a male, in summer plumage was collected 2 miles east of Hadibu on May 17. Soft parts: iris dark brown; bill black; feet dark greyish. Stomach contents: mollusc shell fragments and a caterpillar. Weight 100 gms. This is the first record of the golden plover from Socotra.

Charadrius hiaticula tundae (Lowe): Ringed Plover

One female was collected east of Hadibu on March 13. Soft parts: iris brown; bill black, orange yellow at base; feet pale orange. Weight 48 gms.

Although this Arctic migrant regularly visits the coast of East Africa, this is the first record for Socotra. Forbes-Watson records having seen others on Abd-el-Kuri in March.

Charadrius dubius curonicus Gmelin: Little Ringed Plover

One specimen, a female, was collected near Hadibu on March 9. Soft parts: iris brown; eyelid yellow; bill black with yellow spot on extreme base of lower mandible; feet pale yellow. Stomach contents: insects and grit. Weight 37 gms.

Charadrius alexandrinus alexandrinus Linnaeus: Kentish Plover

Both Ogilvie-Grant and Forbes (1903, p. 54) and Forbes-Watson collected this species on Socotra. The latter found this bird to be common and resident along the ponds and lagoons on the north coast. Eggs and young were noted from March to May. Seven males, five females, and three downy young were collected near Hadibu. Weight: males 34-40 gms.; females 32-39 gms.; downy young 9 gms. Soft parts of adults: iris brown; bill black; feet blackish; tarsus olive grey. Downy young: iris dark brown; bill blackish; feet pale green grey; bare skin on throat dull blackish. The stomachs of the adults contained grit and insect fragments.

Subfamily SCOLOPACINAE: Curlews, Sandpipers, Snipe

Numenius phaeopus phaeopus (Linnaeus): Whimbrel

Forbes-Watson found a flock of seven birds on the rocks near the water's edge on Kaal Firaon.

Numenius arquata subspecies?: Curlew

Forbes-Watson mentions this species in his list of birds seen on Socotra but gives no further data. Vaurie (1965, p. 424) states that migrants "south to east Africa" appear to be chiefly intermediate between nominate *arquata* and *orientalis* Brehm and cannot be identified with certainty as to subspecies.

Limosa lapponica subspecies?: Bartailed Godwit

Forbes-Watson records having seen the bartailed godwit on Socotra. This is the first record for the island.

Tringa totanus subspecies?: Common Redshank

Ogilvie-Grant and Forbes (1903, p. 54) found the redshank common on the rivers near Hadibu. It was not seen by Forbes-Watson.

Tringa nebularia (Gunnerus): Greenshank

Ogilvie-Grant and Forbes (1903, p. 54) found the greenshank to be common at the mouths of the rivers traversing the Hadibu Plain. On March 13 Forbes-Watson collected a female 1 mile west of Suk. Soft parts: iris brown; bill blackish on tip, olive green at base; feet pale olive green, joints darker. Weight about 100 gms.

Tringa glareola Linnaeus: Wood Sandpiper

A wood sandpiper was collected by Riebeck at Kallansiya (Hartlaub, 1881, p. 956). One specimen of this Palearctic migrant, a female, was taken near Hadibu by Forbes-Watson on March 11. Soft parts: iris brown; bill blackish; base of lower mandible greenish; feet green yellow; joints and toes greenish. Stomach contents: insect fragments. Weight 56 gms.

Tringa hypoleucos Linnaeus: Common Sandpiper

This species was recorded from Abd-el-Kuri by Ogilvie-Grant and Forbes (1903, p. 54). Forbes-Watson collected two males near Hadibu on March 11 and 15. One specimen had the feathers of the upperparts quite worn although the remiges showed signs of recent replacement and the rectrices were undergoing molt. Soft parts: iris brown; bill blackish; base grey green; feet greenish; toes more dusky. Stomach contents: insects. Weight 42 gms. The other specimen, in fresh summer plumage, had the iris brown, bill olive, base of lower mandible paler, feet pale olive. Stomach contents: insect fragments. Weight 60 gms.

Arenaria interpres interpres (Linnaeus): Turnstone

Bennett secured one specimen on Socotra (Ogilvie-Grant and Forbes, 1903, p. 53). Forbes-Watson obtained one male and three females near Hadibu between March 9 and June 12. Soft parts: iris brown; bill blackish; base of lower mandible greyish; feet orange; joints dusky. One stomach contained small crabs. Weight from 87 to 100 gms.

Capella stenura (Bonaparte): Pintail Snipe

Two examples of the pintail snipe were secured by Ogilvie-Grant and Forbes (1903, p. 55) at Homhil, Socotra. None were seen by Forbes-Watson.

Capella gallinago gallinago (Linnaeus): Fantail Snipe

"It was common in the rushy edges of the stream below our camp at Homhil, and proved a welcome addition to our bill of fare"—Ogilvie-Grant and Forbes (1903, p. 55). This species was not seen in 1964.

Calidris albus (Pallas): Sanderling

Forbes-Watson did not record the sanderling on Socotra although Bennett is credited with having obtained a specimen (Ogilvie-Grant and Forbes, 1903, p. 54).

Calidris minutus (Leisler): Little Stint

Two males, representing new records for Socotra, were collected near Hadibu on May 17. Soft parts: iris brown; bill black; feet black. Stomach contents: insect fragments. Weight 20 gms.

Calidris temminckii (Leisler): Temminck's Stint

Ogilvie-Grant and Forbes (1903, p. 54) report having shot a specimen from a flock feeding in the bed of the Hanefu River on Feb. 20, 1899. Forbes-Watson secured two males and one female near Hadibu on March 9, 10, and 13. Replacement of the primaries was almost complete in all of these specimens. In the female, all of the primaries were new except the tenth, which was about half way out of the sheath. One male had replaced all but the ninth and tenth primaries while the other had the tenth half grown. Soft parts: iris brown; bill black; feet green yellow or olive green. Stomach contents: grit and small insects. Weight 20 to 23 gms.

Family DROMIDIDAE: Crab Plovers

Dromas ardeola Paykull: Crab Plover

Professor Balfour found the crab plover common at Kallansiya (Sclater and Hartlaub, 1881, p. 174), but neither of the later expeditions record it.

Family GLAREOLIDAE: Coursers, Pratincoles

Cursorius cursor cursor (Latham): Cream-colored Courser

Plate 4 (bottom)

A series of seven breeding specimens, four males and three females, were collected between March and June by Forbes-Watson. The narrow subterminal black bands on the tail, the wide dark margins on the inner webs of the secondaries, and the large wing measurements (145 to 157 mm.) are all characters associated with the nominate form.

Adults: soft parts: iris dark brown; bill blackish, paler at base; feet white, soles creamy. Stomach contents: seeds, insects, and grit. Weight 100 gms. Juvenal male: some parts: iris brown; bill pale fawn, tip greyish; feet creamy white; bare patch at base of throat pink grey. Stomach contents: grasshoppers. Weight 60 gms. Downy young: soft parts: iris brown; bare patch at base of neck slaty; bill pinkish brown; egg tooth chalky white. Stomach contents: grasshoppers. Weight 13 gms. These birds were common just east of Hadibu and on the Ras Kharma airstrip, and also near Eriosh.

Regarding the breeding behavior of the cream-colored courser, Forbes-Watson made the following observations:

> After a while the presumed female squatted, moved slightly, and again squatted with hunched back and depressed tail and head. The presumed male approached and pattered with its feet near the other bird's tail and mounted, but did not mate. He then jumped off to one side and 'scooped' at her rapidly with his head—this he did several times. They then went off together, and she squatted several more times, but as if on eggs and with head up, and he did not attempt to mount again.
>
> Several call notes were written down on the spot and are recorded as follows:

a parent calling to young made soft deep whistles "wheeout"; the ground alarm "woot"; flight-call "qwut" and "kwit"; in flight "werrau," "mraau" and "wit." In flight the birds look noticeably deep-chested and wide-winged with the head drawn back.

Family LARIDAE: Gulls, Terns

Larus species

Gulls were not generally common but were noted in small numbers all along the north coast. The following species were observed by Forbes-Watson: herring gull, *Larus argentatus* subspecies?; lesser black-backed gull, *Larus fuscus* subspecies?; white-eyed gull, *Larus leucophthalmus* Temminck; and sooty gull, *Larus hemprichii* (Bruch). All but *leucophthalmus* were observed on Abd-el-Kuri also. Ogilvie-Grant and Forbes (1903, pp. 55, 62, 63) reported both *Larus argentatus* and *Larus fuscus* from Abd-el-Kuri but only one species, *Larus argentatus,* from Socotra.

Sterna repressa Hartert: White-cheeked Tern

A pair were seen by Forbes-Watson in early June on the sandbar at the mouth of Kallansiya Lagoon; the next day there were four in the same place, but they were not seen again.

Sterna bengalensis subspecies: Lesser Crested Tern

These terns were seen fishing with *Sterna bergii* at both Qadhub and Kallansiya.

Sterna bergii subspecies?: Swift Tern

The swift tern was the most common species along the north coast and on Abd-el-Kuri. Ogilvie-Grant and Forbes (1903, pp. 55, 62) also report it from both these localities.

Sterna albifrons subspecies?: Little Tern

Regarding this tern, Forbes-Watson made the following comments in his field notes:

> The only examples of *Sterna albifrons* seen were a few pairs being harried by a pair of ravens in late May near Eriosh. These birds were flying inland for about a mile and had just started to make scrapes in the gravel. Most of these scrapes seemed to have white shell fragments (mollusc) nearby. The presumed males were seen offering small silver fish to their mates with wing-lifting and raised crests. This was often done near a scrape, but in many cases was on the bare plains, and often the fish was not accepted, even after many attempts and from

several places; in such cases the female might fly off towards the sea, and the male would either swallow the fish, or persist in following her.

Anous stolidus **subspecies?: Noddy**

A noddy was seen by Forbes-Watson on Ras Hebak in late May.

Family PTEROCLIDIDAE: Sandgrouse

Eremialector lichtensteinii lichtensteinii **(Temminck): Lichtenstein's Sandgrouse**

Six males and five females were collected at Qaysuh in June. Soft parts: iris brown; eye-ring yellow; lid tinged green; bill orange yellow; feet pale yellow. Females averaged slightly paler. Stomach contents: seeds and grit. Weight 100 gms. Forbes-Watson noted these birds only on the Hadibu Plain and on the limestone slopes near Kallansiya: "They seem to prefer fairly thick cover, but when the nests are exposed they are most difficult to find. The sitting birds and eggs are beautifully camouflaged."

Family COLUMBIDAE: Pigeons, Doves

Streptopelia senegalensis senegalensis **(Linnaeus): Laughing Dove**

A series of eight males and five females were collected near Hadibu, at Qaysuh, and in the Hagghier Mountains. Wing length 127-135 (131.6) in eight males and 121-131 (126.8) in five females. Soft parts: iris brown; eye-ring dull maroon; bill and cere black; feet dull maroon. Stomach contents: seeds. Weight: males 79-98 gms., females 70-80 gms.

The Laughing Dove was very common in most places and especially numerous in the date groves near Hadibu and Qaysuh. Nesting was noted in all months during the expedition's stay on Socotra. Many nests were found in boxwood bushes, placed about eight feet from the ground and were typical small twig saucers. In the Hagghiers, a nest was found in a thorny tree about 20 feet from the ground.—A. D. Forbes-Watson.

Oena capensis capensis **(Linnaeus): Namaqua Dove**

Hartlaub (1881, p. 956) reports a male collected by Riebeck at Gollonsir: "Iris dark brown, feet red."

Treron waalia **(Meyer): Bruce's Green Pigeon**

Three males, eight females, and one juvenal were collected at Hadibu in June and at Kishin and in the Hagghier Mountains in April. Soft parts of adults: iris: outer ring bright blue, inner ring pale green; bare skin around eye blue grey; cere dull greyish maroon; bill white, base maroon; feet bright yellow. Females have soft parts generally paler. Stomach contents: fig pulp. Weight 100 gms.

The juvenal specimen had the iris green grey; eye-ring blue grey; bill whitish, base blue grey; cere blue grey; feet pale yellow. Weight 97 gms.

These birds were not particularly common, but were seen near Kishin, especially in fruiting figs, and also in the palm groves near Hadibu where they were eating green dates. Call notes were written as follows: "u-vu," a rising near-whistle, or "ki-yoo," sometimes two in succession, or a rising and falling "u-wu-u!"—A. D. Forbes-Watson.

Family CUCULIDAE: Cuckoos

Centropus superciliosus sokotrae C. Grant: Socotra Coucal

A good series of four males and three females was secured on the Hadibu Plain and in the Hagghier Mountains and foothills in March, April, and May. Soft parts: iris red; bill black; feet blue grey. Stomach contents: grasshoppers. Weight 100 gms.

Five specimens are in adult plumage. The nape and upper back are streaked with white and the tail feathers are greenish black over half their length. Another specimen has the nape and upper back streaked with white but the tail has the barrings usually associated with the immature plumage. Still another specimen has the brown and black head markings of the immature, but the incoming rectrices are greenish black. Friedmann (1930, p. 283) has commented on the variation in the color of the rectrices in immature birds of this species.

With regard to the order of molt of the remiges, several specimens occur in our series from Socotra which have new feathers appearing among the middle primaries, but no sequence of molt is discernible.

This species was not very common and was confined to water courses and their environs. They were rare in the palm groves on the coastal plain but more common in the Hagghiers. Forbes-Watson reports the call note of a pair flying to a roost in late evening as a quiet clicking "te-tu." No evidence of breeding was noted.

Family STRIGIDAE: Owls

Otus scops socotranus (Ogilvie-Grant and Forbes): Socotra Scops Owl

Three males, three females, and one with sex undetermined were taken at Kishin at 2000 feet, and one male at Hadibu between April 16 and May 17. None were in breeding condition although one female had slightly enlarged ovaries on April 19. One female is in body down though fully fledged. Soft parts: iris bright yellow; bill black; feet grayish; soles yellowish white. Wing: males 124-130; females 133-135 mm. Weight: males 64, 70, 78, 85; females 71, 74; immature female 72 gms. Stomach contents: grasshoppers, one centipede, two lizards.

Owls were noted by Forbes-Watson in the Hagghiers and at Hadibu and Qaysuh. The first one seen was behaving more like a nightjar than an owl. It was flying out from a perch and back again in the twilight and appeared to be catching moths (although these insects were not found in the stomach contents after the bird had been collected and examined the next evening).

Ogilvie-Grant and Forbes (1903, p. 45) mention having heard the call on several occasions of a distinctly different species of owl (*Strix?* species) but were unsuccessful in obtaining a specimen.

Family CAPRIMULGIDAE: Nightjars, Goatsuckers

Caprimulgus nubicus jonesi **(Ogilvie-Grant and Forbes): Socotran Nightjar**

This endemic nightjar was described from a specimen shot in the Dimichiro Valley in the Garieh Plain, east Socotra. It was not seen in 1964.

Family APODIDAE: Swifts

PLATE 5 (top)

Apus pallidus berliozi **Ripley**

In April, Forbes-Watson found flocks of smaller swifts flying about the hills and cliffs of the Hagghier Mountains. An examination of 20 males and 11 females collected here and at Hadibu and Kallansiya shows that they represent a hitherto undescribed subspecies (Ripley, 1966, p. 101). Nearly all of these birds were in breeding condition.

Certain aspects of the courtship behavior of this new race have been recorded in some detail by Forbes-Watson:

> In the flocks most birds were in pairs, one bird closely following the other. When collected, the leading bird was invariably the female, the following, the male. Much screaming was indulged in at such times as the birds swooped about; on a few occasions birds were seen to cling to their partner in the air, then they would drop with wings flexed, to break apart again only when they neared the ground. Several times birds were heard to make "whip-crack" noises in the air. This consisted of several rapidly-repeated slaps and the bird appeared rather

stiff when this occurred—presumably the noise was made by the wings, either slapping together or actually cracking like a whip; this may have been some form of sexual display. Birds were seen at the high pink cliffs in the Hagghiers, and were almost certainly breeding in cracks in the cliffs.

In March, Forbes-Watson observed large black swifts with pale throats flying near Hadibu, Kallansiya, and the west end of Abd-el-Kuri. None were collected but they were thought to be *Apus apus*.

Family CORACIIDAE: Rollers

Coracias garrulus garrulus **Linnaeus: European Roller**

A female was taken near Hadibu on March 15. It agrees in the color of the upperparts with a single winter-taken specimen of *garrulus* in the National Collection. Soft parts: iris brown; bill black; tail dull yellow. Stomach contents: grasshoppers. Weight 100 gms.

Coracias abyssinica **Hermann: Abyssinian Roller**

"I [Forbes] picked up on Abd-el-Kuri a skeleton of *Coracias,* of which I brought away the skull, which, on comparing it with a specimen in the British Museum, agreed exactly with this species"—Ogilvie-Grant and Forbes (1903, p. 61).

Family UPUPIDAE: Hoopoes

Upupa epops **Linnaeus: Hoopoe**

Ogilvie-Grant and Forbes (1903, p. 61) report a hoopoe sighted at sea near Abd-el-Kuri.

Family ALAUDIDAE: Larks

Eremopterix nigriceps forbeswatsoni, **new subspecies**

PLATE 5 (bottom)

Type.—United States National Museum No. 518056, adult male, collected Mar. 13, 1961, by Alec D. Forbes-Watson, 4 miles east of Hadibu, Socotra.

Diagnosis.—Similar to *E. n. melanauchen* (Cabanis) of the adjacent African mainland, but having the upperparts more rufous, less brown, particularly on the edgings of the inner secondaries and the middle rectrices. The white patch on the forehead extends farther back from the base of the upper mandible to crown than in neighboring populations (6.5 mm., average of 14 specimens from Socotra, vs. 4.6 mm., average of 5 specimens from Ethiopia, Eritrea, and

Somaliland, and 5.3 mm., average of 3 specimens from Aden). The Socotran series differs further from the Arabian form, *sincipitalis* (Blyth), in being decidedly darker above and having the upperparts more rufous brown, less sandy grey. Females are indistinguishable from those of other races.

Soft parts.—Iris brown; bill whitish; feet white flesh.

Weight.—15 gms.

Range.—Island of Socotra only.

Remarks.—

This was one of the commonest birds on the plains. It was usually found in flocks of from half-a-dozen to about fifty birds which would rise up just ahead of one and settle some way off. The favorite habitat on the plains was where the very shortest bushes grew. At Kallansiya, where the bush is taller, only two pairs were seen. They were often seen drinking in the heat of the day at the freshwater pond a mile to the east of Hadibu, and those seen at Kallansiya were drinking at the brackish lagoon there.—A. D. Forbes-Watson.

Calandrella cinerea subspecies?: Short-toed Lark

A single specimen in rather worn plumage was collected on the west end of Abd-el-Kuri on March 21. It is one of the paler southwest Asian forms and Mrs. B. P. Hall of the British Museum, to whom we are indebted for her courtesy in examining this specimen, suggested that it may possibly be *artemisiana* Banjkovski, but the race cannot be identified with certainty. Soft parts: iris brown; bill brown horn; feet flesh brown. Wing 94 mm. Culmen 13.5 mm. Weight 19 gms. Stomach contents: insect fragments and a few seeds.

Family HIRUNDINIDAE: Swallows

Ptyonoprogne obsoleta arabica (Reichenow): Pale Gray Martin

Forbes collected several specimens of the pale gray martin in the Hagghiers during the 1898–99 expedition. The present series consists of two males and two females collected at Adho Dimellus in May. The males have wing measurements of 110 mm. The females are somewhat larger, having wing length ranging from 113 to 115 mm. Soft parts: iris brown; bill black; base of lower mandible yellowish; gape and palate yellow; feet dusky, soles white. Stomach contents: beetles. Weight 13-14 gms.

Hirundo rustica rustica Linnaeus: Swallow

One female was collected by Forbes-Watson near Hadibu on May 17. The underparts are white with only a slight trace of pinkish buff. Weight: 17 gms.

Riparia riparia riparia **(Linnaeus): Sand Martin**

This Palearctic migrant may be added to the list of Socotra birds based on two males and one female collected near Hadibu in May 1964. Weight 11-13 gms.

Delichon urbica **subspecies?: House Martin**

Forbes-Watson reports having seen this martin on several occasions in mid-May flying over Hadibu town.

Family LANIIDAE: Shrikes

Lanius elegans uncinatus **Sclater and Hartlaub: Socotra Shrike**

Plate 6 (top)

Fourteen males and 12 females of the Socotra shrike were collected at or near Hadibu, near Kallansiya, and in the Hagghier Mountains. Wing lengths 97-104 (100.7) in 14 males and 92-103 (98.5) in 17 females. Weight 50-60 gms. Stomach contents: mostly grasshoppers but also centipedes and small lizards. Forbes-Watson reports this bird to be common and conspicuous, occurring from sea level to at least 4500 feet.

Family STURNIDAE: Starlings

Onychognathus frater **(Sclater and Hartlaub): Socotra Chestnut-winged Starling**

Eight males and nine females of this endemic species were collected near Hadibu, Kallansiya, and Kishin, in the Hagghier Mountains. This is a longer billed, shorter tailed species with no sexual dimorphism in color. Wing length 157-163 (159.5) in seven males and 148-156 (151.5) in nine females. Tail 139-146 (141.8) and 127-136 (131.2). Culmen from feathers 28-32 (29.2) and 27-29 (27.8). Soft parts: iris chestnut brown; bill and feet black. Weight 100 gms. Stomach contents: largely green fig pulp and grasshoppers. (Critical comments on the sympatric distribution of this species and *O. blythii* are discussed on p. 7.)

Onychognathus blythii **(Hartlaub): Brown-winged Starling**

Plate 6 (bottom)

Fourteen males, eight females, and one sex unknown, were secured during the 1964 expedition near Hadibu and Kishin in the Hagghiers. This is the shorter billed, longer tailed species with pronounced sexual dimorphism in coler. Wing length 165-175 (171.0) in 10 males and 155-164 (159.2) in 7 females. Tail 172-190 (177.0) and 155-169 (163.2). Culmen from feathers 23-25 (24.3) and 22-24 (22.6). Soft parts: iris chestnut brown; feet and bill black. Stomach contents: beetles, large black seeds. Weight 100 gms. This species was also found on Abd-el-Kuri.

Family CORVIDAE: Crows

Corvus ruficollis ruficollis **Lesson: Brown-necked Raven**

One female was secured on April 17 from the Hagghier Mountains. It was one of a pair, but no signs of breeding were noted. Stomach contents: bones of a reptile. Weight 150 gms.

Family MUSCICAPIDAE: Insect Eaters

Subfamily SYLVIINAE: Warblers

Sylvia communis **subspecies?: Whitethroat**

Ogilvie-Grant and Forbes (1903, p. 59) report one specimen having been obtained on Abd-el-Kuri.

Phylloscopus collybita **subspecies?: Chiff-Chaff**

Ogilvie-Grant and Forbes (1903, p. 59) secured a single example on Abd-el-Kuri.

Cisticola incana **Sclater and Hartlaub: Socotra Warbler**

Forbes-Watson collected a fine series of these lively little warblers that are endemic to the island of Socotra. The bird, in plumage pattern and wing formula, closely resembles *C. fulvicapilla* from southern Africa. It is, however, very pale fulvous brown on the upper parts, with a slightly paler, faintly tawny head (the tawny tone varies, being absent in some specimens) and darker, blackish-brown tail. The tail has terminal white tips on the under surface, the lateral tail feathers in some specimens having subterminal white bars on the inner web. The primaries are dark brown with whitish outer edges. Wing length 49-53 (50.8) in 12 males and 46-51 (48.5) in 10 females. Tail 43-48 (45.2) and 41-47 (43.1). Some parts: iris tawny; eye-ring brown; bill black and pale brown; feet pinkish to orange flesh. Stomach contents: insects. Weight 9-12 gms. This bird was found on the plains near the foothills and up to at least 4500 feet in the Hagghiers, and also on the more thickly covered plains at Ras Kharma and Kallansiya.

Cisticola juncidis haesitata (Sclater and Hartlaub): Socotra Cisticola

This is an endemic subspecies found only on the island of Socotra. It has the same wing formula and plumage pattern as *juncidis* and appears merely paler, more washed out in plumage. The 1964 expedition was fortunate in obtaining five males and one female in March and April. Wing length 45-50 (47.6) in five males and 43 in one female. Soft parts: iris tawny; bill blackish with cutting edge of upper and lower mandible yellowish to pale yellowish horn; feet pale flesh. Stomach contents: insects. Weight 6-8 gms. Ogilvie-Grant and Forbes (1903, p. 41) say that the adult males have the inside of the mouth bluish black while the females have this part flesh colored.

In his field notes, Forbes-Watson has recorded the following observations:

> This species is by no means common, and was only found in two localities—one and one-half miles to the west of Hadibu, just below the foothills of Ras Hebak in light scrub, and a family group at 2800′ on the upland meadow near Adho Dimellus. These latter were seen on the two days April 16 and 17; the habitat here was short grass with clumps and scattered bushes, with a stream flowing through. The birds also foraged just over the edge of this plateau, where the bush was thicker. The male sang from the top of these or in flight; this was an emphatic and abrupt "chit! . . . chit! . . . chit! . . .," etc., regularly spaced at around one-half second intervals; there was also a quick and subdued "tititi . . ." after alighting or at the end of a song from a bush. Apart from this family group of two parents and three young, no signs of breeding were noted. The other birds were foraging in the bushes, but at a lower level (in the bush) than was normal for *incana*, and it is doubtful if the two species compete much.

Subfamily TURDINAE: Thrushes, Wheatears

Oenanthe deserti oreophila (Oberholser): Desert Wheatear

Nine females and one male were collected near Hadibu in March. Another male was collected during the same month on Abd-el-Kuri. Although Vaurie (1959, p. 347) lists *atrogularis* as occurring on Socotra in migration, the large wing measurements (100 mm. in both) and the large white area in the wing touching the shaft indicate that they should be placed with the more southerly race *oreophila*. Soft parts: iris brown; bill black; feet black. Stomach contents: insects. Weight: males 20-23 gms., females 20-27 gms.

Oenanthe isabellina (Temminck and Langier): Isabelline Wheatear

One specimen of this chat was collected on Socotra by Professor Balfour (Sclater and Hartlaub, 1881, p. 167).

Family MOTACILLIDAE: Wagtails, Pipits

***Motacilla alba dukhunensis* Sykes: White Wagtail**

A series of two males and five females collected in March near Hadibu have the upperparts considerably paler than nominate *alba* and are closest in this respect to *dukhunensis*. Their measurements, however, were consistently smaller than those usually given for *dukhunensis*: wing 80-85 mm., tail 81-87 mm., culmen 10-11 mm., tarsus 21.5-23 mm. Soft parts: iris brown; bill black; feet black. Stomach contents: insects. Weight 18-29 gms.

***Budytes flavus* subspecies?: Blue-headed Yellow Wagtail**

Professor Balfour obtained three specimens of the blue-headed yellow wagtail (Sclater and Hartlaub, 1881, p. 168), but neither Forbes nor Forbes-Watson observed it on Socotra.

***Anthus campestris campestris* (Linnaeus): Tawny Pipit**

Ogilvie-Grant and Forbes (1903, p. 60) saw a pair on Abd-el-Kuri and secured a male.

***Anthus similis sokotrae* Hartert: Socotra Long-billed Pipit**

PLATE 7 (top)

Both Ogilvie-Grant and Forbes (1903, p. 60) and Forbes-Watson recorded the long-billed pipit as common and generally distributed over all parts of the island. A large series of 33 specimens were taken between March and June. Soft parts: iris brown; bill blackish horn; feet yellowish to orange flesh. Stomach contents: insects generally; one stomach contained a scorpion pincer. Weight: male 26-35 gms.; female 25-31 gms. This species was not noted on Abd-el-Kuri.

Family NECTARINIIDAE: Sunbirds

***Cyanomitra balfourii* (Sclater and Hartlaub): Socotra Sunbird**

A total of 33 sunbirds were collected near Hadibu and in the Hagghier Mountains. Soft parts: iris orange brown; bill and feet black. Stomach contents: insects, fruits, and seeds. Weight 8-15 gms.

Since little is known of the life history of this endemic species, the detailed observations made by Forbes-Watson and recorded in his field notes are quoted in full:

This is another species with a large altitudinal range, occurring from sea-level to at least 4500′. It is found in ones or twos or small family parties and groups in any place where there is sufficient vegetation—they prefer fairly reasonably-sized trees and bushes, and so are most numerous in the hills, both in the Hagghiers and on the foothills, and are not found on the bare limestone plateaux. Nor are they to be seen on the Hadibu plains proper, but they do occur in the thicker cover of the Kallansiya plains. Their call notes are typical of the family, and the song is a very quick cascading tinkle of characteristic sunbird-like notes.

Unlike sunbirds in Africa, this species was not seen to visit flowers at all, so nectar probably figures little in their diet. Most food was collected as the birds hopped about in the branches of trees and shrubs, and insects were seen to be picked off leaves and twigs, and were also caught in aerial flight. Occasionally birds would fly down onto bare ground to catch an insect. Insects were the main food but were mostly unidentifiable; one bird had a small cicada in the bill when shot, and another together [sic] with a small crab-spider in the throat. But vegetable matter was also an important item; this consisted of small fruits, fruit-stones and seeds, the commonest of these latter being large oval black seeds, and a flat seed was found in one stomach. An immature bird was seen picking fruits off a *Euphorbia* bush near Qaysuh, and had great difficulty in swallowing them, but managed eventually after a great deal of head-stretching and gasping.

Several stages in the breeding cycle were noted, but always too late to find the eggs, so they still remain unknown. In mid-April an empty nest was found at c. 1500′ in the Hagghiers, which, a day or two later, was half torn apart. The young were found in an identical nest on May 1, at 3100′ near Adho Dimellus. This nest was found while a pair of agitated Sunbirds were being watched, when the male soon took food in his bill to feed the young, which were just ready to fly, and were waiting side by side in the nest with their bills on the edge of the entrance. One flew when approached, but the other was collected; this was a male with very small testes, and weighed 8 gms.; it had a brown iris (not orange brown as in the adult), bill with the upper mandible blackish, lower pale yellowish, except for the edges at the base, which were dusky, gape pale yellow, palate orange-yellow, feet dark greyish with paler soles. Insect fragments were the only contents of the stomach.

As with the other nest, this one was built at the base of a small vertical cliff (but another old nest, near Qaysuh, had no such protection), and was not suspended as in most species of the family, but was surrounded by branches and was not hanging free. It was built *in* the top of a small bare twiggy tree around 8 feet above the ground, and the entrance faced towards the cliff. The nest, which was collected, was a small inconspicuous structure of typical sunbird form; it was neat and frail, and was not suspended, but was supported at top and sides by small branches which were incorporated into the walls. It was a pear-shaped purse with a rather large oval entrance topped by a short indefinite porch of plant-down. The overall height was around 80 mm.; greatest depth from front to back around 60 mm.; greatest width (near the bottom) around 55 mm.; the entrance was around 40 mm. in height, around 24 mm. wide near the top and around 20 mm. wide near the bottom. The lining was of silky plant-down, rather patchy in parts (especially at the attachments), and this was surrounded and bound together with fine greyish twiglets, grass, etc., and cobwebs, with a few dead leaves and one spider egg-case on the exterior. All this blended in very well with the surroundings.

Young birds were seen being fed by a parent on a few occasions, when the young solicited with quivering wings and querelous calls—in each of these cases only one young was noted. The clutch, therefore, may usually be only one, with the occasional around two, but this data is insufficient, and these single birds may be the survivors of a larger brood. In any case, it is probably not ever more than two, which is the normal clutch-size in African sunbirds.

Display was only seen once, when a male was singing sustainedly from the top of a tree, with his yellow pectoral tufts spread widely. Chases, presumably territorial, were often noted, but, although known pairs were watched for long periods, no other signs of nuptial activity were seen.

Family ZOSTEROPIDAE: White-eyes

Zosterops abyssinicus socotranus Neumann: Socotra White-breasted White-eye

Plate 7 (bottom)

With the exception of one bird taken near Kallansiya, all of the 35 additional specimens of this endemic subspecies were taken in the Hagghier Mountains. Soft parts: iris tawny; bill dusky; feet blue grey. Stomach contents: small fruits and seeds. Weight 8-15 gms.

The flock call is a thin descending whistle "seeoo," and this noise is one of the commonest and most characteristic sounds in the mountains. These birds have a peculiar habit of sipping water from a thin smear on the rocks rather than drinking from the pool below. The Bedu catch and eat a certain number, but apart from this, no predation of the species was noted.—A. D. Forbes-Watson.

Family PLOCEIDAE: Sparrows, Weavers

Passer insularis insularis Sclater and Hartlaub: Socotra Sparrow

Plate 8 (top)

We would place this species in a superspecies with *iagoensis* as it is distinctly patterned on the upper parts, lacking any brown except for the buffy-tawny superciliary and shoulder patch. A series of 51 Socotra sparrows were collected on the main island. Weight 20-35 gms. Wing length 72-78 (75.2) in 28 males and 68-78 (73.7) in 23 females.

This species was widespread and abundant. It probably breeds throughout the year. A nest in a house at Hadibu was occupied successively from early March to late June. Certainly two broods were successfully reared, and a male sparrow, perhaps the original builder of the nest, pulled it apart and rebuilt it in another site in the same ceiling when the first brood had flown. Other sites were noted—several in holes in the trunks of *Adenium* and Dragon's Blood Trees, a few in holes in rock, the formation of limestone being particularly suitable, and one untidy nest was found in a thorny tree. All the accessible ones were empty, so the eggs are still unknown, but, as three young were seen from the nest in the house at Hadibu, the clutch can be presumed to be at least three.

Away from habitations, the birds go about in flocks of varying sizes, the largest being seen at Qaysuh, where 50 or so were commonly seen together, and they reminded one strongly of weavers in Africa—was it such a flock that Balfour mistook for weavers as no other observer has noted any species of weaver on any of the islands.—A. D. Forbes-Watson.

Passer insularis hemileucus Ogilvie-Grant and Forbes: Abd-el-Kuri Sparrow

Seven of the pale sparrows (four males and three females) were collected on Abd-el-Kuri. This form has a marked white band below the buff shoulder patch. Stomach contents: vegetable matter. Weight 20-25 gms. Wing length 71-74 (72.7) in four males and 67-71 (69.0) in one female. Ogilvie-Grant and Forbes (1903, p. 58) found them only in the hills, where they were very wild. Forbes-Watson made a similar observation upon his arrival on Abd-el-Kuri, but later found them behaving much like *P. domesticus* about a small settlement on the north coast. Since there is no surface water on the island, it is difficult to understand how these birds survive in this inhospitable environment.

Family FRINGILLIDAE: Finches

Rhynchostruthus socotranus socotranus Sclater and Hartlaub: Golden-winged Grosbeak

With the exception of 1 male collected near Kallansiya, the remaining specimens (10 females, 20 males, and 4 unsexed) were all collected in the Hagghiers. The skull of our anatomical specimen, examined by Dr. Richard Zusi, bears a strong resemblance to the pine grosbeak and to the New World evening grosbeaks, which are in themselves members of the cardeuline assemblage linked to the Palearctic and Himalayan rose finches. As Ripley stated (*in* Ripley and Rabor, 1961, p. 16), *Rhynchostruthus* bears a certain resemblance to *Rhodopechys*. We feel that this finch is related as a relict to the Himalayan fauna in the same way that some Arabian species seem so related (Ripley, 1954, p. 246). Soft parts: iris brown; bill blackish; feet pale brown flesh. Stomach contents: seeds, fruit pulp, and other vegetable matter. Weight 25-39 gms. Wing length 85-91 (88.4) in 20 males and 81-86 (83.7) in 10 females. Tail 50-55 (52.2) and 47-52 (49.2). Culmen 14-17 (15.5) and 14-15 (14.4).

Forbes-Watson observed these birds in the Hagghier Mountains and has written the following notes concerning their behavior:

> Where they are found they are not uncommon, but can easily be missed, as they are shy and inconspicuous and feed in restricted areas. Their daily routine is as follows: in the early morning they descend from the highest parts of the

> Hagghiers, where they probably roost in the thickets at 4500′ or so. They fly down the valleys in loose flocks, flying very fast with a dipping flight, and often not alighting till they reach the feeding grounds, which may be as far down as 500′ above sea-level. Here they feed on berries and rest until evening, when they return as they came.

Regarding their feeding habits, he says further:

> The bird would clamber onto a bunch of small purple fruits (this was the favorite food) and pick off individual fruits, which would then be "mumbled" between the mandibles, and so much of the fleshy outside pulp was removed and dropped. This fruit is sticky, and the bills of all those birds collected were encrusted with this dried latex. The seeds were not crushed, however, as one would expect them to be from the enormous size of the bill, and were entire in all crops examined.

Family EMBERIZIDAE: Buntings

Fringillaria tahapisi insularis **Ogilvie-Grant and Forbes: Cinnamon-breasted Rock-bunting**

Twenty-five males and four females comprise this series taken by Forbes-Watson at or near Hadibu, near Kallansiya, and in the Hagghier Mountains. Soft parts: iris brown; bill dark dusky lemon; cutting edge and lower mandible yellowish; feet orange flesh. Stomach contents: small seeds. Weight 13-17 gms.

Fringillaria socotrana **Ogilvie-Grant and Forbes: Socotra Mountain Bunting**

Plate 8 (bottom)

With the exception of 3 birds (2 males and 1 female) taken in the Hagghiers, the remaining specimens in this series (11 males and 3 females) were taken near Kallansiya. Soft parts: iris brown; upper mandible dusky; lower yellowish; feet pale orange flesh. Stomach contents: small seeds and grit. Weight 13-16 gms.

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TABLE 1.—Some resident birds of Socotra and their habitats (+ = present, blank space = absent)

Species	Lowlands (0-200')					Highlands (200-4000')					Bleak highlands	
	shore	towns	lagoons and pools	man-groves (Goba)	plains	foothills	hill valleys	hill slopes	thickets	grassy uplands	limestone plateaus (1500-2000')	Hagghier peaks (4000-5000')
Neophron percnopterus	+	+	+	+	+	+	+	+		+	+	+
Falco peregrinus	+				+							+
Falco tinnunculus		+	+		+	+				+	+	+
Buteo buteo	+				+	+	+	+		+	+	+
Pandion haliaetus	+		+									
Charadrius alexandrinus	+		+									
Cursorius cursor			+		+							
Eremialector lichtensteinii			+		+							
Streptopelia senegalensis		+	+	+	+	+	+	+	+			
Treron waalia			+			+	+	+	+			
Centropus superciliosus			+				+	+	+			
Otus scops			+			+	+	+	+			
Caprimulgus nubicus					+							
Apus pallidus	+	+	+		+					+	+	+
Eremopterix nigriceps			+		+							
Anthus similis			+		+	+	+	+		+	+	+
Cisticola incana					+	+	+	+	+	+		
Cisticola juncidis					+					+		
Lanius elegans		+	+		+	+	+	+		+		
Corvus ruficollis	+	+	+		+	+	+	+		+	+	+
Onychognathus frater		+	+		+	+	+	+	+	+		+
Onychognathus blythii		+	+		+	+	+	+	+	+	+	+
Zosterops abyssinicus			+		+	+	+	+	+	+		
Cyanomitra balfouri						+	+	+	+	+		
Passer insularis	+	+	+	?	+	+	+	+	+	+	+	+
Rhynchostruthus socotranus					(+)	+	+	+	+	+		
Fringillaria tahapisi		+	+		+	+	+	+	+	+		
Fringillaria socotrana					+				+			+

A dragon's blood tree and the Hagghier Mountains on Socotra.

Hagghier Mountains from the Hadibu Plain on Socotra.

West end of Socotra, the habitat of *Fringillaria socotrana*.

Village on Abd-el-Kuri in the area where *Passer insularis hemileucus* occurs.

Sula dactylatra melanops in flight.

Buteo buteo in flight.

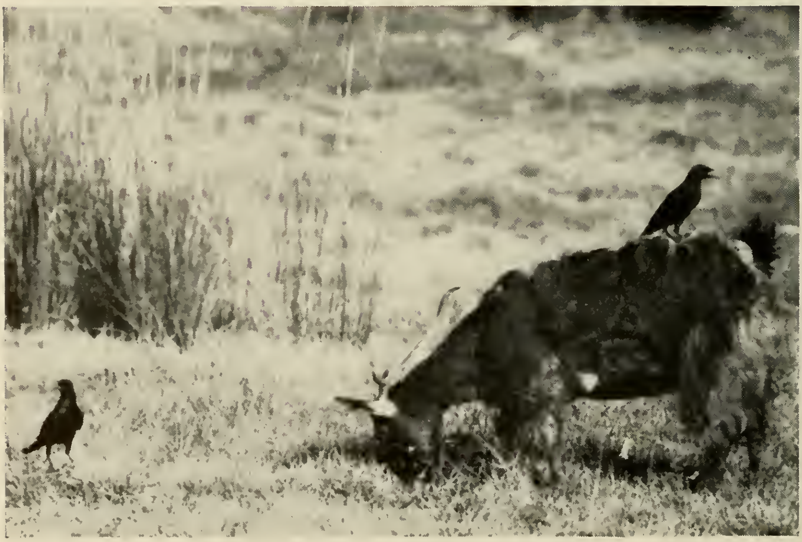
Neophron percnopterus percnopterus.

Cursorius cursor cursor settling on eggs.

Swift in flight near Hadibu Town.

Male *Eremopterix nigriceps forbeswatsoni.*

Lanius elegans uncinatus.



Onychognathus blythii and an island goat.

Anthus similis sokotrae.

Zosterops abyssinicus socotranus.

Passer insularis insularis male at Hadibu.

Frigillaria socotrana.

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 151, NUMBER 8
PUBLICATION 4683

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(WITH SIX PLATES)

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PORT CITY PRESS, INC.
BALTIMORE, MD., U. S. A.

CONTENTS

ACKNOWLEDGMENTS

The research described in this paper was conducted in the Department of Zoology at the University of British Columbia, in the Vancouver Zoological Gardens, at the Smithsonian Tropical Research Institute in the Panama Canal Zone, at the Biological Station near Acapetahua in the State of Chiapas Mexico, and at the U.S. National Zoological Park. The project was supported by funds from a grant to Dr. Eisenberg from the National Research Council of Canada, a General Research Board Grant from the University of Maryland, and Grant No. GB-3545 from the National Science Foundation.

The authors express their indebtedness to Dr. Hugh Campbell-Brown for his aid in photographing the captive specimens. In addition we gratefully acknowledge the support and kindness of Mr. A. Best, director of the Vancouver Zoological Gardens; Dr. M. Moynihan, director of the Smithsonian Tropical Research Institute; Mr. J. L. Grimmer and Dr. T. Reed of the U.S. National Zoological Park; Dr. D. Johnson, Curator of Mammals at the Smithsonian Institution; and Dr. M. Alvarez del Toro of the Departamento Biologico, Tuxtla Gutierrez, Chiapas, Mexico.

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(With Six Plates)

INTRODUCTION

The study of primate behavior experienced a renaissance in the past ten years, and today a concerted effort is being made to study primates in both field and laboratory settings. The major focus of recent effort has been on the anthropoid apes and the Old World ground-dwelling macaques and baboons. The only monographic studies of Neotropical primates include the pioneer efforts of Carpenter (1934) on *Alouatta* and the recent study by Moynihan on *Aotes*. Although the howler monkey has been the subject of several recent publications the remainder of the New World primate genera have virtually escaped attention.

In order to extend the descriptions of primate behavior we undertook a preliminary study of the spider monkey, *Ateles*. We wished to approach this study in both a field and a captive setting in order to develop refined techniques for quantifying behavior and also to observe the effects that captivity had on the expressed behavior patterns of the animals. In the laboratory special emphasis was given to the forms of auditory and visual communication. The zoo setting allowed a quantitative description of the social structure and a determination of some of the mechanisms responsible for group coordination and cohesion. The field observations served as a control situation for testing the hypotheses generated by the captive studies.

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The study of primate social behavior need not be an end in itself. In fact it is highly desirable to integrate the specific conclusions reached through the study of one primate species not only with the studies of social behavior in other primates but also with the studies of other orders of mammals. To this end the discussion sections have been used to integrate the observed trends in primate behavior with those trends discernible in other mammalian taxa.

THE BEHAVIOR PATTERNS OF *ATELES*

Methods and Specimens

A colony of four *Ateles* was established in the laboratory at Vancouver on August 2, 1963. Judging by the descriptions in Kellogg and Goldman (1944) three species were represented: a male and a female *A. belzebuth,* designated A and C respectively; a male *A. paniscus,* designated B; and a female *A. geoffroyi pan,* designated D. These specimens were judged to be adult at the time of acquisition. Since they were purchased from a commercial dealer, no accurate information with respect to origins or past histories could be ascertained.

The animals were maintained in individual cages measuring 4 x 4 x 4 feet. Each cage was provided with an overhead exercise bar and a bench for resting and sleeping. The sides, top, and bottom of the cages were of wire. The specimens were fed and watered in the morning and late afternoon. Their food ration consisted of fresh fruits and vegetables, nuts, bread, and a liquid vitamin supplement. Cooked hamburger was offered once a week and three of the specimens accepted this meat supplement readily.

The animals were housed in a heated room, 15 x 18 feet. In this same room was the exercise cage, 5 x 10 x 8 feet, which contained a swing. Approximately every second day each subject was released into this large cage, giving him space and implements for exercise. The exercise cage was also utilized as an encounter arena. Two animals could be released into the cage simultaneously and the resultant interaction recorded.

The encounter series was initiated a week after the arrival of the animals. All combinations of male-female and female-female encounters were run once in order to formulate a description of the behavioral elements involved in their social interaction. From August 29, 1963, to January 1, 1964, a formal series of encounters was run according to the following plan. The observer sat in full view of the animals and verbally recorded the interaction patterns with a tape recorder. The verbal descriptions were then transcribed on paper with a 10-second time interval signal. Thus a measure of the temporal patterning of the behaviors could be made. Any sustained behavioral unit was recorded as occurring once if it was less than or equal to 10 seconds in duration. Short-term activities of less than 5 seconds having a clear onset and termination could, however, be counted twice or more within a given interval of 10 seconds.

From January 3 to March 17, 1964, the subjects were observed from an adjoining room through a pane of one-way glass. In this way the bias induced by the observer was removed and certain aspects of the animals' sexual behavior could be noted.

The period of observation was not fixed and an encounter was sampled over intervals ranging from 10 to 40 minutes. During the weeks when the animals were allowed to encounter, not all encounters were recorded on tape. Photography, both still and moving, as well as handwritten notes of interaction patterns, and tape recordings of vocalizations were made during the encounter periods and supplemented the formal recordings. Altogether 52 encounters were studied and of these 34 were verbally recorded in detail. On April 10, 1964, the colony was disbanded.

To supplement the controlled observations in the laboratory we have also introduced data from observations and recordings made at the Vancouver Zoological Gardens (see pp. 29-31) and the U.S. National Zoological Park. At the National Zoological Park the following specimens were available for study during the fall and winter of 1964-65: a group consisting of a mated pair of *A. belzebuth* with their single offspring and three adult female *A. geoffroyi* and a group of four adult *A. fuscisceps robustus.* The *A. fuscisceps* group consisted of one male and three females. One female had an infant born during the study and a second female had a juvenile with her during part of the study.

Description of the Behavioral Elements and Their Functional Contexts

In this section the units of behavior displayed by *Ateles geoffroyi* will be defined and interpreted. The behavior patterns are similar for all four species observed and no attempt will be made to enumerate species differences systematically. The field observations pertinent to the functional interpretation of the behavioral units will be introduced at this time.

MAINTENANCE BEHAVIOR

Locomotion

Ateles employs four primary modes of locomotion: the quadrupedal crossed extension pattern, the bipedal run or walk, leaping, and brachiation. Descriptions of locomotion are complicated by the fact that the prehensile tail, as well as the limbs, is involved in arboreal activity. Free-living spider monkeys seldom descend to the ground, but in captivity terrestrial locomotion is common (table 10).

During terrestrial activities the animals employ a typical crossed extension pattern of quadrupedal locomotion with the fore and hind limbs of the opposite sides of the body in synchrony. They may, however, gallop with the fore and hind limbs alternately striking the ground. The bipedal mode of locomotion is adopted for short periods and the arms are often held up at head level to maintain balance. During both bipedal and quadrupedal locomotion the tail may be held in an S shape or wrapped around the animal's body.

During arboreal locomotion the tail is constantly employed to grasp branches and provide support whether the animal is moving quadrupedally or bipedally and even when brachiating (figs. 1 and 2). When the animal is moving bipedally in the trees it is surrounded with branches so that the hands and tail are continually providing support. The animal thus is able to distribute its weight over several small branches and twigs and effectively support itself at the extremities of tree crowns. Brachiation and leaping are employed during rapid, arboreal progress. Leaping may involve a vertical descent to a lower level in the foliage, and leaps of 15 to 25 feet are not at all uncommon. When climbing vertically the animals employ either a crossed extension synchrony of limb movements or a series of hops. The hop involves an alternate extension of the body while supporting with the hind feet, followed by a grasp with the forefeet, and pullup while releasing the hind feet.

In addition to the common methods of locomotion, the animal may slide along a tree branch on its stomach, chest, and forearms while propelling itself with the limbs. In captivity an animal may adopt a scooting method of locomotion where it propels itself with the arms while sliding on its rump or thighs. This latter behavior pattern is common in infants and juveniles (table 10).

Manipulation of the Environment

The hands, feet, teeth, lips, and tail are all employed in feeding and in testing objects. The genus *Ateles* is characterized by the

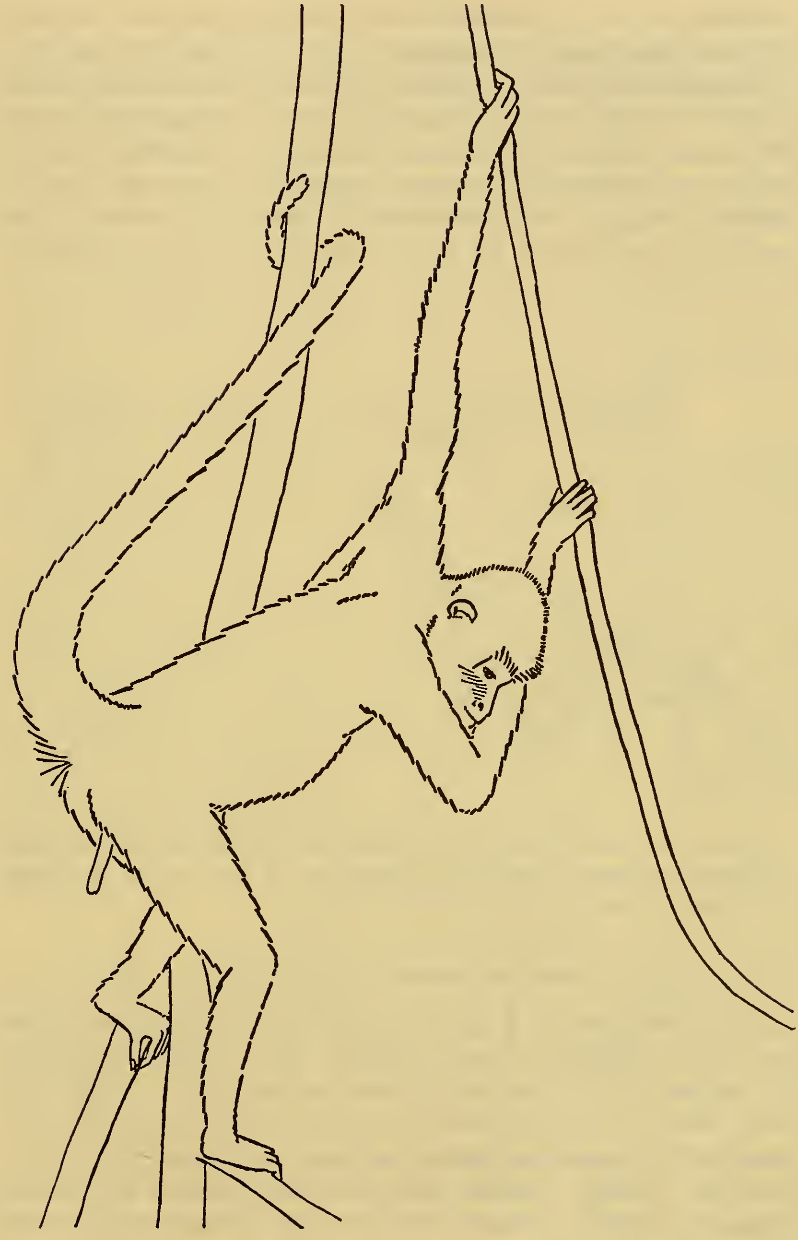

FIGURE 1.—Hanging by the forelimbs and the tail. Note the clitoris of this female *A. geoffroyi.* This is the most obvious visual character for differentiating the sexes. (Drawing made from a photograph taken in Panama.)

reduction or loss of the thumb so that the forepaws are effectively converted into hooks for grasping and hanging during locomotion. The manipulative ability is severely curtailed when compared with *Cebus* or the Old World macaques. Objects are carried and grasped with hands, feet, and tail, and, although fine manipulation of artifacts is not possible, the animals experience no apparent inconvenience in foraging. When retrieving an object the hand tends to be used as a scoop with all the digits pressing an object into the palm.

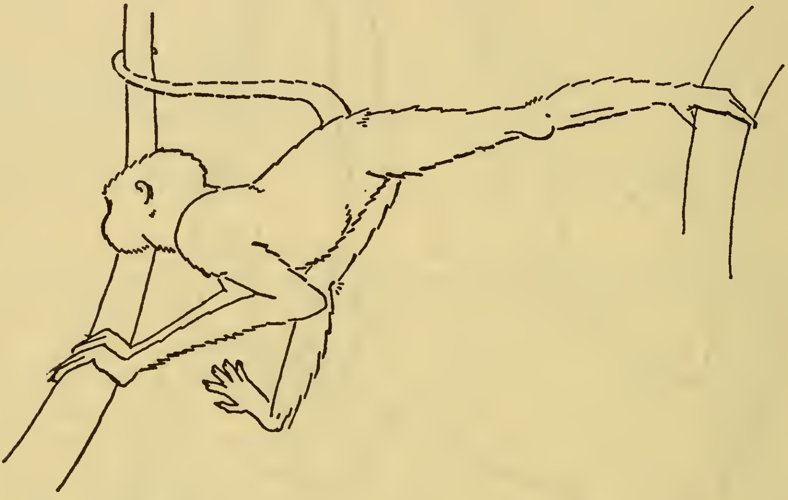

FIGURE 2.—Crossing between two branches in a tree crown. All four limbs and the tail are used to distribute the weight over as large an area as possible. (Drawing made from a photograph taken in Panama.)

POSTURES DURING REST AND SLEEP

The animals rest in a variety of postures including both prone and supine variations. They frequently adopt a supine posture in the sun and thus expose a maximum surface area to solar radiation. During rest the animals may support their body axis on a branch while the tail and limbs grasp the nearest branches to provide additional stability. During sleep or during showers the animals expose the minimum of body surface to the air and adopt a sitting position with their arms wrapped around their legs while their heads are lowered onto their chests. Two or three animals often sleep together, embracing each other while doing so.

Feeding and Drinking

Great individual variation was noted in feeding patterns. While feeding in the field the animals are prone to hang suspended by three limbs and the tail or any combination of limbs and tail, including suspension by the tail alone. Hanging upside down while feeding on fruits effectively prevents juice and pulp from running down on the animal's limbs and chest. The hands are primarily utilized to pick fruits and nuts, but the feet and tail may be employed to hold foodstuffs. Small fruits may be picked with the teeth and lips alone. Foodstuffs are generally sniffed at before picking and it would appear that the animals can discriminate ripe from unripe fruit by odor. Even so, many fruits are rejected after a bite or two and apparently taste is equally important in determining palatability.

It is not uncommon for captive animals to eat directly from the ground without necessarily picking up the food with the hands, but rather utilizing the lips and teeth to retrieve pieces of fruit and nuts. Seed hulls and rinds are often spat out and not ingested, but individual variation is common. In the laboratory group female D always spat out grape skins, whereas male B would eat whole grapes without rejection of the skin. Seeds or pits were spat out if large, but again individual variation was common. Female D was prone to reject date pits, but male B swallowed over half the pits ingested.

Drinking was generally performed by lapping water. In the field and in the zoo, specimens were often observed to hang suspended above a pool and by dipping one hand in the water they were able to lap up the drops adhering to their fur and palm.

Comfort Movements

Urination and defecation are performed without apparent regard to a specific locus. The animal may urinate when standing or squatting but it may shift its position somewhat to avoid urinating on its limbs. The animals generally flex their hind limbs slightly when defecating. During both urination and defecation the animal is momentarily motionless. This pause in activity is prolonged and more predictable with defecation than with urination.

During yawning and stretching the limbs and torso are extended and flexed in the typical vertebrate patterns. Care of the coat is primarily a function of the hands and feet. Most carnivores, rodents, and ungulates employ the tongue, teeth, and lips in this care of the body surface, but *Ateles* relies less on the mouth as a cleaning organ and more on the hands. The fingers may be licked after feeding and the fur also may be licked, but the most common comfort movement is scratching. Scratching may involve either the hands or the feet, and generally the whole hand or foot is rubbed over the surface to be "scratched." Discrete finger movements may be employed in scratching, but it is far more common for the lower surface of the fingers or toes, as well as the palm or sole, to be employed. A self-grooming pattern involving the mouth and hands does occur, but it is infrequently shown. This grooming pattern involves parting the fur with the fingertips and licking the exposed skin, or removing foreign particles with the lips, tongue, or teeth. If an animal has been bitten it treats the wounded area with similar movements—parting the fur and licking the bite. The animals may rub their bodies against branches or, in the case of captive animals, against artifacts such as wire or wooden posts. The mouth may be rubbed on leaves after feeding, and the chest may be rubbed on branches. A frequent movement distinct from scratching includes stroking downward with a forepaw from the pectoral gland (pp. 18, 26) to the abdomen. This has been termed the *pectoral stroke.*

Ateles also engages in sunning, which has been described on page 6. Sunning generally occurs in the early hours of the morning after feeding or in late afternoon. If the animals become wet during a rainstorm they generally sun themselves whenever the first opportunity presents itself. The pectoral stroke is often associated with sunning, and one is led to hypothesize that the secretions from the pectoral gland may be deliberately spread on the fur during exposure to the sun. If these secretions are reingested when the fur is licked, it is possible that the pectoral gland secretions are involved in the synthesis of some essential dietary supplement. Further research is necessary to clarify this point.

Self-manipulation of the external genitalia is not common either in females or males. The pendulous clitoris of the female is often examined but little attention beyond tugging or licking is shown to the external genitalia. During an erection the males may touch their penises or lick them from time to time but no induced ejaculations were observed.

Young animals frequently exhibit finger-sucking.

Several patterns are included in this subsection which remain ambiguous as to their function. These include urinating on the fingers and spitting on the fur. Occasionally female C was observed to place her hand in the stream of urine which she was releasing. The urine-soaked fingers were licked slightly and no further attention to the hand was noted. Spitting on the fur involved a repeated expulsion of saliva by C onto the hair of her abdomen or thighs. This saliva was then spread with tongue or fingers. Urinating on the hands was noted with captive *Cebus* (Fiedler, 1957). Ulrich (1954) noted excessive salivation in *Lagothrix* accompanied by smearing the saliva on the cage walls and then rubbing the breast in the deposited saliva.

PATTERNS OF SOCIAL BEHAVIOR

Expressive Movements

1. Head shake.—While looking directly at the partner the head is moved back and forth in the horizontal plane. This pattern was seen in the field and captive settings. It accompanies an initial contact or a renewed contact where the animal is ambivalent in its approach. It may also occur when a contact situation is about to break up as a result of mixed agonistic tendencies on the part of the other animal. Head shaking could be elicited from our captive specimens when human observers imitated the movement.

2. Turn away.—This movement may involve the head only or head and body. It was frequently shown by an animal apparently indifferent to the approach of another.

3. Grooming solicitation.—The whole body is turned exposing the back and the animal sidles toward the partner. Such a movement is to be distinguished from the simple turning away.

4. Look at.—Obvious meaning. Again the head alone or the whole body may be involved.

5. Grimace.—A facial expression involving partial opening and retracting of the corners of the mouth combined with raising the upper lip, thus exposing the teeth. This expressive movement was seen in the field, zoo, and laboratory. It may be accompanied by a rush, moving away, or a slap; however, the expression itself is often sufficient to induce moving away in an approaching animal. The signal value for the grimace appears to alter with experience. In the encounter series the effect of the grimace in inducing moving away varied for each encountering pair of animals considered (table 1). In the A-C encounter series, the male's grimace had little initial effect in inducing moving away by the approaching female. However, the male did not reinforce the grimace with slaps or chases. After a month, including 10 encounters, a recheck on the signal value of the grimace indicated the male was reinforcing about 40 percent of his grimaces with slaps or chases and achieving a high response

from female C. In the C-B encounter series, the male virtually ignored the grimace of the female in the initial two encounters; however, the female was reinforcing about 50 percent of the grimaces. A subsequent sample indicated a higher response rate by the male and about the same reinforcement level for the female. In the D-B series, the female D often reinforced with bites and slaps, achieving a high level of moving-away responses from the male. In a later sampling, the female's grimace rate had fallen considerably as a result of the stable relationship achieved (fig. 3).

TABLE 1.—*Changing signal value of the grimace.*

Subjects	Initial two encounters			Average of three encounters 20 to 40 days following		
	n	Prop. ma	Prop. reinf.	n	Prop. ma	Prop. reinf.
A to C	9	.22	.00	15	.66	.40
C to B	10	.00	.50	19	.68	.53
D to B	20	.80	.30	6	1.00	.33

Legend: n—total number of grimaces. Prop. ma—proportion of grimaces that induced moving away. Prop. reinf.—proportion of grimaces reinforced by a slap, rush, or bite.

6. Pursed lips.—A facial expression involving an extension of the lips. The teeth are rendered virtually invisible. This expression is assumed during contact-promoting behavior (pl. 1a).

7. Open mouth.—An ambiguously defined expression involving four subtypes. The mouth may be partially or widely opened. In either case canines may be exposed or unexposed. A partially opened mouth with canine exposure differs from the grimace only in that the corners of the mouth are not retracted.

8. Pilo-erection.—Varying degrees of hair erection were noted when the animals were highly aroused. This pattern was not quantified.

9. Shaking the branches (or bars).—A movement performed by jumping up and down alternately flexing and extending all four limbs while gripping a fixed object with the tail.

10. Chin-up.—The face is thrust forward by tilting the neck, presenting a "chin-up" posture.

11. Eye closure.—Eye closure ranged from wide-open eyes with pronounced scalp retraction to eyes almost completely closed. Generalized correlations among selected expressive movements are included in table 2.

VOCALIZATIONS

Unless specified, the following definitions apply to sounds produced by adults. When physical measurements are given the species from which the recordings were made will be designated. Although the vocal patterns appear similar for all species it is not intended that a set of measurements from one species be generalized to all species.

1. Tee tee.—A sound of approximately one-half second duration with the greatest energy concentrated between 2,200 and 4,500 cps (*A. geoffroyi*). Although it may be repeated two to three times, the sound is not repetitive in character. Each individual call consists of three to four pulses, each rising and falling within about .20 seconds over a range of about 2,300 cps. This call is given at the approach of a troop member or familiar attendant and appears to function as a greeting call. The call has been noted for *fuscipes, geoffroyi,* and *belzebuth.* (pl. 1b).

TABLE 2.—*Correlations among selected expressive movements.*

1. Open mouth	
a. Canines exposed	Generally correlated with a direct stare
b. Canines unexposed	Correlated with head shake and varying degrees of eye closure
2. Pursed lips	Variable associations including slitted eyes and head shake but most frequently the brows are raised with concomitant scalp retraction
3. Grimace	Associated with a direct stare
4. Lips almost closed	Associated with partial eyelid closure and the production of high-pitched sounds
5. Head shake	Most frequently associated with pursed lips or open mouth with no canine exposure
6. Chin-up	Can be associated with almost any facial expression and appears to be a concomitant of tensing the throat for high-pitched sounds; it is most frequently associated with slitting of the eyes and the whinny or chirp series

2. Whinny.—A sound of 1.5 to 2.5 seconds in duration. It has a vibrato form with the greatest energy concentrated from 1,000 to 4,600 cps (*A. geoffroyi* and *A. belzebuth*). At any given emission the sound is relatively pure in tone. It is strongly correlated with feeding when the animals are dispersed. It would appear to function in maintaining spatial awareness or assembly, but it does not promote

physical contact (see pl. 3a). The lips are virtually closed during this vocalization. This sound has been noted for all species studied.

3. Chirp series.

a. Slow whinny.—A series of sounds with each element lasting .15 seconds in duration and separated from the next element by an equal quiet interval. The chirps are uttered in a series about 2 to 3 seconds in total duration. The greatest energy lies between 1,700 to 3,300 cps (*A. fusciceps*). The sound is harmonic in structure and repetitive, but the energy is more broadly distributed than is the case with the true whinny. It has been noted in all species and appears to accompany contact-seeking behavior. Generally the chin is up and the lips are virtually closed during this vocalization (pl. 2a).

b. Yip yip.—A variant of the preceding vocalization, which appears under similar circumstances. The lips are pursed and evidently modify the tonal quality of the sound. It was repeatedly noted with *A. fusciceps.*

4. Twitter.—Similar to the preceding but higher in pitch and softer. It is harmonic with the greatest energy at 3,500 and 5,500 cps (*A. fusciceps*). The sounds are less than .1 second in duration and are delivered in a burst of evenly spaced sounds. Each burst lasts about 1 to 2 seconds. Each discrete sound rises and falls over a range of about 500 cps. This vocalization has been noted in adult females and juveniles in a contact-seeking circumstance. It has been heard in *A. geoffroyi* and *A. fusciceps.* (pl. 2b.)

5. Grunt-Trill.—A relatively pure sound with harmonics, consisting of a sustained series of individual pulses. It generally ascends the scale with energy concentrated at 2,000-3,500 cps (*A. fusciceps*) or 1,900-3,650 cps (*A. belzebuth*). The sound may be delivered rapidly with fusion of the individual pulses (pl. 3b) or delivered more slowly with a full recognition of the individual elements. Often the call terminates with a nonharmonic grunt termed the *caw.* The caw is discussed separately at the end of this section. Much energy may be contained in the upper harmonics of 8-9,000 cps in the call of *A. fusciceps.* It is generally given when one animal is isolated from another or it may be given when seeking contact.

6. Squeak.—A simple note often repeated and having an average duration of .35 seconds with the energy of the signal concentrated at 3,600 to 4,100 cps (*A. belzebuth*). This sound was given by the captive female C when she was seeking contact with a male but at the same time approaching slowly as a result of a previous rebuttal. It was also given by the female during the initial phases of primary

sexual behavior. The sound was heard in juvenile and adult *A. geoffroyi* in different contexts (see end of this section and pl. 4a).

7. Chitter.—A complex, pulsed sound with several defined harmonics. The sound may be given once or repeated two or three times. Duration ranges from 1.0 to 2.0+ seconds. The energy is concentrated in two major distributions: 1,000 to 1,500 cps and 7,400-7,900 cps.

All species exhibited the sound, and recordings were analyzed for *A. paniscus* and *A. fusciceps.* The sound was always associated with extreme autonomic arousal (e.g., piloerection and labored breathing). The animal would frequently leap at the cage and shake the bars. One could discern definite elements of threat in the behavior (pl. 4b).

8. Ook ook.—A short, grunting sound repeated rapidly. Harmonic structure is blurred; the maximum energy in the signal, however, is concentrated from 1,000 to 1,400 cps. The individual utterances average .28 seconds in duration. This sound is 100 percent correlated with grappling, both in the field and laboratory (pl. 5a). It is recorded for *A. belzebuth* and *fusciceps,* but noted as well for *geoffroyi.* The ook ook varies slightly in its tonal quality depending on the facial expression accompanying the sound production. With the lips pursed the sound is hollow, but, if the mouth is open with the canines exposed while vocalizing, the tone is flat and harsh. This latter expression may be shown before a transition to growling and the accompanying vocalization has been termed the ak ak variant (see p. 16).

Low ook ook.—This differs from the preceding in its low intensity (see p. 19).

9. Bark.—A short but intense sound often repetitive and noted in all species. The duration averages .38 seconds. Although the sound is harmonically structured, the harmonics are blurred. The energy distribution ranges from 500 to 3,400 cps (*A. belzebuth*). This sound is commonly displayed in situations where novel animate stimuli are encountered. In the field it is a common initial response to the presence of human observers (Carpenter, 1935; Wagner, 1956) (pl. 5b).

10. Growl.—A sound of about .5 seconds duration with a blurred harmonic structure. The maximum energy distribution ranges from 700 to 2,600 cps (*A. belzebuth*). The sound was noted in all species and is associated with aggressive arousal (table 3, pl. 6a).

11. Roar.—A sound similar to the growl but longer in duration,

generally exceeding one second. It also is associated with aggressive arousal.

12. Cough.—This vocalization is quite discrete in its onset and termination and has virtually no harmonic structure. The energy tends to be concentrated from 700 to 2,000 cps. It is associated with a strong tendency to rush or slap (pl. 6b).

13. Scream.—A harsh shriek, often repeated. This is given by an injured animal as a result of fighting. It was not recorded but was noted for *A. geoffroyi.*

14. Hiss.—An unvoiced expiration during aggressive interaction.

15. Champing.—Sound produced by striking the teeth together and associated with aggressive arousal.

TABLE 3.—*Vocalization patterns and their associated circumstances.*

Vocalization	Circumstances and Supposed Function
1. Tee tee	Given by a group member at the approach of second member who has been absent for some time; the sound appears to function as a greeting call
2. Whinny	Given by group members at the onset of feeding; the sound appears to function as a feeding call and although it promotes assembly it does not promote physical contact
3. Chirps	Given during contact promoting behavior—often shown between juveniles
4. Twitter	Circumstances and function similar to above
5. Grunt-trill and caw	A sound produced by an isolated animal; function unknown
6. Squeak	Given by an approaching animal, often after it has been repulsed; it appears to function as an appeasement and contact promoting signal
7. Chitter	Correlated with a strong autonomic arousal, generally induced by an alien stimulus
8. Ook ook	Completely correlated with grappling; a low intensity variation accompanies primary sexual behavior
9. Bark	Response to an alien stimulus serves to alert group and focus attention on the responding animal
10. a. Growl b. Roar c. Cough d. Hiss	Agonistic sounds which accompany threat or attack behavior
11. Scream	Response of injured or frightened animal

Additional sounds occasionally heard but not recorded or adequately defined include the following: *oo oo*—a low sound uttered by young and adults; *caw*—heard several times in the field from *A. geoffroyi* and given by an animal isolated from the main group, may grade into the grunt-trill; *low squeaks*—heard between two animals during mutual aid at a crossing point (see pp. 53-54); *rapid squeak series*—approximating a chitter and heard when an infant *geoffroyi* slipped and fell to a lower branch while climbing.

It should be stressed that many of these sounds are heard in conjunction with a second or third sound type. As we have mentioned, the grunt-trill and caw are often associated. In a similar fashion the animals can move from a chirp series to a twitter and from a twitter to a chitter apparently depending on the, as yet undefined, interaction of external stimuli and the motivational state of the animal. Ook ook may grade into a growl or roar but these sound types are generally distinct. The tee tee, whinny, bark, cough, scream, and squeak are least frequently associated with other call types.

The infantile and juvenile sounds are necessary to complete a description of the origin and functional change in the elaboration of the vocal repertoire of *Ateles.* Although our present ontogenetic data are incomplete it would appear that the infant II and juvenile I age classes produce the twitter, squeak, chirp, and chitter sound types. The whinny, bark, cough, growl, and roar appear later on in development. This is not to imply that the infant is incapable of producing all major sound types. In the normal course of development the young animal clings to the mother and is often not presented with a stimulus situation which would elicit the strongly agonistic calls. Thus the brief comments concerning infant and young juvenile calls merely reflect the relative frequency with which the call types were noted.

Table 4 compares the best defined sounds with respect to four characteristics: duration, repetition rate, predominant frequency, and tonal purity. As can be seen, the sounds can be grouped into three classes: sounds with high frequencies and a rather discrete tone; sounds with low frequencies and a blurred harmonic structure or broad spectrum energy distribution; and a class of intermediate sound types. Class A sounds are associated with contact maintenance or contact promotion, whereas Class C sounds are agonistic in part. The series twitter, squeak, tee tee, grunt-trill, and whinny make a related group of sounds that differ chiefly in their duration as do the agonistic series cough, growl, and roar. The Class B sounds of ook ook, bark, and chitter form in some respects an intermediate group with respect to the four polar attributes of duration, repetition rate, pitch, and tonal clarity. These latter three sounds form a series from short to long and repetitive to nonrepetitive. Bark and ook ook are related to the agonistic sounds with respect to pitch and tonal clarity, whereas chitter is related to the agonistic sounds with its nonrepetitive character. Because of its inherent difficulty in measurement the parameter of sound intensity has been left out of consideration.

TABLE 4.—*Classification of the physical characteristics of Ateles vocalizations.*

Sound Type	Characteristics							
	Duration		Repetitive	Nonrepetitive	Dominant Frequency		Clear Tone	Blurred Harmonics
	Long	Short			High	Low		
A.1. Twitter		xxx	xx		xx		xx	
2. Squeak		x	xx		xx		xx	
3. Tee tee		xx		x	xx		xx	
4. Chirp		x	x		x		x	
5. Grunt-trill	x		xx		xx		xx	
6. Whinny	xx		xx		xx		xx	
B.7. Ook ook		xxx	xxx			x		x
8. Bark		xx	xxx			x		x
9. Chitter	xx			x	x		x	
C.10. Cough		xxx		xxx		xx		xxx
11. Growl		x		xx		xxx		xxx
12. Roar	xx			xxx		xxx		xxx

Table 3, insofar as possible, summarizes the correlations between circumstances of occurrence and vocalization pattern, while table 5 includes the correlations between facial expression and vocalization. The configuration of the mouth influences the tonal quality of certain vocalizations. For example, the ook ook has a deep resonant quality when the lips are pursed, but if the animal shifts to an open mouth the sound becomes flat and harsh. This can then grade into a roar if the sound is prolonged rather than pulsed. As mentioned previously the yip yip sound appears to be a variant of the slow whinny with the former sound involving pursed lips and the latter sound accompanying a virtually closed mouth expression.

Patterns of Interaction

1. Unspecified patterns.

a. Approach.—One animal moves toward another by any of the described modes of locomotion. Generally the approaching animal looks directly at the other. No special facial expression or sound necessarily accompanies an approach.

b. Move away.—The animal moves away by any of the major types of locomotion. There is no particular associated facial expression or vocalization.

2. Contact and contact-promoting patterns.

a. Extend.—The act of extending an arm, leg, or the body in order to touch another animal.

b. Touch.—Contacting a second animal by touching lightly with the foot, hand, or mouth.

c. Embrace.—This behavior pattern may be mutual or performed by one member of an interacting pair. It involves placing the arms around the body of the second animal.

Table 5.—*Major correlations of expressions with vocalizations.*

	Expression					
	Open mouth					
Sound Type	Canines exposed	Canines unexposed	Pursed lips	Lips closed or slightly parted	Chin-up	Head shake
1. Tee tee				xxx	x	
2. Whinny				xxx	xx	
3. Chirp series			xxx	xxx	xx	
4. Trill			xx	x	xx	
5. Twitter			xx	xx	xx	
6. Chitter		xx	xxx		xx	
7. Squeak				xx		
8a. Ook ook	x	xxx	xxx			xx
b. Ak ak (variant)	xxx					
9. Bark	xx	xxx				
10. Growl-Roar	x	xxx	x			
11. Cough		x (head jerked up and down)				
12. Hiss	x	x				
13. Scream	xx					
14. No sound	xxxx					

xxxx = very strongly associated (12-15 associations)
xxx = strongly associated (7-11 associations)
xx = often associated (3-6 associations)
x = occasionally associated (1-2 associations)
From a total of 117 recordings

d. Pectoral sniff.—A complex act which occurs only during an embrace. It involves lowering the head and placing the nose or mouth close to the pectoral gland or axilla of the partner.

e. Anal-genital investigation.—A pattern whereby the nose and mouth are brought near to the anal-genital area of the partner.

f. Grooming.—This act may involve soliciting (see p. 9). The groomer parts the hair of the groomed individual with its forepaws and (employing the tongue, lips, and teeth) licks and nibbles at the skin and fur.

g. Grappling.—A complex pattern accompanied by the ook ook vocalization. Grappling involves elements of the embrace: pushing away, pulling toward, mock biting, and slapping. Ook ook sounds may grade into roars and the bout may end in a chase. Certain elements of sexual behavior including mutual manipulation of the genitalia with the mouth, hands, or feet also occur. In the field, ook ook sounds were common in the early evening just after sunset. These sounds often graded into roars and clearly suggested that male-female grappling was in progress. Since grappling may be a prelude to sexual behavior (see p. 19) we assume that much of the sexual behavior of *Ateles* takes place at dusk in the sleeping trees.

h. Face to face.—During an embrace or when sitting or hanging together, the animals will often bring their faces together.

3. Agonistic and Avoidance Patterns.

a. Chase-flight.—This behavior may involve all mixtures of quadrupedal, bipedal, and brachiating locomotion.

b. Slap (tag).—A directed movement of one limb, resulting in a blow to the partner's body, often including a grimace expression.

c. Bite.—A swift slash with the canines or a hard incisor nip.

d. Kicking.—A directed blow with one or both hindfeet, often while hanging suspended by the arms or tail.

e. Rushing.—A swift movement toward the partner, involving any of the various modes of locomotion. A rush may conclude with a chase but if the partner faces the oncoming animal certain attitudes of threat may occur.

f. Threat.—A nonspecific term which includes roaring, hissing, champing or coughs while facing the partner. Branches or cage artifacts may be shaken and slaps may be directed at the partner.

4. Sexual patterns.—Complete sexual behavior has not been described for *Ateles* and it is seldom observed in the field or captive situation. There is reason to believe that primary sexual behavior takes place at night as we have outlined in the previous section.

The paucity of data prompts us to include here a partial description of the sexual behavior of *Ateles belzebuth*:

March 17, 1964; 1435-1550; Animals A and C.
Following a grappling bout the female approached uttering the repeated squeak; her lips were pursed from time to time. The male was sitting on the swing, producing a very low intensity ook ook sound. The female hung above the male and then sat in his lap; they embraced face to face and sat together vocalizing for slightly over one minute. They then separated for twelve to fifteen minutes, The male then initiated a low ook ook series and was observed to have an erection. He approached the female who was braced standing upright in a corner of the cage. The male braced himself in front of her and exhibited a pelvic thrust, whereupon he turned and brachiated away to sit on the swing. The female followed, giving the squeak vocalizations and sat in his lap; she then moved away, followed by the male. They hung facing one another for perhaps ten seconds when the male turned and returned to the trapeze followed by the squeaking female. This move-follow sequence occurred four times within a minute after which the male suddenly remained hanging and manipulated his genitals. The female hung opposite, facing him while the male exhibited a pelvic thrust. She moved away and he remained hanging. She approached again and manipulated his genitals. The male moved away and the female followed. Again they faced one another still producing their respective sounds. The male exhibited a pelvic thrust, then the male moved to the swing and sat. The female followed and hung over him. The male manipulated her clitoris, and then hanging up behind her he grasped her legs with his feet and thrust. The female moved slightly, froze, and then moved away to hang suspended and facing the male.
Total time elapsed—23 minutes.

Although intromission was not actually seen, several definite elements of sexual behavior can be described: (1) contact behavior including the embrace, (2) genital manipulation, (3) erection, (4) pelvic thrusts by the male, (5) sitting in the lap, by the female, (6) mounting by the male. It is noteworthy that the low ook ook and squeak vocalizations were associated with this interaction. Previous observations of A and C had shown all these elements except (4) and (6). The female played an active role in approaching the male and sitting in his lap. The male also approached the female and attempted mounting and thrusting. In any case, no clearcut dominance was exhibited by the male over the female.

Elements 3, 4, 5, and 6 of sexual behavior were not seen in the field; however, all other elements of social interaction described in this section were observed in the free-living group studied in Panama.

The Organization of the Behavior Patterns

THE ENCOUNTER*

The two-animal encounter initially followed a typical course of action. After a 2-week separation the animals exhibited a variable contact latency ranging from 20 minutes to less then 1 minute. Contact was established after a series of approach, touch, and withdrawal maneuvers. After the initial touch phase, an embrace with a pectoral sniff generally occurred. Contact was furthered by anal-genital investigation and embracing. Depending on the animals involved, the course of the encounter could then lead to mutual indifference, avoidance, and mild agonistic interaction, or grappling which often led to elements of sexual behavior.

Animals B and C were judged to be younger than A and D. Female D was quite old and in general avoided strong interaction and grappling. Male A was also prone to avoid the playful attentions of female C, but he could dominate her when aroused. Male B and female C were active and playful, but male B could be aroused to dominate female C. Table 6 summarizes the total interactions of the four animals in terms of chasing, biting, and the ratio of moving away to approaches. Whenever molested or teased the older female D responded by chasing or biting. This happened rarely and the younger animals (B and C) soon learned to leave her unmolested. Male A never formed a stable relationship with her, but she was not completely dominated by him. Male A could displace female C, but B and C were very evenly matched. The older female tended to move away submissively when approached by B and C, but this in no way reflected her inability to defend herself—it rather indicated her tendency to avoid the advances of the younger animals. By the same token male A tended to move away from female C as often as he approached her but this again did not reflect dominance but rather a tendency to avoid the younger animal's attempts to initiate play. Clearcut dominance, then, did not often manifest itself. Differences in behavior were more strongly correlated with the age of the animals rather than their respective sexes.

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* The following discussion refers to the two-animal encounters run in the laboratory at Vancouver (see pp. 2-3).

THE EFFECT OF SUCCESSIVE ENCOUNTERS

The B-D Series

Successive encounters between the male *paniscus* and female *geoffroyi* were characterized by a sharp decline in the intensity of interaction. Early attempts by B to engage in grappling were met by chases and bites from female D. Encounters in later months proved to be very stable with only nasogenital investigation by the male remaining as a contact-promoting behavior. The animals would sit side by side or ignore each other except for occasional periods when D groomed B or solicited grooming from B (fig. 3).

Table 6.—*Relations among the laboratory Ateles.*

		Chase				Bite				Ma/App			
Recipient →		A	B	C	D	A	B	C	D	A	B	C	D
Effector	A	–	–	4	0	–	–	4	0	–	–	1.0	.72
	B	–	–	4	0	–	–	0	0	–	–	.69	.92
	C	0	6	–	0	0	1	–	0	.69	1.9	–	.50
	D	7	2	1	–	1	6	1	–	.92	4.0	2.8	–

The B-C Series

The male *paniscus* established no contact relationship with the female *belzebuth* until early December. Their interaction from September to late November consisted of a continual interplay of approach, tag, and move away. This interaction was quite stereotyped and involved a sustained dispute over the possession of the swing. In general the male was more approach-prone. As soon as he would leave the swing the female would take possession of it, only to be eventually displaced by the male. In late November male B became ill with an intestinal ailment. During the phases of recuperation female C was allowed to encounter with him. At this time his overall activity was depressed and a stable contact relationship was established. During subsequent tests in January a grapple form of interaction was present (fig. 4).

The A-C Series

This was the only series of male-female encounters where the animals were of the same species. Aside from the male's tendency to avoid the sustained play engagements of the female, the animals indulged in contact-promoting, grappling, and sexual patterns of behavior.

The A-D Series

The male *belzebuth* was never able to establish a stable relationship with the female *geoffroyi*. Grappling was virtually absent while grimacing; biting and slapping were of common occurrence. The male never ceased to approach the female except after being bitten.

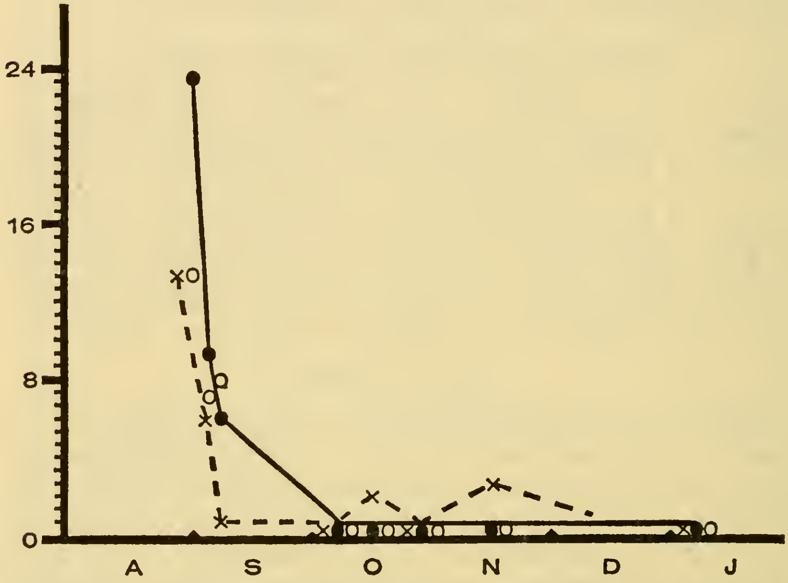

Figure 3.—Stability of the B-D relationship. Open circles refer to bouts of grappling; dots refer to tagging by B to D; crosses refer to grimaces by D to B. Acts were totaled for 20-minute encounters sampled over a 5-month period. Note the decline in all behaviors after the initial three encounters.

The female was generally willing to move off when approached, but she would not tolerate attempts at grappling or sexual contact.

In summary we can say little concerning the effect of species and age differences on the type of encounter displayed; however, it is surprising how consistent the encounter form was for any given matched pair of animals. Once initial contact had been made and the animals had learned the idiosyncrasies of their partner, the course of a given encounter was quite predictable.

Discussion

A captive study utilizing an encounter technique has several limitations. Cage pathologies such as grappling with the self and stereotyped movements in a confined space must be evaluated and deleted from a normative description. As one can see in the description of the behavioral elements several behavior patterns simply do not appear in a confined situation. A captive encounter results in an intensification of behavior which may result in severe distortions with respect to frequency and intensity of display. It is noteworthy, however, that in utilizing the field as a control situation almost all captively determined elements were found to be represented in the field in situations comparable to the captive ones. It is our belief that much critical work can be accomplished with confined populations, but only if a field check is available to correct any interpretations of pathological behavior induced by confinement.

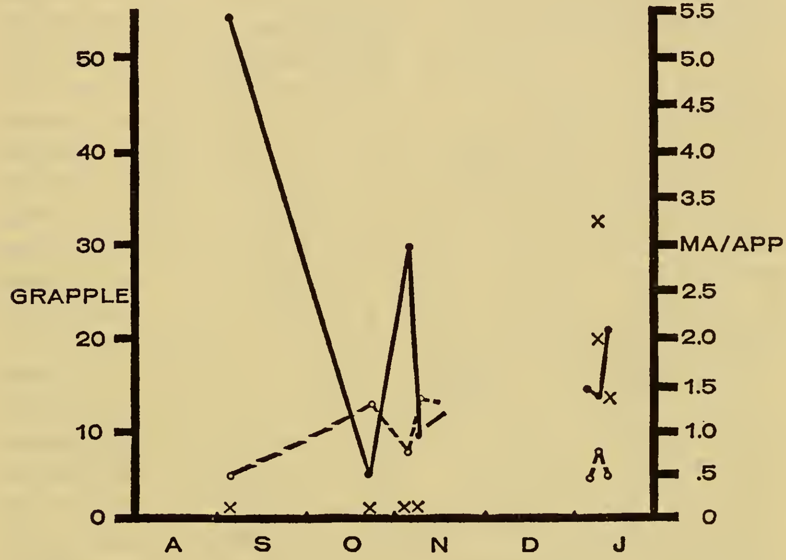

Figure 4.—Change in grappling intensity in B-C relationship. Crosses refer to bouts of grappling; dots refer to C and open circles to B with respect to their approach-move away ratios. B retained a low tendency to move away whereas C exhibited a higher but more erratic tendency to move away. Note the onset of grappling following B's illness.

Species differences in the defined elements of behavior were not obvious. Our sample is too small to permit a detailed analysis, but the major behavior patterns of *geoffroyi* appeared to be identical with *belzebuth, fusciceps,* and *paniscus.* Although variations in the patterns of vocalization were noted, these could well have been a result of individual variation. We have no doubt that species differences exist, but the differences are probably slight. It would seem that differences in coat color and odor would be most likely to insure correct sexual selection in cases of sympatry rather than differences in the overt behavioral elements.

The maintenance behaviors of *Ateles* are similar to those of other Cebidae and Cercopithecidae. Locomotion by *Ateles* involves brachiation, a characteristic shared by the closely related *Lagothrix* and *Alouatta.* With the exception of the gibbon *Hylobates,* the siamang, *Symphalanges,* and the orang-utan, *Pongo,* which are members of the superfamily Hominoidea, the Old World primates have not evolved brachiation to such a high degree. *Ateles* shares with the cebid genera *Lagothrix, Brachyteles, Alouatta,* and *Cebus* the characteristic of a prehensile tail. This organ not only modifies locomotion, but it also is used to hold and manipulate objects. On the other hand the manipulative ability of *Ateles* is restricted when compared with other higher primates because of the loss of the all important thumb.

The movement and vocalization patterns occurring during social interaction present a special problem, since all movements performed in the vicinity of a partner may be of communicatory significance. The patterns of communication displayed by primates have been reviewed exhaustively by Marler (1965). Our findings for *Ateles* conform in broad outline to the findings of other workers in their studies of cebids and cercopithecids. We have approached the problem of communication by describing the sounds, movements, and postures which have an inherent communicatory value; however, information content can be rigorously established only when an outside observer can consistently correlate a presumed signal from a sender with a predictable response by a receiver. We attempted to employ this rigid criterion to the grimace, and, as demonstrated in table 1, the signal value or information content seems to alter with the experience of the interacting animals. Many presumptive patterns of communication are correlated with a given set of circumstances and may be called "situation-specific," but their information content is not firmly established (tables 3 and 5).

Andrew (1963 a, b) has discussed the origin and evolution of expressions and vocalizations in primates. He asserts that an expression does not necessarily reflect a specific emotional state of the sender. This would seem to be true for many expressions such as the grimace shown by *Ateles,* since it can occur when the animal is about to slap or when the animal is mildly disturbed and is tending to avoid contact. In either case the grimace often induces moving away or checks an approach. It is interesting to note that in *Macaca mulatta* the grimace is associated with avoidance and not with a potential attack. This has led Hinde and Rowell (1961) to describe this expression as a "fear" grimace in *M. mulatta.* These observations lead to a further conclusion which may be stated most simply: that similar expressions found in two or more species do not necessarily have the same presumptive information content.

Visual communication appears to be of potential significance in primates. The diversity of color patterns within the genus *Ateles* strongly suggests that these conspicuous markings act not only to promote species recognition but also as signals to permit visual contact when the animals are feeding and moving in the trees. Sexual dimorphism with respect to size or coloration is virtually absent in adult *Ateles.* Adult males are slightly larger than females but the pendulous clitoris of the female is a far more obvious visual signal which may permit recognition of the sexes at considerable distance. With the exception of the grimace and pursed lips, facial expressions are difficult to associate with any consistent stimulus situation. It would appear that a raised chin and a virtually closed mouth are the physical concomitants involved in producing loud, high pitched sounds with relatively pure harmonics. This facial expression is common during distance communication but also during nonagonistic contact. The pursed lips are associated with contact receptivity whereas the grimace is the antithesis of this expression, both in appearance and context. The open mouth without canine exposure does not appear to be an expression associated with an attack tendency, but the open mouth with canine exposure is associated with agonistic vocalizations and an attack or withdrawal tendency (table 5).

The facial expressions of *Ateles* are apparently not as rich as those shown by the genera *Cercocebus, Cercopithecus,* and *Macaca.* The eyelids are not contrastingly colored and the many expressions observable in certain species of Old World monkeys are lacking completely. However our descriptions of *Ateles* facial expressions fell within the general primate range as set forth by Van Hoof (1963).

Tactile communication appears to be facilitated by touch, embrace, grooming, anal-genital investigation and manipulation, and grappling. With the exception of the embrace and grappling activities, these are all common mammalian patterns. Chemical communication is strongly implied during the anal-genital investigation and the pectoral sniff. The presence of a pectoral gland lying at the top of the sternum has been described by Wislocki and Schultz (1925). The ritualized embrace-pectoral sniff implies a role for this gland as a mediator of chemical information, although the axillary glands may be equally or more important.

Auditory communication by *Ateles* appears to be well established for some sounds, especially the whinny, ook ook, squeak, and the high-intensity agonistic sounds such as the roar and cough. Rowell and Hinde (1962) divide the calls of *Macaca mulatta* into "harsh" and "clear" calls. As in *Ateles* many of the harsh calls are agonistic in their character, a trait also noted by Tembrock for a variety of mammals (Tembrock, 1959). However there remains the problem of the harsh calls which are obviously not entirely agonistic in *Ateles* and *Macaca.* It would appear that these calls involve other important parameters such as repetition rate and intensity that may be important in delineating the overall tonal gestalt to the receiving monkey. The auditory repertoire of *Ateles* consists of 16 sounds, including the discernible intermediate calls. Of these, 10 are frequently heard. This is a slightly lower number than the possible 20-30 calls which Rowell and Hinde postulate for *Macaca.* Schaller (1963) described 22 sounds for the gorilla (*Gorilla gorilla beringei*); however, only 8 of these occurred with any appreciable frequency. Carpenter (1940, 1934) describes 9 calls for the gibbon, *Hylobates lar,* and 20 for the howler monkey, *Alouatta palliata.* It would appear then that *Ateles* lies within the range of known primate "vocabularies."

As was indicated in table 6, overt aggressive behavior is exhibited with a very low frequency of occurrence. This is in marked contrast to baboon and macaque studies. Primary sexual behavior is also seldom observed and probably takes place at night. There are no ritualized mounting patterns employed in social control which are characteristic of old world macaques and baboons. Penile erection displays as noted for the cebid genus *Saimiri* (Ploog and MacLean, 1963) are also absent, but the male *Ateles* will exhibit an erection during precopulatory interaction. The signal value of this pattern has not been evaluated.

In concluding this discussion, the behavior patterns of *Ateles* will be contrasted with three orders of mammals which exhibit a range of behavioral adaptations and are sufficiently unrelated to provide a broad basis for comparison. For example, when one compares the maintenance behavior of *Ateles* with species of insectivores, carnivores, and rodents, several obvious differences are apparent. The movement patterns of *Ateles* have stereotyped elements but the elements are combined in a versatile manner. Stereotyped, complex sequences of cleaning movements found in rodents (Eisenberg, 1963; Bürger, 1959) are not present in *Ateles.* Rather, we find a stereotyped wiping and scratching movement utilized in a much less ritualized pattern. Locus specificity in urinating and defecation, so common in rodents, carnivores, and insectivores (Eisenberg, 1963, 1964), is lacking in *Ateles.* The stereotyped elements of behavior utilized by some rodents, carnivores, and insectivores in burrowing, nest building, and food caching are also completely lacking in *Ateles.* We find instead in *Ateles* and other cebid and cercopithecid primates a lack of many stereotyped sequences of maintenance patterns and a versatility with respect to those maintenance behaviors which they possess (table 7). When we turn to the social behavior patterns of *Ateles,* certain obvious differences set this and other primates apart from most rodents, carnivores, and insectivores. During an initial encounter, the spider monkey promotes contact by first reaching out and touching the partner and then embracing with a pectoral sniff. The embrace brings the animals face to face and the pectoral sniff evidently functions in chemical communication. Small rodents, carnivores, and insectivores being quadrupedal will generally initiate contact by touching noses (Eisenberg, 1963, 1964). Nasoanal patterns of contact are common to the spider monkey as well as small rodents, carnivores, and insectivores. During a male-female encounter, rodents typically further contact by the process of social grooming (Eisenberg, 1963); however, *Ateles* is not prone to groom during an initial contact. Although grappling, with sexual overtones, serves as a form of social interaction, social grooming in *Ateles* appears to develop out of a longer period of association than is the case with many species of rodents. As with all social mammals, *Ateles* exhibits contact-promoting behaviors during an encounter even in the absence of primary sexual consummation.

Referring again to table 7 it can be seen that *Ateles* and other higher primates differ from many small insectivores and rodents by the persistence of groupings of adults of both sexes; however, primate groupings do not generally exhibit a persistence of parental care by the male except for the marmosets, the Titi monkey, *Callicebus,* and the night monkey, *Aotes* (Grüner and Krause, 1963; Mason [pers. comm.]; Moynihan, 1964). Some male parental care

TABLE 7.—*Behavioral comparisons among selected mammals.*

Behavior Patterns	*Sorex vagrans*	*Perognathus parvus*	*Tamiasciurus* hudsonicus*	*Ateles* geoffroyi*	*Canis lupus*
1. Nest building	nest and tunnels	nest and tunnels	leaf nest and tree cavities	none	earth burrow
2. Cleaning movements	simplified	elaborate stereotyped	elaborate stereotyped	labile elaborate	elaborate
3. Caching food	some	elaborate	elaborate	none	some
4. Defense of an area by group or individual	nest defense	nest and burrow defense	nest and surrounding area	reduced tendency	social unit closed to outsiders
5. Social group composed of adults of both sexes which moves as a unit	none	none	none	present	present
6. Contact promoting behavior outside of the primary sexual behavior	none	none	none	elaborate	elaborate
7. Pair bonding	none	none	none	none	present
8. Provisioning of female and young by male	none	none	none	none	present

* Diurnal and arboreal

is shown by *Macaca fuscata* and *M. sylvana,* but this is in no way comparable to the previously mentioned neotropical genera. On the other hand, some rodents live in closed social groups or colonies and a few insectivores show persistent social groupings based on a family group structure (Eisenberg, 1965). Within the carnivora certain species such as the wolf, *Canis lupus,* form social groupings of adults of both sexes, and male parental care is exhibited by means of food provisioning. This latter trait is unknown among the infrahuman primates (table 7).

In conclusion then, it is not the case that a sharp dividing line separates primates from other mammals with respect to their social behavior. The primates exhibit, as a taxonomic order, all variations of sociality and, further, no linear evolution of sociality is distinguishable in any given family (Eisenberg, 1965). What appears to set many higher primates aside into a special category of sociality are the facts that adult males and females may move together as a unit and many higher primates have a rich repertoire of sounds and facial expressions with a presumptive communication function. However, the communicatory value of these sounds and expressions remains to be thoroughly investigated, and social groups of mixed sexes, although typical of higher primates, are not the prerogatives of primates alone within the class mammalia.

SOCIAL STRUCTURE IN A CAPTIVE COLONY

Introduction and Definitions

A colony of *Ateles geoffroyi geoffroyi* was studied in detail from July 1963 until March of 1964 at the municipal zoological park in Vancouver, British Columbia. The number of animals in the colony fluctuated from 14 to 16 in the course of the study. After some practice each animal in the colony could be identified by means of individual markings and expressions. A list of the animals, including pertinent age and sex class data is included in table 8. Three of the animals suffered from a malformation of the hind legs, probably as a result of a vitamin deficiency during critical growth phases. These animals, A, H, and J, are therefore not included in the locomotion analyses. There were 10 adult females; 4 of these (E, F, L, N) had an associated infant or juvenile. Two of the remaining 6 females (B and C) were judged to be old and perhaps postreproductive. The other 4 females (J, D, A, and I) were mature but not carrying infants; D, however, was judged to be less than 3 years of age. Two additional females were immature. M was an Infant-2* to Juvenile-1 in the course of the study. Female O was born during the study and passed from Infant-1 to Infant-2 before her death on February 29, 1964. There were 4 males of which only one, G, was an adult. Throughout most of the study K was a Juvenile-1, whereas H and X were designated Juvenile-2s. Male X died from a fall before the formal analysis was initiated.

TABLE 8.—*List of members of the zoo colony.*

Code letter	Sex	Age class	Remarks
A	female	adult	cripple, not *geoffroyi*, probably *vellerosus*
B	female	adult	no attached young
C	female	adult	no attached young
D	female	young adult	no attached young
E	female	adult	mother of H
F	female	adult	mother of K
G	male	adult	
H	male	juvenile-2	cripple
I	female	adult	no attached young
J	female	young adult	no attached young; cripple
K	male	juvenile-1-2	
L	female	adult	mother of M
M	female	infant-2 to juvenile-1	
N_1	female	adult	mother of O; designated N_2 after O's death
O	female	infant	born Nov. 1, died Feb. 29
X	male	juvenile-2	died Aug. 1963, before the formal study

Data were obtained by speaking into a tape recorder while observing the animals. The behavioral elements were coded and later transcribed onto sheets of paper employing a 10-second interval criterion for quantification (see Methods on page 3). In addition, actual durations of some acts were computed directly from the tapes. Two types of data were obtained: 1. Each animal was observed as an individual for 30 minutes during four separate periods of the day: morning, noon, afternoon, and during the late afternoon feeding period. This gave us 120 minutes of observations for each animal sampled during four distinguishable periods of the day. (2) Grouping data were recorded by sampling throughout the day and described the size and

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* Age classes as described by Carpenter, 1935.

individual composition of every discernible group. The recorded behavioral elements were defined in the same manner as those listed under the Behavior Patterns of *Ateles*. In addition, the following definitions were employed:

Grouped (Social)—the animal was moving interactively with other animals or resting in contact with, or resting while interacting with, other animals.

Alone—moving or resting free of contact with other animals and without mutual interaction with other animals.

Resting—maintaining a single locus for at least 2 seconds with no more than 2 seconds interruption at any one time. Changes of body position at a given locus could occur.

Moving—locomotion which changed the locus of the body by more than one body length or width, lasted more than 2 seconds, and was not interrupted for longer than 2 seconds.

Since only one adult male was present in the zoo colony (see pp. 29-30) most analyses of the behavior patterns refer to age classes. The term "young-free adult" refers to the adult male or a female without an attendant infant or juvenile. The terms "young-associated adult" or "mother" refer to a female with an attendant juvenile or infant (females E, F, L, N_1).

Locomotion and Activity Analysis

The data in table 9 clearly indicate that regardless of age, sex, or time of day the captive animals spent about 87 percent of their time resting. The length of uninterrupted rest averaged 8.67 10-second intervals, whereas the average length of time spent in continuous movement was slightly less then 10 seconds. The percent of the total time spent in locomotion for each of the five locomotion forms is presented in table 10. Quadrupedal climbing and running or walking were about equal in frequency and accounted for about 73 percent of all locomotion. Brachiation and bipedal walking comprised roughly 20 percent of the locomotion time, but females with infants walked bipedally only half as much as did those adults without a clinging infant. Infants and juveniles climbed more and scooted significantly more than did the adults. The bipedal walk was virtually absent in the juvenile and infant monkeys.

Self-Care Analysis

A full consideration of self care (grooming, scratching, and licking) is best deferred until the rank order is discussed. The

TABLE 9.—*Activity analysis.*

Category	Measure	Class	MNA	F
Resting	Prop	Y-fr	.884	.837
		M	.870	.830
		J & I	.910	.898
Moving	$\bar{D}$	Y-fr	10.40	5.28
		M	7.79	3.91
		J & I	10.59	10.03
	$\bar{D}$	Y-fr	1.00	.95
		M	.80	.76
		J & I	.74	.72

Probability of a difference between MNA and F or between animals in a class or between classes were greater than .10 and judged to be not significant.

Legend: Prop—proportion of 30 min. observation period. $\bar{D}$—mean number of 10 second intervals/30 minutes observation period. MNA—average for morning, noon, and afternoon periods. F—average for feeding periods. Y-fr—young-free adults. M—mothers. J & I—juveniles and infants.

amount of self grooming is, to an extent, inversely correlated with the amount of social grooming in which the animal engages. Higher ranking animals indulge in more social grooming and thus exhibit less self grooming. Table 11 presents the proportion of self-care behavior devoted to scratching and grooming. The average duration of a scratching bout is remarkably constant for all age and reproductive classes (4.0-5.6 sec.); however, the average duration for self grooming is quite variable (3.0-26.8 sec.). All animals spent less than 10 percent of their time engaging in self care. Scratching was the most frequent self-care pattern shown and accounted for roughly 70 percent of the total time spent in self care.

THE SOCIAL STRUCTURE

Given the definition of a social group in section A, exact records of the individuals composing a group were kept. It was therefore

TABLE 10.—*Locomotion analysis.**

	Quadrupedal					
Class	Plane surface	Climb	Jump	Scoot	Bipedal	Brachiate
Y-fr	.370	.357	.018	.026	.124	.106
M	.325	.407	.009	.067	.069	.124
J & I	.227	.369	.002	.299	.000	.102

* Figures represent the proportion of the total time spent moving.

possible to compare the proportional distribution of the observed group sizes with a proportional distribution derived from the supposition that grouping occurred with equal probabilities for joining or avoiding another individual or group of individuals (fig. 5). Before the death of infant O, the most frequently observed group size was four. After the death of O, the most frequently observed size shifted to three.

Table 11.—*Self-care analysis.**

Subjects	Scratching		Grooming		Pd T
Y-fr	Pd	$\bar{D}$	Pd	$\bar{D}$	
A	.70	4.0	.29	7.3	.090
B	.62	5.6	.38	13.8	.081
C	.79	5.3	.21	5.6	.051
D	.97	4.6	.03	3.0	.028
G	.87	5.0	.11	6.5	.040
I	.41	3.7	.59	26.8	.120
J.	.89	5.2	.11	6.1	.072
N_3	.76	5.1	.23	16.7	.090
Mothers					
E	.98	5.1	.02	5.0	.057
F	.99	4.5	.01	1.0	.067
L	.94	4.7	.06	3.2	.037
Inf. & juv.					
H	1.00	5.6	–	–	.036
K	.88	4.8	.12	13.0	.048
M	1.00	9.2	–	–	.051

Legend: $\bar{D}$—average duration in seconds of the specified act. Pd T—proportion of time spent for all observation periods in self care. Pd—proportion of the total duration of all self care for all observation periods.

* Licking has been left out and accounts for the remaining proportion.

The calculated maximum frequency of group size based on chance alone for the same two periods ranged from eight to seven. Clearly then the grouping tendencies were not based on a model which assumes a constant probability for joining regardless of group size. Further, if the identity of the individuals comprising a group of a given size were held constant and the frequency of occurrence of each combination calculated, then 50 percent of all constant composition combinations sighted were within the size range of two to four individuals. There are two other significant departures from a chance process of aggregation: 1. If we calculate the probability based on equal chance alone of observing only young-free adults or only young-associated adults in a group, we find that the observed combinations are not in accordance with an equal-chance model. There is a tendency for the young-free adults to form subgroups separate from the young-associated adults (table 12). 2. When large groups were formed in the cage, the females with young were present in these groups with a frequency exceeding that frequency calculated by assuming an equal chance process (table 13). Therefore we feel that group formation in this colony of *Ateles* was structured, and although the females with young tended to form a distinct subgroup, they also served as a focus to promote grouping whenever large numbers of animals began to join a resting group. The mothers

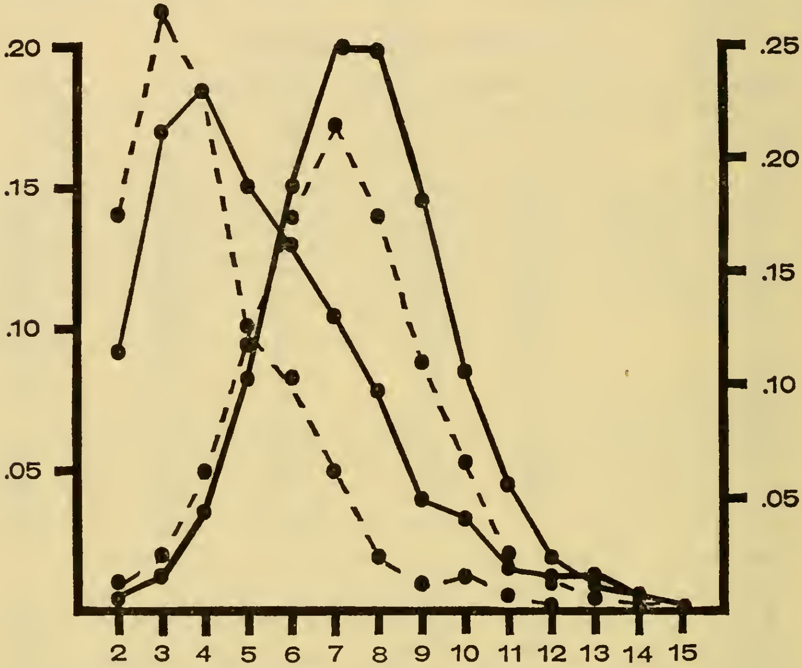

FIGURE 5.—Proportional distributions by sizes of possible and observed combinations for *Ateles* groups. Solid lines based on data before O's death; dotted lines represent theoretical and observed values after O's death. Theoretical values are based on a binomial expansion assuming an equal probability for joining or avoiding a group regardless of the group size. Graph was based on the following data: Before O's death, total observed combinations, 872; number of observation periods, 27. After O's death, total observed combinations, 415; number of observation periods, 15.

TABLE 12.—*Proportions of possible and observed combinations in each class of adults.*

Class	Possible		Observed	
	p	f	p	f
Young-free only	120	.004	56	.064
Mothers only	247	.008	57	.065
Mixed combinations	32385	.988	759	.871
Totals	32752		872	

Legend: p—proportion of total. f—frequency of occurrence.

may serve as a nucleus for grouping because they are less mobile; however, this assumption appears to be invalid because movement of females with young was equal to that of the young-free adults (table 9). We believe, therefore, that the mothers may promote grouping because they dispense a considerable amount of grooming to those animals which join their group, and equally important the mothers also receive grooming from many individuals (pp. 41-42).

Within the zoo colony certain grouping tendencies were observed more often than others. There were definite preferences and antagonisms which appeared to reflect a subtle series of dominance relationships. The animals were seldom overtly aggressive and fighting or chasing were infrequent. At the same time, one cannot say that the subjects were extremely demonstrative of interindividual dependency.

TABLE 13.—*Theoretical and observed probabilities of the presence of mothers in combinations of varying sizes.*

	Number of mother-infant pairs							
	All 4 pairs		At least 3		At least 2		At least one pair	
Group size	e	o	e	o	e	o	e	o
2	–	–	–	–	–	–	.038	.053
3	–	–	–	–	–	–	.114	.326
4	–	–	–	–	.004	.037	.224	.795
5	–	–	–	–	.022	.295	.360	.970
6	–	–	.001	.025	.064	.558	.506	.992
7	–	–	.006	.101	.143	.780	.652	1.000
8	.0001	.016	.022	.194	.263	.839	.781	1.000
9	.001	.050	.063	.350	.424	.875	.883	1.000
10	.007	.036	.145	.750	.608	1.000	.952	1.000
11	.026	.273	.219	.818	.798	1.000	.988	1.000
12	.077	.500	.508	1.000	.930	1.000	1.000	1.000
13	.200	.600	.771	1.000	1.000	1.000	1.000	1.000
14	.467	1.000	1.000	1.000	1.000	1.000	1.000	1.000
15	1.000	–	1.000	–	1.000	–	1.000	–

Social grooming was of minor importance in the life of an individual *Ateles* when compared with the social grooming activities of macaques and baboons.

In order to determine the differences in social responsiveness for each individual within the colony, the data were analyzed and all two-animal encounters were abstracted. Whenever two animals interacted outside a defined group their behaviors when approached were categorized either as "Avoid" or "Stay." From these data two calculations were made for each individual, giving numerical results which are termed the induction ratio and the response ratio. The response ratio represents the number of times the approached animal moved away, divided by the total number of times it was approached. The induction ratio represents the number of times the approaching animal caused a second animal to move away, divided by the total number of times the approaching animal initiated a contact. Thus a low response ratio indicates that the subject moved away seldom when approached, whereas a high induction ratio indicates that the subject often elicited avoidance when it approached another. Table 14 summarizes the ratio for each individual adult. The adult male, G, had the highest induction ratio. Almost one half of the subjects he approached moved away. The remaining adult females have remarkably uniform ratios and indicate no significant rank order. When one considers the response ratio, some differences occur. The

TABLE 14.—*Response and induction ratios for the adults.*

Response ratio			Induction ratio**		
Subject	Ratio	n	Subject	Ratio	n
*N_1	.00	13	G	.43	43
*L	.08	66	*F	.26	42
G	.13	30	D	.25	64
*F	.16	36	C	.24	34
C	.18	28	*E	.23	62
I	.25	36	A	.21	43
N_2	.31	19	B	.21	24
*E	.31	36	N_2	.21	29
B	.33	57	I	.20	41
J	.36	45	J	.19	26
A	.39	23			

* Mothers. Note E's baby (H) is a juvenile-2 and the most nearly independent of the four.

** L and N_1 were omitted since number of encounters were too low for significant computation. Criterion for inclusion was at least 25 encounters.

adult male G, the older female C, and the three young mothers are not prone to move away at the approach of another animal. Female I seems to fall intermediate between the preceding category and the second category of females with nearly grown (E) or no young (N_2, B, J, A, and D). This latter series has a uniformly higher tendency to move away when approached. Using the response ratio as the sole criterion for determining a dominance order would be fallacious, since the induction ratio already suggests quite a different interpretation from that of the response ratio. We believe that the simultaneous integration of several behavioral measurements is a necessary procedure and therefore postpone further discussion along these lines until page 41.

TABLE 15.—*Summary of adult two-animal interactions for the Ateles colony.*

Responder	A	B	C	D	*E	*F	G	I	J	*L	*N_1	N_2	Σ_1
A	–	1,4	1,0	4,5	0.1	1,2	0,0	2,8	2,4	1,9	0,0	0,1	45
B	8,1	–	0,5	2,2	0,2	1,2	0,2	1,0	2,1	0,1	0,2	0,1	33
C	0,0	1,2	–	0,2	3,1	1,9	0,4	1,0	2,1	0,4	0,3	0,0	34
D	3,4	6,9	1,5	–	5,8	0,0	3,8	1,1	2,9	0,3	0,3	0,0	71
*E	2,4	2,6	1,2	9,6	–	0,1	1,4	1,4	1,3	0,7	0,2	4,7	68
*F	2,1	2,5	1,5	2,2	2,0	–	0,2	2,8	0,2	0,3	0,1	1,1	42
G	1,0	6,2	1,1	1,0	1,2	3,4	–	2,3	2,3	2,4	0,0	1,1	39
I	0,3	0,1	0,1	3,3	0,1	0,5	0,1	–	5,2	1,4	0,1	0,1	33
J	0,2	0,4	0,1	4,1	1,3	0,0	0,1	0,0	–	0,8	0,1	0,0	26
*L	0,0	1,1	0,0	2,0	1,1	1,1	0,2	0,1	2,3	–	2,0	0,0	17
*N_1	1,0	0,0	0,2	0,0	0,2	0,2	0,0	0,0	0,0	1,12	–	0,0	20
N_2	1,0	1,4	0,1	4,1	12,4	1,4	0,2	0,2	3,1	1,4	–	–	46
Σ_2	32	58	28	53	49	38	30	37	50	65	13	21	–

Legend: Numbers refer to: left entry—total move away and flee; right entry—total stay responses.

* Mother.

Σ_1 Sum of all approaches or chases involving the given animal.

Σ_2 Sum of all responses for the given animal.

There were differences in the intensity and form of interaction when one inspects each possible class of two-animal encounters. Table 15 summarizes the data for all two-animal interactions where the interacting individuals were outside any defined group. Chase-flight patterns as well as moving-away patterns are included in this tabulation. The negative relationships included a persistent antagonism for: B to A; E to D; N_2 to E; G to B. These data only partially reflect direct unquantified observations of these relationships. Definite preferences included the following: 1. "mother" associations E to L, N to L; 2. female associations A to I, A to L, C to F, D to J, E to B, F to I, J to L; 3. male-female associations D to G. Female E and D initiated the most approaches; conversely, females B, D, E, J, and L received the most approaches.

When one analyzes the data for pectoral sniff and social grooming, additional inferences can be made concerning the social structure. Table 16 summarizes the data for two types of pectoral sniff, mutual and individual. In the latter case the act was performed by the initiator. Male G and female F were involved in the greatest number of pectoral sniffs. Female A, who was an outcast in many respects, received the least number of sniffing interactions. It is worth noting that after N lost her baby she dropped to a small number of sniffing interactions. Of additional interest is the fact that female B sought out male G on three occasions to perform a pectoral sniff and yet throughout the course of the study male G tended to respond negatively toward her.

TABLE 16.—*Frequency of engagement in the pectoral sniff.*

		Individual sniff		
Subject	Mutual sniff	Initiator	Recipient	Total
A	1	0	0	1
B	4	3	1	8
C	5	1	1	7
D	4	0	2	6
*E	2	1	2	5
*F	9	2	3	14
G	7	2	3	12
I	6	2	0	8
J	2	1	1	4
*L	3	3	2	8
*N_1	4	0	2	6
N_2	1	2	0	3

* Mother.

An examination of the grooming relationships yields more evidence for the existence of a social rank order. Figures 6 and 7 attempt to indicate several trends. Although not highly significant, figure 6 suggests that as an animal gives more grooming it is liable to receive more in return. Figure 7 indicates two possible trends: 1. within all observation periods as the total duration of social grooming decreases for an animal, the total duration of all self-grooming increases. 2. in a similar manner, as the total duration of social grooming received decreases, the total duration of self-scratch periods increases. With this in mind an analysis was run on the relation among the duration of social grooming given, the duration of social grooming received, and the number of different individuals from which a subject received grooming. Table 17 summarizes the results.

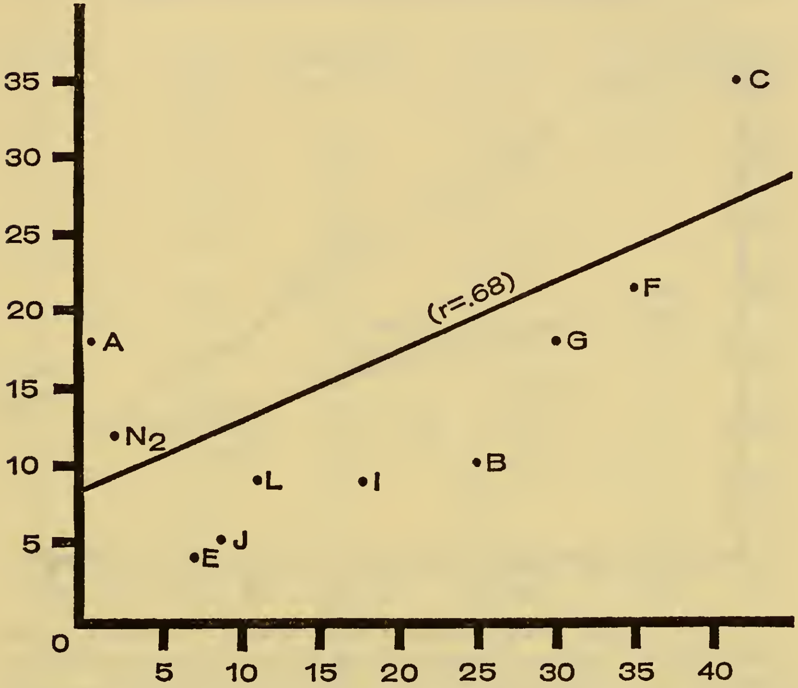

FIGURE 6.—Relation between amount of social grooming received and amount of social grooming given. Ordinate—total amount of social grooming received; abcissa—total amount of social grooming given. Units indicate number of 10-second intervals corrected to nearest five seconds. An *r* of .68 is significant at the .05 level of confidence.

In this table the animals are listed provisionally according to the rank order determined by the response ratio in table 14. The juveniles and infants are included in an arbitrary order after the adults. It can be seen that in terms of the total time spent in giving grooming to another, the top ranking mothers (L, M) and adults C and G dispensed the most grooming. When a grooming ratio is calculated by dividing the time spent receiving grooming by the sum of the total times grooming was given and received, the mothers and top ranking adults (C and G) have low ratios. The mothers L and F have ratios less than .50 when their infant grooming is excluded, which indicates that they give more grooming than they actually receive. Animals receiving a great amount of grooming included the infants and the low ranking females A, B, and N_2. The ratios of J and D are out of line with their response rank and this may be a result of their relative youth. A further discussion of this point will follow. It is also interesting to note that female E with her almost-grown juvenile does not rank with the mothers L and F. It would be interesting to know if a female's status changes with the change in her reproductive state, but the data on N, before O's death, are insufficient for a comparison with the subsequent rank of N. Such data as are available indicate that N had a high grooming ratio even when she was carrying O.

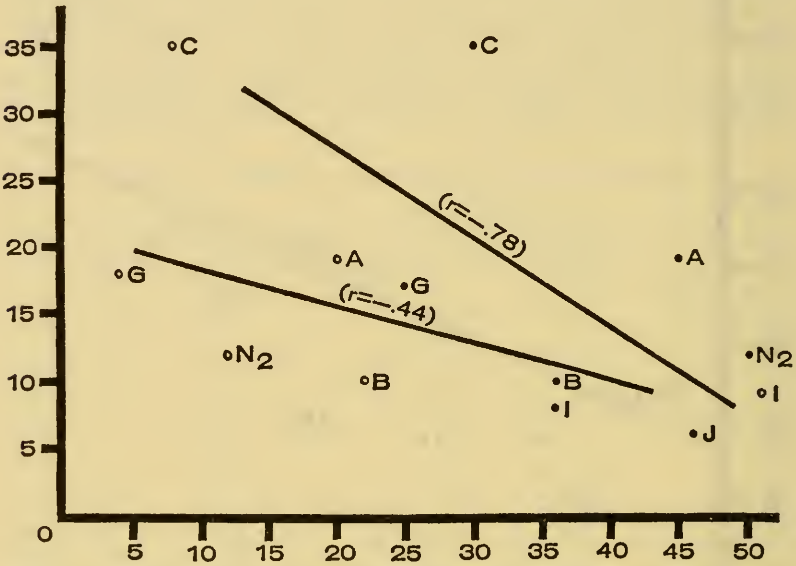

FIGURE 7.—Relation between amount of social grooming received and amount of self-care given. Ordinate—total amount of social grooming received; abcissa—closed circles: total amount of scratching; open circles: total amount of self-grooming. Units as in figure 4. An *r* of —.44 is not significant but an *r* of —.78 is significant at the .01 level.

The last column in table 17 indicates how many different individuals were groomed by, and how many individuals gave grooming to, a given subject. The low ranking females and infants gave grooming to few animals. The high ranking adults (C and G) groomed many individuals but received from only a few. The mothers L and F gave to many and received from many. The data describing interindividual relationships are summarized in figure 8. This is a sociogram modeled after those of Kummer (1957). In this diagram, male G and female C have been placed in the top category and the mothers in the second category. This change in rank order is consistent with our interpretation that the response ratio does not completely reflect the "relative rank order" but rather that the rank, based on the high number of animals groomed, coupled with a low number of animals received from, does reflect a consistent order. When the animals are arranged in order, based on a consideration of the response ratio and the number of animals from which grooming was received, there is a general

TABLE 17.—*Response ratio and grooming correlations.*

Subjects	Response ratio	Total seconds grooming given	Grooming ratio	No. of individuals	
				Groomed	Groomed by
*N_1	.00	–	.758	3	3
*L	.08	304	.232	6	5
		(192)	(.324)		
G	.13	175	.498	8	3
*F	.16	693	.230	9	6
		(335)	(.361)		
C	.18	416	.455	8	2
I	.25	175	.346	4	3
N_2	.31	15	.888	3	3
*E	.31	71	.333	2	3
		(15)	(.706)		
B	.33	25	.800	1	4
J	.36	85	.418	4	4
A	.39	0.0	1.00	0	7
D	.45	35.1	.373	3	4
O	–	0.0	1.00	0	3
M	–	76	.666	3	2
K	–	11	.971	2	3
H	–	0.0	1.00	0	5

Legend: ( ) includes corrections for mothers where infant-mother grooming has been subtracted.

* Mother.

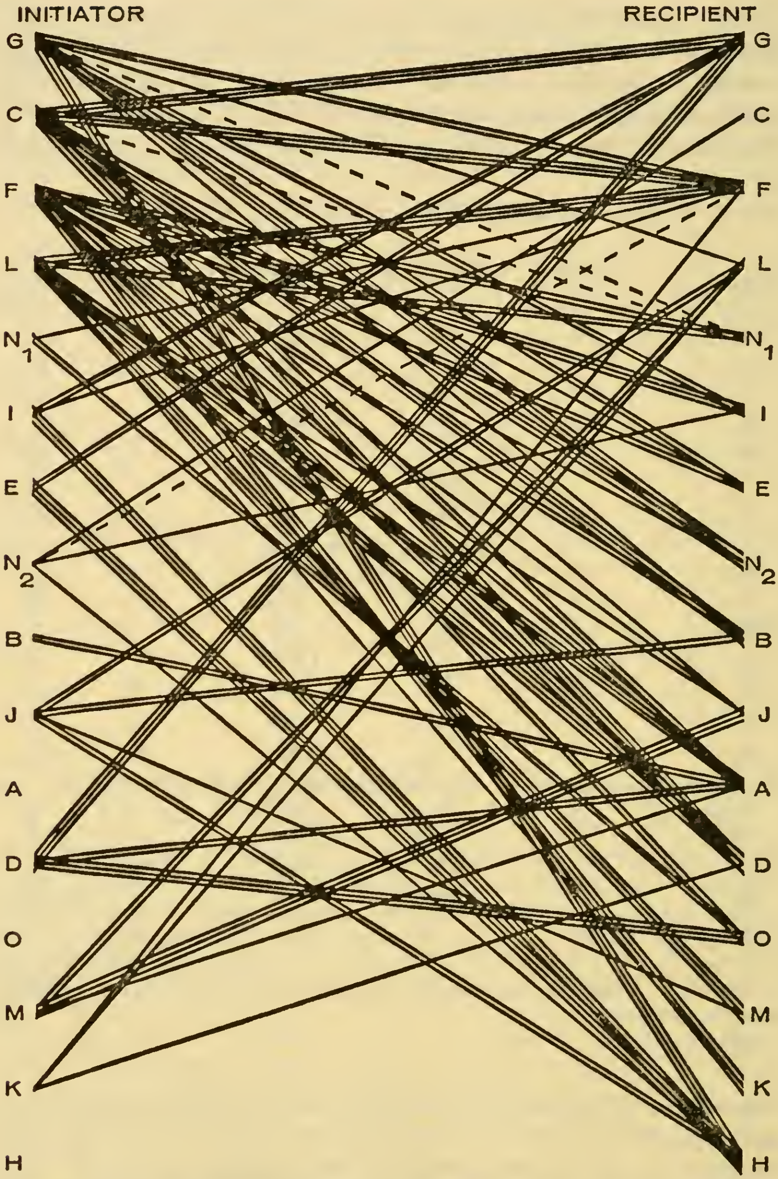

FIGURE 8.—Grooming relationships in an *Ateles* colony. Letters refer to the individual specimens. The left column indicates the groomer; the right column designates the recipient. The lines indicate cumulative durations of grooming. Dotted lines refer to less than 5 seconds. One solid line indicates more than 5 seconds but less than 10. Two lines indicate on the average 10 to 45 seconds, and three lines indicate 50 to 400 seconds. These solid lines correspond roughly to a frequency of 1, 2 to 6, and 7 to 20 times.

trend indicating that higher ranking animals groom lower ranking animals more frequently than the reverse situation.

The facts that the mothers consistently give more grooming than they receive and are less easily displaced contribute to their rather high position in the determined rank order. Mothers may be, on the other hand, somewhat outside the typical adult rank order in a manner similar to mother langurs, *Presbytis entellus,* discussed by Jay (1963). This sociogram shows a clear trend in that higher ranking tend to groom lower ranking animals with the greatest frequency.

TABLE 18.—*Noninclusion in large groups.*

	Frequency for the group sizes					
Subjects	10	11	12	13	14	Total
G	9	3	2	3	0	17
C	14	1	0	0	0	15
*L	5	2	0	0	0	7
*F	9	3	0	0	0	12
I	11	6	2	0	0	19
*E	12	1	0	0	0	13
*N_1	5	2	1	1	0	9
B	11	4	5	4	1	25
J	13	4	2	0	0	19
A	20	7	4	2	0	33
D	13	5	2	0	0	20
O	5	2	1	1	0	9
M	3	2	0	0	0	5
K	8	3	0	0	0	11
H	13	3	2	1	0	19

Observations based on: 27 occasions; 52 combinations; 56 sightings.
* Mother.

G and C formed a grooming relationship, and the only consistent transgression of rank occurred when infants or juveniles groomed high ranking individuals. Since female D consistently displayed this juvenile tendency, we conclude that this reflects an incomplete socialization by a young animal as was found by Kummer for his young juveniles in a *Papio hamadryas* colony (Kummer, 1957).

An analysis was undertaken in order to determine the degree of absence from large groups. We reasoned that as a group becomes very large there would be a pronounced tendency to join the group and exclusions would be equally improbable for all animals in the colony. An inspection of table 18 indicates that such was not the case. The mothers were almost always in the larger groups as were their infants. The young-free adults and juveniles were less prone to be found in large groups. The most frequent absences from large groups included the juvenile male H, the low ranking females A and B, and the adult male G. In view of G's otherwise high status we are led to conclude that perhaps adult males are less bound to core groups (pp. 53-55).

A final analysis was undertaken to determine the effect of feeding on the tendency to group. It was found that at feeding time the young-free animals were less grouped during the 30-minute observation period, but the tendency to be alone fell off at the end of 20 minutes (tables 19 and 20). A similar trend existed for the mothers but it was not significant.

TABLE 19.—*Sociality at feeding time.*

Category	Class	MNA	F
Proportion of 30 minute period(s) social	Young-free Adults	.581	.230*
Average duration of 30 minute period(s) social	do.	18.99	3.50*

Legend: MNA—Morning, noon, afternoon. F—Feeding.
* Significant at the .01 level.

TABLE 20.—*Average number of seconds alone throughout the feeding period.*

	Quarters			
Class	First	Second	Third	Fourth
Young-free adults	294	339	340	198
Mothers	103.3	85	168.9	38.3

SUMMARY OF THE DIFFERENT ROLES AND RELATIONSHIPS WITHIN THE ZOO COLONY

THE MATERNAL-YOUNG RELATIONSHIP

Mother and infants show a close bond. The infant clings to the female's ventrum for about the first 4 to 5 months of its life. Gradually the infant begins to ride on the female's back and is carried for another 1 or 2 months. During this stage of life the infant (*geoffroyi*) has a dark, dusky pelage which changes to the adult bicolor pattern toward the end of its first year. Following Carpenter's (1935) terminology we have designated young animals as a Juvenile-1 when they are in the transition phase of coat color and Juvenile-2 at the stage of adult pelage. Male H was a Juvenile-2 during most of the study and figure 9 indicates the percentage of time he spent with his mother, female E. His average of approximately 20 percent is in marked contrast to Juvenile-1 K and Infant-2 M, who were bound to their mothers 85 percent of the time.

The infants nurse from the mother and are groomed in turn by the mother and other associated females. An Infant-1 may be carried by other females but this was observed only once. Juveniles and Infant-2s groom themselves, their mothers, and associated animals.

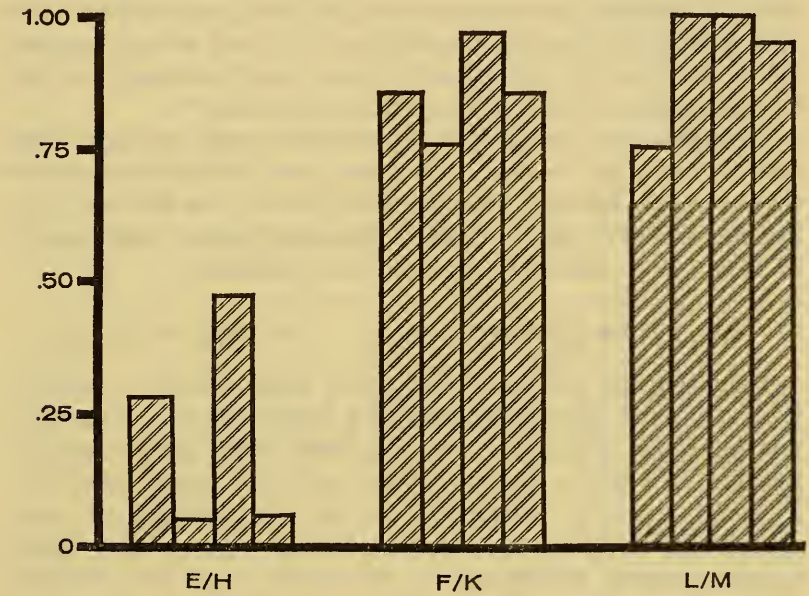

Figure 9.—Percent of total observation period in which the infants were associated with their mother. The four separate divisions for each of the three mother-infant pairs refer to the morning, noon, afternoon, and feeding periods of observation.

THE ROLE OF FEMALES WITH YOUNG

Mothers are characterized by moving away less when approached. This does not seem to be correlated with a high dominance status since they induce little moving away. Mothers with young infants spend more time grooming other animals than they do grooming themselves. This probably results from an overall increase in their grooming tendency as a result of the stimuli from the infant. Mothers dispense grooming to and receive grooming from several other adults. The mothers with infants are prone to form a separate subgroup but this subgroup evidently promotes grouping by other animals. In short, within the zoo colony the mothers act as group promoters.

THE SOCIAL ROLE OF THE ADULT MALE

Male G appeared to enjoy a status only approximated by female C. As discussed previously, G and C shared several social traits which led us to consider them the top animals in social rank. The male groomed many individuals but received grooming from just three animals: female C, his coequal; young female D, and female F. The male induced the maximum moving away and was not a group promoter. He was often found outside large social groupings and may be considered less bound to the core "mother-group."

Attempts at the introduction of new adult males into this colony have indicated that several adult males cannot tolerate one another without severe fighting. Crandall (1964) comments that successful breeding groups of *Ateles* cannot be maintained without a high number of adult females relative to the adult male population.

THE RELATIONSHIPS AMONG YOUNG-FREE FEMALES

The young-free females exhibit a loose dominance order. Motherhood appears to alter the behavior of a female but we cannot say if females revert back to an original status after their infant has matured. We believe that motherhood confers a greater stability on a female's status by virtue of the fact that she associates with other mothers and is less easily displaced by the approach of a second animal; however, maintenance of an original status may definitely occur as was suggested by the data from N before and after her infant's death (table 17).

THE SOCIAL STATUS OF THE JUVENILES AND YOUNG ANIMALS

The juvenile male H ranked very low in the social order and did not enjoy social mobility as did the postjuvenile female D. It is noteworthy that H was roughly groomed and played with by many of the older young-free females. H rarely approached the adult male G. Juvenile and postjuvenile male mortality is high in this colony and no young males have survived to adulthood. This is surely caused by a heightened social tension in the confined area of the zoo colony.

The young females as typified by D evidently enjoy an undefined social status until they reach puberty. The exact age of sexual maturity for females is not known, but the evidence suggests that 3½ years is approximately correct.

Discussion

A comparison of *Ateles* with *Papio* and *Macaca* is appropriate since the latter two closely related genera are distantly related to *Ateles* and have been well studied in both the field and under captive conditions. *Ateles geoffroyi* does not exhibit ritualized presenting, as an appeasement gesture, or ritualized mounting as an exhibition of dominance as do *Macaca mulatta* (Hinde and Rowell, 1962; Altmann, 1962; and Carpenter, 1942) and *Papio hamadryas* (Kummer, 1957). Ritualized brow-raising, floor-slapping, and neck-biting shown by *Papio* and ritualized lip-smacking exhibited by *Papio* and *Macaca* are also absent in *Ateles*.

In general one could say that overt aggression and sexuality were more reduced in the *Ateles* group than was the case in the *Macaca* and *Papio* groups studied by Altmann and Kummer. Although relative dominance is a function of age, sex, and reproductive state, a strict linear dominance order in *Ateles* cannot be defined. One can describe a rather loose rank order between and within given age or sex classes only by utilizing several different behavioral measures. The adult male *Ateles* did not serve as a focus for controling group activities. He was not sought out by frightened animals as was the case in the *Papio* colony studied by Kummer. On the other hand, he would occasionally approach two fighting animals, generally causing the fight to terminate, but he did not overtly assert himself with ritualized neck bites as did the dominant male in the *Papio* study.

THE BEHAVIOR OF FREE-RANGING SPIDER MONKEYS

Introduction

Carpenter (1935) conducted a 7-week field study and survey of *Ateles geoffroyi panamensis* in Panama. Within one observation quadrant at least four distinct groups were noted with a total population of approximately 100 animals. One typical group contained 33 animals that utilized in common the same trails, feeding sites, and sleeping trees within a given area. Carpenter noted that a given group tends to subdivide into subgroups ranging in size from 3 to 17 animals. With respect to age and sex composition, the subgroups could be divided into four types: all male, several mothers and their young, a single mother and her offspring, or a group of several females and their young, plus one or more males. Within the total population, adult females outnumbered the adult males. The evidence strongly suggested that adult males are in part intolerant to one another when they accompany sexually mature females.

Wagner (1956) reported on *Ateles geoffroyi vellerosus* in Chiapas, Mexico. He concluded that the social structure of spider monkeys varied, depending on the hunting pressure and food supply. His populations in undisturbed habitats tended to exhibit a family group structure with one adult male and one or two adult females with their juvenile and infant offspring comprising a cohesive social unit.

In order to confirm and clarify these observations on *Ateles,* two preliminary field studies were undertaken. In 1964 and 1965 the senior author spent a total of 8 weeks in Panama studying the behavior of an introduced group of *Ateles* on Barro Colorado Island. In addition, in 1965, 8 days were spent in the west coastal mangrove region of Chiapas in order to census a wild population of *A. geoffroyi* living in a habitat conducive to the formation of small groups.

Patterns of Behavior in an Artificial Group

INTRODUCTION AND METHODS

In 1960 and 1961 several attempts were made to introduce post-juvenile specimens of *Ateles geoffroyi panamensis* on Barro Colorado Island in the Canal Zone Biological Area. One group of four females and a male has established itself. And in the spring of 1966 each of three females bore one young. The group was initially provisioned but now derives almost all of its food independently, and although exceedingly tame, the animals move freely and are quite independent of man. This group was selected for a preliminary study because it permitted almost continual contact by a human observer. This is not, of course, a "natural" group, but it did serve as a partial control for our captive observations.

Intensive field observations were made during a 4-week period from May 17, to June 11, 1964, and in 1965 supplementary observations were made from July 19 to August 8. Handwritten notes of the behavior patterns were taken down and the feeding, sleeping, and resting areas as well as the paths of movement were indicated on sketch maps. In addition the following technique was adopted to permit a quantification of the gross activity patterns. Four categories of activity were defined: moving, resting, feeding, and playing. For the purposes of this study, tagging, chasing, and grappling were lumped into the category play. This introduces a degree of imprecision, but these adult females did exhibit a certain amount of behavior generally found only in juveniles. To facilitate recording, the artificial category play was adopted.

Using a stop watch, the activity of the group was censused every minute, and the number of animals engaged in each activity was recorded in this fashion, including at least four periods of observation for each hour of the day beginning at 0600 and ending at 1900. The average number of monkeys in sight during a given minute equalled 3.0. On four mornings the animals were followed from their sleeping tree and on four evenings the animals were observed until they came to rest in a sleeping tree. Aside from distinguishing the male and one female, the other three animals were not individually distinguishable with any accuracy.

GENERAL ACTIVITY

As indicated on page 23, the most frequently observed behaviors in captivity were also observed in the field. The females engaged in embrace and pectoral sniff, grappling, grooming, and chasing. Locomotion by climbing, bipedal walk, brachiation, and quadrupedal walk were all observed in approximately the same proportions as was the case in the captive colony. Vocalizations and their contexts have already been discussed on pp. 11-16. It is noteworthy that this tame group did not often exhibit the barking responses to human observers which is so characteristic of wild troops (Carpenter, 1935; Wagner, 1956). Only once did the group bark at an observer and this occurred early in the morning when their arousal was being observed.

TABLE 21.—*Activity analysis for free-living Ateles.*

	0600 through 1800 hours												
Category	6	7	8	9	10	11	12	13	14	15	16	17	18
Rest	.00	.43	.43	.34	.50	.61	.67	.58	.92	.37	.17	.11	.22
Move	.35	.16	.40	.29	.30	.30	.13	.30	.07	.23	.36	.13	.28
Feed	.65	.26	.15	.24	.04	.09	.00	.12	.00	.29	.34	.65	.61
Play	.00	.15	.02	.13	.06	.00	.20	.00	.01	.11	.13	.11	.00

The quantitative data on activity are presented in table 21. It is evident that the animals have two primary peaks of feeding activity: an early morning peak from 0630 to 0730, and a later afternoon peak from 1600 to 1830. Resting, consisting of sitting or hanging by the tail, reached peak values at 1200 and 1400 hrs. Movement, either directed or shifting in the same tree, was distributed evenly except during 1400 hrs. Play behavior was common during and after feeding in the morning and in the afternoon. From dawn to dusk the animals spent their time in the following proportions: .25 moving, .40 resting, .26 feeding, and .09 playing. Compared with the zoo colony the free-living animals were at least twice as active.

RESPONSES TO THE ENVIRONMENT

Figure 10 indicates the major patterns of movement and the major areas of utilization within the group's home range during the 1964 study. At least three sleeping trees were used and the animals moved out from these trees and spent the rest of the day foraging and resting. Certain trees which were in fruit served as loci for sustained feeding behavior. A definite trail stereotypy was shown and the same branches were used over and over again as the animals passed to and fro. The animals frequently crossed the two streams in their home range. Definite crossover points were used and in one case a palm tree was used to swing on, over a small ravine. This palm had been used so often that it was permanently sprung out of line. The palm crossing discussed previously is one example of the utilization of the elasticity of branches in order to gain momentum when leaping. A frequently employed technique involved jumping up and down on a limb while hanging onto a second branch with the tail. After several jumps the tail hold was released and the leap combined with the rebound of the branch contrived to impart a great deal of force to the jumping animal.

The animals were strictly diurnal. Dawn occurred at about 0530 and sunset at 1830. Four arousal times ranged from 0550 to 0645 whereas settling generally occurred from 1820 to 1835. Rain had an overall effect of depressing activity. Late afternoon showers caused the animals to move from the crowns to the understory of the trees. During severe downpours the animals moved close to the trunks of trees and huddled in groups of two or three. They often responded to the sound of an approaching shower with roars and increased activity. If the animals became wet or moved during a light shower they wiped and scratched continually at their fur. Wiping movements ranged from 27 to 39 strokes per minute when an animal's fur became soaked.

The choice of food trees appeared to be largely a function of habit and a matter of which trees were fruiting. In addition to an unidentified fungus the animals fed most frequently on the pods of

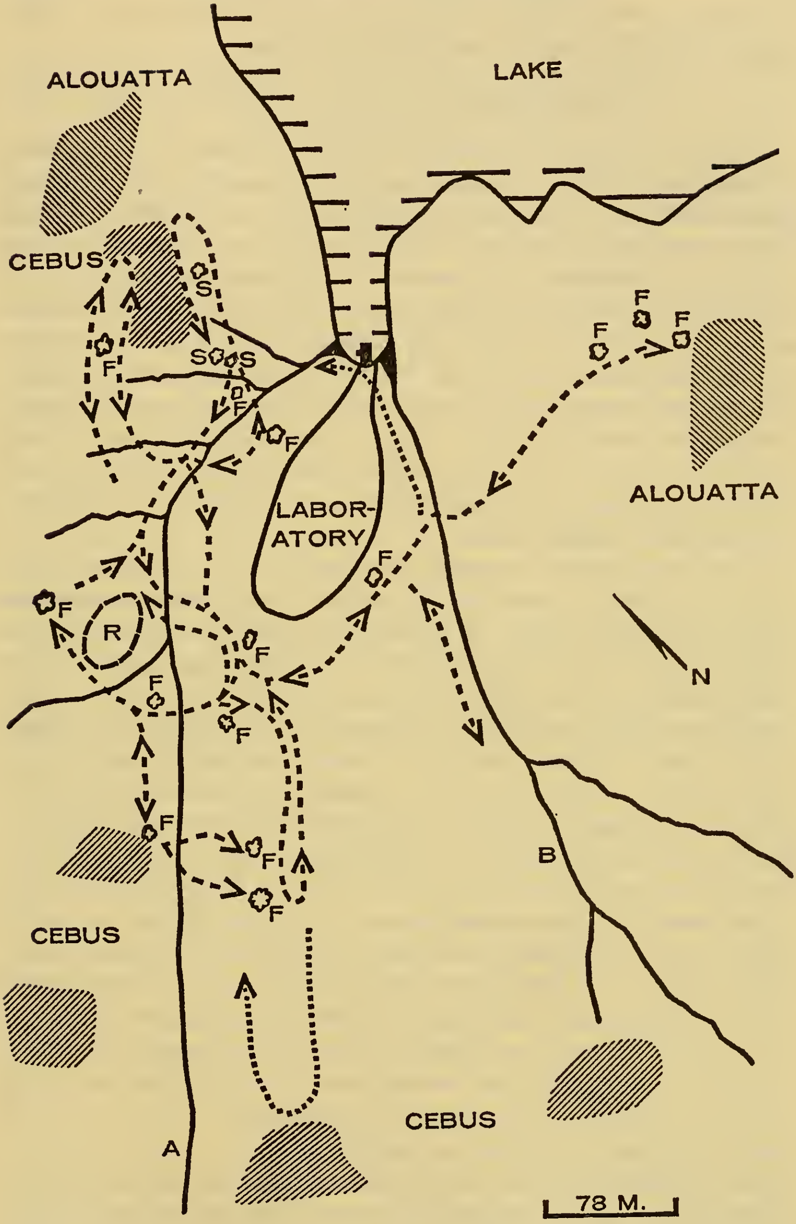

FIGURE 10.—Major routes for the free-ranging *Ateles* troop. This map indicates the major movement patterns of the *Ateles* troop. A and B refer to the two canyons flanking the laboratory clearing (lab). R indicates the primary midday resting area. Partial ranges of neighboring cebus and howler troops are indicated by crosshatching. Food trees are designated F and sleeping trees S.

Cecropia sp. and *Anthodon panamensis,* and on the fruits of *Ficus* sp., *Enocarpus panamensis,* and *Mangifera indica.*

RESPONSES TO OTHER SPECIES

Carpenter (1935) and Wagner (1956) have described the responses of free-living *Ateles* to the approach of a human observer. Barking, branch-shaking, breaking branches, dropping branches, and defecating are common responses, but the half-tame group observed for this study was so habituated to humans that it displayed barking only once and branch-shaking by the male on only two occasions. Specimens of *Cebus capucinus* and *Alouatta palliata* were frequently contacted by the *Ateles* group. On several occasions the spider monkeys fed in the same tree or very near a howler troop with no apparent interaction. The spider monkeys were seen on four occasions feeding in the same tree as the capuchins but again no interaction took place. One morning the spider monkey group appeared to be moving with or in the same direction as a capuchin troop.

In addition to these neutral relationships there were several instances of positive interaction as well as overt agonistic responses which are worth relating. A solitary male howler was observed for 2 days in A canyon (figure 10). This animal slept alone on one night and appeared to be detached from the main howler group which was living farther up the hill. A female *Ateles* contacted the animal on both days. On the first day a female approached, touched, and embraced the howler. The initial embrace was followed by about 8 minutes of interaction during which time the female repeatedly approached and withdrew, often tagging or pulling the howler's tail. The howler eventually moved off. On the second day the female was again observed to approach the howler—this time without an embrace—and engage in tagging. At one point she bit his tail, whereupon the howler roared and chased her for some distance. The howler was not observed thereafter in the well-utilized part of the spider monkey's range. During late June 1964 a female spider monkey was seen carrying an infant howler monkey. How she acquired the young animal was not determined, but she continued to carry it for several days until it died of apparent malnutrition.

The relationship of the five spider monkeys to the neighboring *Cebus* troops was exceedingly complex. On one occasion in a peripheral section of the home range the male *Ateles* was observed to leave the four females and actively follow a *Cebus* band moving to a new feeding area. On another occasion a *Cebus* troop was passing single file along a branch which was serving as a sunning perch for a female spider monkey. The female did not move but continued to remain in a prone position while three juveniles paused and in succession groomed her for periods of 1 to 3 minutes. Although the females were generally tolerant of neighboring *Cebus* monkeys, on four recorded occasions the spider monkeys engaged in bouts of chasing and roaring with the *Cebus*. The most prolonged bout in 1964 occurred on June 1 when the male was with the female group. The area of conflict was one in which the *Cebus* had never been seen before and was generally used by the *Ateles* for feeding in the late afternoon. From 1706 to 1715 the *Ateles* interacted by chases and roars with the *Cebus*. The male was the most prone to chase and by 1720 the *Cebus* had departed. About 1735 three juvenile *Cebus* returned to the area and fed unmolested.

Carpenter (1934) mentions the tendency for *Ateles* and *Cebus* to form temporary mixed species groups when feeding. This habit of interspecific association should be investigated in much greater detail with natural populations before definite conclusions can be drawn. It may well be that troops of different species, such as *Cebus* and *Ateles*, can share areas of their home ranges and even move together; however, it appears from these data that the novelty of finding other animals in a heavily utilized portion of the home range can result in agonistic interactions.

The *Ateles* were also observed to interact with the semiarboreal coati (*Nasua narica*) and tayra (*Eira barbara*). A solitary male coati was "teased" for several minutes as he climbed—one female hung above him tagging at his tail. The male and four females responded to two courting tayras in quite a different fashion. Initially they barked for approximately 20 minutes while moving in the branches directly above the two animals. The male would descend to within a few feet causing the tayras to growl and hiss. Even after the barking response had ceased, the spider monkey group continued to observe the tayras and remained in the same tree for over 40 minutes.

On one occasion the female spider monkeys were in the same tree observing a three-toed sloth (*Bradypus tridactylus*). The sloth was moving and attracted the attention of two animals which approached and hung above it. At no time did they attempt to touch or slap at it and after several minutes they moved on.

SOCIAL RELATIONS

The four females were extremely cohesive in their movements. They slept together in the same tree, played in groups of two, three, or four, and were slightly scattered only when resting or feeding. Even during these latter periods they were in vocal contact. When moving, the leading animal's movements were copied by the followers, especially at crossing points and often with respect to routes along specific tree branches. Assistance was rendered at crossings and two examples are noteworthy. In one instance a female had successfully bridged a gap between two branches and then turned to confront the following female. The follower made several attempts to reach across and then uttered several low squeals. The lead animal reached out, while holding the branch with her tail, and the animals grasped each other's arms. The follower then released her tail hold and swung across. Immediately after reestablishing footholds the animals embraced and mutually gave a pectoral sniff. In a second instance the lead animal reached across a gap and held onto the last branch with her tail. The follower then crawled across the bridge formed by the first animal's body.

Play was common in the female group and almost always involved grappling followed by growls and chases. At times all four animals could be engaged in a four-way grappling bout, hanging by their tails. This prolonged grappling behavior with its sexual overtones is here interpreted as abnormal. In the natural groups observed in Chiapas, play was confined solely to the juveniles (Carpenter, 1935). It can be assumed that these females without young were exhibiting abnormally prolonged juvenile behavior.

There was some indication of dominance within the female group, especially when settling for the night. Two of the animals generally slept huddled together while the third generally attempted to keep the fourth away as she settled next to the compatible pair. Usually the interaction was reconciled within 10 minutes with the fourth animal joining the huddled pair and the third animal resting about 3 feet away.

The male was typically more independent in his movements. In 1964 he was observed with the females on only 7 days out of the 26 days of observation. At other times he could be found feeding, moving, and resting alone. When he was alone the male was difficult to locate and was often not spotted for 3 days at a time. The dates of his extended association with the females include May 17, 18, 19, 26, 31, and June 1 and 4. Interactions between the male and the females included approaches, tagging, moving away (by females), grappling with ook ook and roar vocalizations by the male, chasing by the male, and grooming of the male by the females. On May 26 the male followed the females throughout the afternoon and one female attached herself to him. They were seen moving independently from the three females until dusk. There is every reason to believe that they formed a pair relationship throughout the night.

The male would grimace, cough, and shake branches at a human observer. This behavior coupled with his occasional agonistic reactions to the *Cebus* and the deference that the females exhibited toward him sharply demarcated his behavior from the females.

BEHAVIOR AND GROUPING TENDENCIES IN A NATURAL POPULATION

From July 7 through July 14 a population of *Ateles geoffroyi vellerosus* was censused in southern Mexico, roughly 30 km west of Acapetahua, Chiapas. The study area included four "islands" of high ground within a strip of mangrove swamp approximately ½ by 3 kilometers. One island comprises the field station of the Departmento Biologico, Tuxtla Gutierrez. During this period, nine groups were observed and counted. Of these nine groups four were censused completely with respect to age and sex classes. It is reasonably certain that these four counts were carried out twice each on the same two groups. These data are summarized in tables 22 and 23.

TABLE 22.—*Group size in free-living ateles.*

Location	Date	Time	Group size
Island I	7/11/65	0840	4
Island II	7/10/65	1100	3
Island III	7/ 7/65	1015	4
	7/ 7/65	1400	6
	7/ 9/65	1440	6
	7/ 9/65	1500	4
	7/10/65	1700	6
	7/14/65	0710	5
	7/14/65	0750	6

This mangrove swamp is not a typical *Ateles* habitat and must be considered as a special situation conducive to the extreme fractionation of *Ateles* groups. Primary feeding is confined to the restricted areas of high ground which support a variety of food plants. At this time of the year the animals were visiting the study areas primarily to acquire the late fruiting *Sideroxylon* sp. (Sapotaceae). Throughout the year at various seasons they are sustained by *Attalea gomphococca,* *Spondias lutea, Chrysophyllum cainito, Heliostylus ojuche, Ficus* sp. and *Oreopanax oligocarpum.** In addition, the monkeys utilized various cultivated plants which have been introduced by the human inhabitants of the islands.

Table 22 indicates the small size of the groups counted, which ranged from three to six with an average of 4.9 animals per group. In table 23 compositions of the two groups from Island III are presented. Troop A was encountered twice, whereas troop B was encountered four times. These troops were characterized by having only one fully adult male attached to them and conform to one type of social grouping observed in Chiapas by Wagner (1956). Furthermore these two groups utilized the same habitat but did so at different times. We have then a case of home range overlap but mutual avoidance.

TABLE 23.—*Composition of troops A and B from Island III.*

	Adults		Juveniles		Infants		
Troop	Male	Female	Male	Female	I	II	Σ
A	1	2	1	1	–	1	6
B	1	1	1	1	–	–	4

Observations of these two groups indicated that the males could initiate movements of the whole troop thus assuming a temporary leadership function. On the other hand the female with the Infant-II was observed on two occasions to move away separately, and on three occasions an adult male moved off without any immediate following response on the part of the associated female and juveniles. The female and associated juveniles or infant presented a much more cohesive social subunit.

DISCUSSION

Wagner (1956) reports that *Ateles geoffroyi* in Chiapas is typically found in family bands consisting of an adult male, several females, and their young. The males typically approach human intruders and bark, break branches, and drop branches on intruders. Females with young may participate in this threatening behavior, but generally retire to the rear. When spider monkeys are hunted such overt hostile behavior is often reduced or absent and concealing behavior is adopted. Wagner further comments that in the coastal lowlands of Mexico

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* List provided by José H. Vasquez.

larger troops of 100 or more animals may be formed from the discrete family bands. He attributes these larger groups to the artificial conditions of hunting pressures. Dr. M. Alvarez del Toro (pers. comm.) described a typical *Ateles* group from the montane forests of Chiapas as consisting of four adult males, eight females and associated juveniles and infants, giving a total of some 20 animals. In addition, he reports the presence of solitary males in a given population. It should be remembered that there is no way to be certain that the presumptive isolated males are truly unattached or whether they are actually attached to a group of females but temporarily moving alone.

Carpenter (1935) found that *Ateles geoffroyi* in Panama lives in clans or troops that utilize a common home range and sleeping trees. Each troop is typically composed of subgroups. Fighting among males has been observed, and the evidence strongly suggests that adult males may join cohesive female groups and defend them against the close approach of other males. Males may also associate compatibly but it appears that when a male associates with a group of females he may be prone to react antagonistically to the approach of other males. It is entirely possible that young males need to escape the mother group and to form a separate subgroup with both other older and younger males. In captivity, the young males are perhaps severely stressed as they mature in a confined social group.

Undoubtedly the social structure of *Ateles* groups varies with the habitat. In an environment such as the mangrove swamp, cohesive groups may be small and approximate a family group structure. In other habitats with a more uniform distribution of food trees the troops may be large and more plastic in their structure.

Certainly the most cohesive social units within an *Ateles* troop are the groups of females with young. Peripheral groups of males may be loosely associated with a given female group but one or two males may by dominance attach themselves exclusively to an adult female group.

GENERAL DISCUSSION AND CONCLUSIONS

Most species of the Cebidae, Cercopithecidae, and Pongidae are group-living, gregarious mammals. The night monkey, *Aotus,* and the lar gibbon, *Hylobates lar,* are exceptional because they appear to live in family groups (Moynihan, 1964; Carpenter, 1940). The orangutan, *Pongo pygmaeas,* appears to be semisolitary, but an adequate appraisal is difficult because of the reduced populations of this species (Schaller, 1961). The gregarious primates have several common social trends:

a tendency for females with young to form a "core group" which is very cohesive; a dominance order for adult males and adult females which is often enforced through nonviolent, subtle communication mechanisms; contact-promoting behaviors involving vocalizations and mutual grooming, and a history of socialization which occurs as an infant matures in a rather stable social matrix. In addition, organized primate groups tend to utilize a given home range with some areas being almost exclusive to a given group and other areas overlapping with the home ranges of neighboring groups. Maintenance of an exclusive area may be accomplished by hostile display and aggressive behavior in *Macaca mulatta,* ritualized vocalizations in *Alouatta palliata* and *Hylobates lar,* or undefined but subtle mechanisms of interaction as in *Papio ursinus* and *Presbytis entellus* (Southwick, 1962). The evidence indicates that *Ateles geoffroyi* is characterized by the above trends, but it differs significantly when further comparisons are made with other primates.

The ground-dwelling macaques and baboons typified by *Macaca mulatta* (Carpenter, 1942; Altmann, 1962) and *Papio ursinus* (Hall, 1962a, b; Washburn and Devore, 1962; Bolwig, 1958) differ from *Ateles* in certain important respects. These ground-dwelling primates are sexually dimorphic and exhibit a strict dominance hierarchy, the male hierarchy being separate from that of the females. One or more dominant males serve as a focus for the group's movements and this male group is centrally located in a moving troop in association with the core mother subgroup. The young males are chiefly in the lead and on the periphery. The males are much larger than the females and actively defend the troop. Macaques and baboons are overt in their sexual behavior and ritualized mounting serves as a means of asserting dominance.

The terrestrial pongids exhibit still different syndromes of social behavior. *G. gorilla beringei* forms cohesive bands of mixed sexes. The dominant male definitely coordinates the movements of the group and plays a defensive role when the group is disturbed; however, overt aggressive and sexual behaviors are reduced when compared with macaques and baboons (Schaller, 1963). The chimpanzee, *Pan satyrus,* is characterized by an extremely loose social organization. Mother groups are common but shift in their composition. Overt male dominance is reduced and strict linear hierarchies are not determinable (Reynolds, 1963).

When we turn to arboreal species, the langur, *Presbytis entellus,* is characterized by troops of mixed sexes with a strict hierarchy among the adult males, but a loose and amorphous rank order among the females. Tolerance among males is shown and the troop moves in a cohesive fashion. Males which leave a given troop are generally prevented from readily reentering and a number of males may be solitary or organized into loose associations outside an organized troop (Jay, 1963). The howler monkey, *Alouatta palliata,* is similarly organized into groups of mixed sexes. The howler group is very cohesive and the males are strongly dimorphic. In addition to their role in offensive and defensive display toward enemies, the adult males engage in vocal chorusing behavior which appears to aid in spacing out neighboring troops. Overt aggressive and sexual behavior appear to be reduced when compared with macaques and baboons.

Ateles is not a strongly dimorphic genus. The males are only slightly larger (Hill, 1962) and only the pendulous clitoris of the female renders her conspicuously different from the male. Although males appear to take the initiative in expressing hostile behavior to intruders, the males do not serve as a focus for troop movement and there is good reason to believe that adult males are relatively intolerant of each other when they are associated with an adult female group. Furthermore, the dominance relations among group members are not strongly expressed and a classical, linear hierarchy appears to be absent. Cohesion among troop members is not pronounced, with the possible exception of the core mother group and their associated young. *Ateles* is not overtly sexual and ritualized mounting as a form of dominance is lacking.

The phenomenon of a complex social life is not unique to the primates. Groups of mixed sexes may be found in some species of ungulates, carnivores, and cetaceans (Eisenberg, 1965). It may be argued that male ungulates are seasonal in their association with females and that during the breeding season male ungulates form harems and are intolerant of other adult males, but harem formation is not solely confined to nonprimate gregarious mammals and appears to be the rule for *Papio hamadryas* (Kummer and Kurt, 1962). Furthermore, the harem mating system is not the rule for all ungulates. Mating orders may be established through a dominance hierarchy, and several males may well associate with more cohesive female groups in such species as *Bos taurus* (Schloeth, 1961) and *Bison bison* (McHugh, 1958). The persistence throughout the year of groupings of mixed sexes in primate societies is somewhat unique, but the wolf forms cohesive social units throughout the year (Murie, 1944) as does the horse (Antonius, 1938; Zeeb, 1961). We wish to emphasize that although complex sociality is a characteristic phenomenon in the order Primates, this trait is not expressed in a uniform fashion. While similar in many ways to other primates, *Ateles* appears to differ in the structure of its social organization so that in some ways it exhibits a structural complexity intermediate between the loose social organizations of some primates, many nonprimate mammals, and the cohesive, organized societies so typical of the macaques, baboons, and gorillas.

SUMMARY

The behavior of *Ateles geoffroyi* was studied in a laboratory, zoological garden, and field setting. In addition captive studies were conducted with *A. belzebuth, A. paniscus,* and *A. fusciceps.* Expressions, postures, and vocalizations were described in detail. Insofar as possible the functional role of these communication patterns was determined. Lip-smacking, tongue protrusion, and ritualized presenting so common in macaque and baboon expressive repertoires, are lacking or nonritualized in *Ateles.*

The following conclusions were drawn concerning the social structure of *Ateles geoffroyi*:

1. The social groupings are loosely organized; however, females with infants and juveniles may form a cohesive group.
2. Overt sexual behavior and aggressive behaviors are reduced when compared with macaques and baboons.
3. A loose dominance order is present within a group, but it is subtle and not as strictly delineated as is the case with groups of macaques and baboons.
4. Grooming relationships in a captive group reflect a rank order within a social group since high ranking animals groom more individuals but receive grooming from only a few animals.
5. Females with young are in some respects outside the normal dominance relationships.
6. In contrast to macaque and baboon groups, the adult males do not serve as a focus for social activity.
7. Tolerance and a reduced aggressive tendency permit the formation of large, loosely organized troops; however, the troops vary in numerical composition. The cohesive units are the small subgroups of females, infants, and juveniles that compose a troop dwelling in a given home range.
8. Adult males may dominate and attach themselves semi-exclusively to adult female subgroups.

9. All-male subgroups are common in a loosely organized troop.

The Cebidae, Cercopithecidae, and Pongidae are generally extremely social mammals, although differences among the social organizations of different species indicate a spectrum of social types. No sharp break in the form of primate social organizations appears to set them apart from the social organizations of some ungulates, cetaceans, and carnivores.

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PLATES

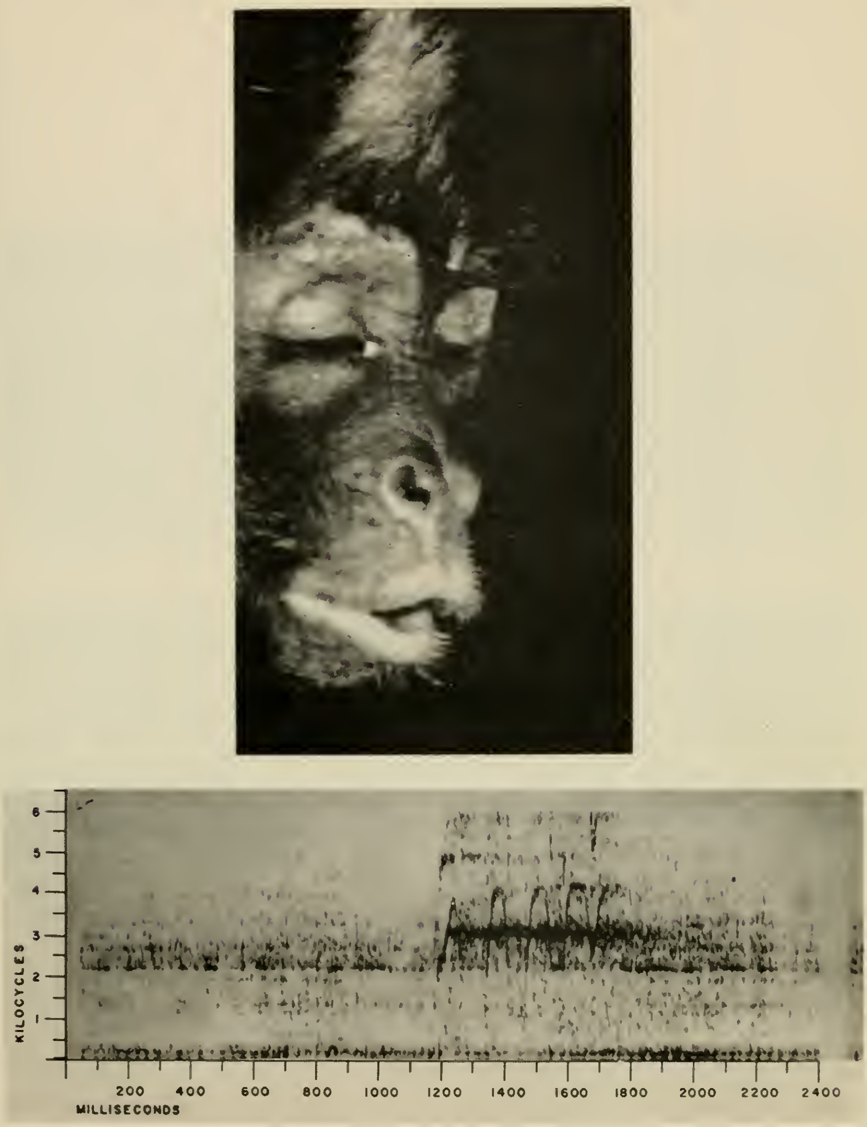

Plate 1

a. Pursed lips. This expression is the antithesis of the grimace and frequently accompanies the low ook ook and twitter vocalizations.

b. The tee tee sound. Neglect the constant background noise. The signal occupies the third quarter of the kymograph tracing (recorded from *A. geoffroyi*).

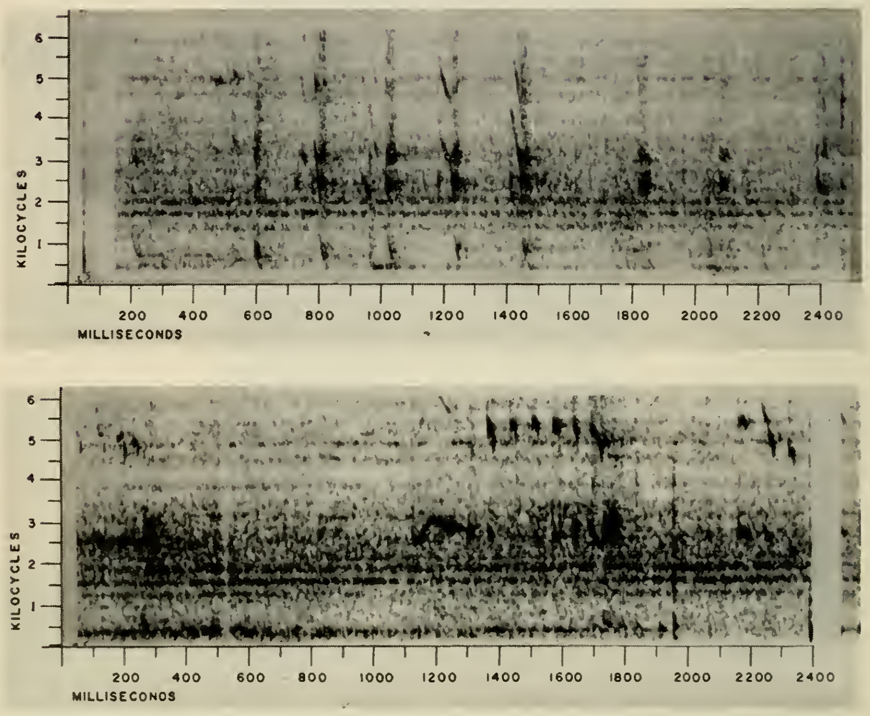

Plate 2

a. A series of eight chirps recorded from *A. fusciceps*. Disregard the constant background noise in this and the following tracing.

b. Portions of three twitter series. Note the double set of harmonics.

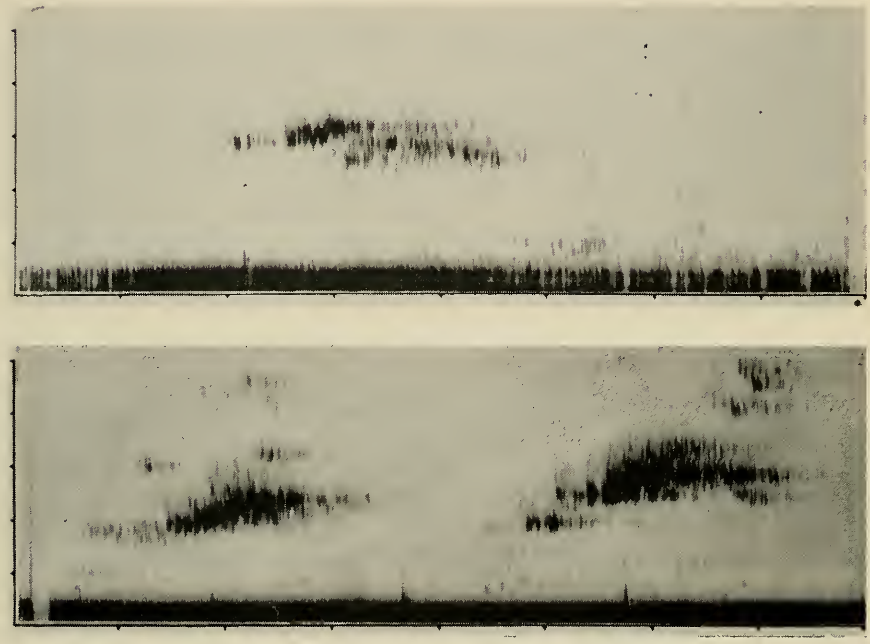

Plate 3

a. Whinny (*A. belzebuth,* male). (Note: unless specified, plates 3 through 6 display an ordinate of 1000 cps increments and an abcissa of .3 sec. increments).

b. Grunt Trill (*A. belzebuth,* male).

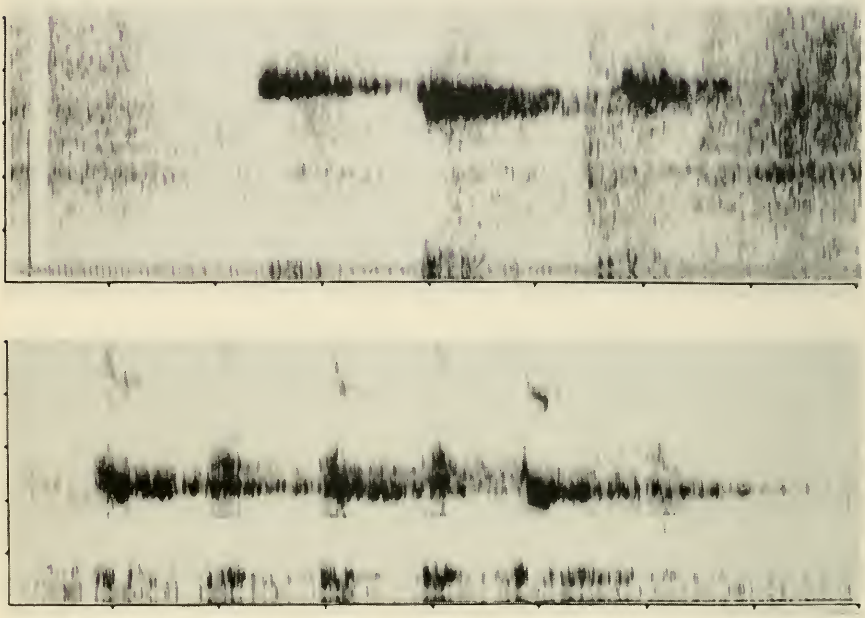

Plate 4

a. Low squeak. Note the relatively narrow frequency range.

b. Chitter; very high pitched, pulsed sound. Ordinate in 3000 cps increments; abcissa in .1 sec. increments. (*A. paniscus,* male).

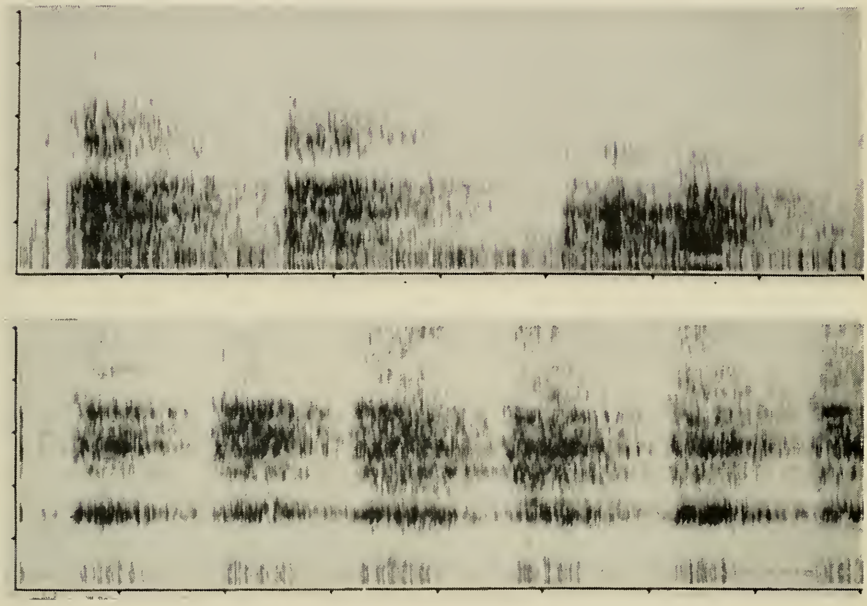

Plate 5

a. Ook ook (*A. belzebuth,* male).

b. Bark (*A. belzebuth,* male).

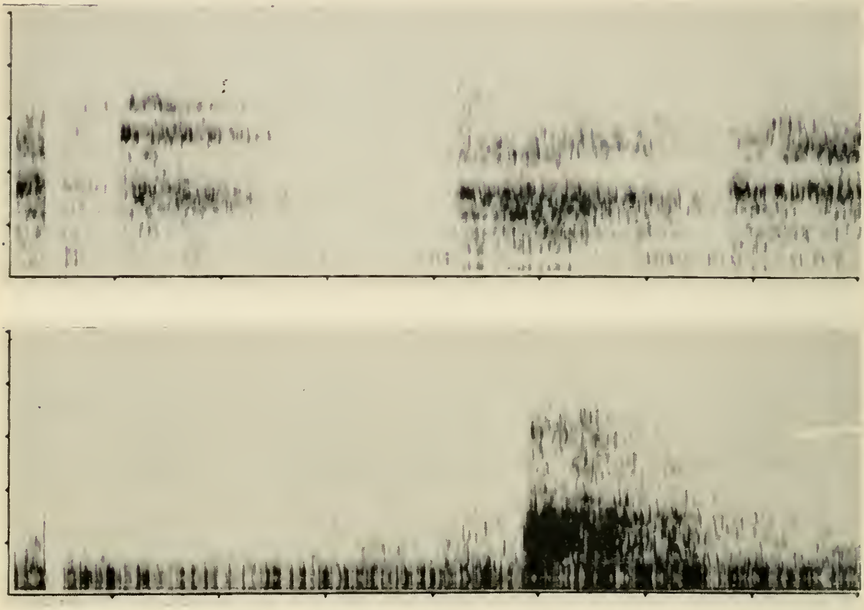

Plate 6

a. Ook, followed by a growl (*A. belzebuth,* male).

b. Cough (*A. belzebuth,* male).

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(With One Plate)

Two new species of *Cassidulus*—one of *Echinocyamus* and one of *Fibularia*—are described from the middle Eocene Upper Scotland Formation in Barbados. The specimens were collected by Alfred Senn and A. J. Mestier in 1937 and sent to me for study by H. G. Kugler.

The new species of *Fibularia* is particularly interesting because of the large number of specimens available, making possible a study of its variation and ontogeny. Although it occurs throughout the Upper Chalky Mount Member, no evolutionary trends were found within the species.

It was necessary to reexamine the American species in order to compare the Barbadian species of *Echinocyamus* and *Fibularia* with the American, most of which have been inadequately described and illustrated. All available specimens have been measured and the data are presented on scatter diagrams. Drawings are included of their tests, showing for the first time the location of their petal pores, the most diagnostic feature in these species.

PREVIOUS WORK

Only three species of echinoids have been described from Barbados, *Cystechinus crassus* Gregory (1889, p. 641), *Eupatagus abruptus* (Gregory, 1892, p. 163), and *Echinolampas anguillae* Cotteau (Guppy, 1911, p. 692). All these species are from the Oceanic Formation which is considered to be Middle Eocene to Oligocene. The species described below are the first that have ever been recorded from the Upper Scotland Formation.

SMITHSONIAN MISCELLANEOUS COLLECTIONS, VOL. 151, NO. 9

The Barbadian Upper Scotland mollusca have been described by Trechmann (1925), the crustaceans by Withers (1926), the larger Foraminifera by Vaughan (1945), the corals by Wells (1945), and the Nummulites by Cizancourt (1948).

AFFINITIES OF ECHINOIDS

It is rather surprising, considering the large number of echinoids known from Eocene rocks in the Caribbean and southeastern United States, that all the four species from the Upper Scotland Formation are new and quite distinct. Vaughan (1945, p. 20) reported a similar situation among the Foraminifera with 9 out of 12 species new, and in the corals Wells (1945, pp. 1-2) found 16 new species of corals with only 2 previously known from other localities.

ECOLOGY

Evidently the echinoids lived in the sediment in which they were fossilized. The Upper Scotland Formation is a sand or a conglomerate in most localities where the echinoids were collected. Two of the echinoid species are fibularids and according to Mortensen (1948, p. 162) members of this family commonly live in sands and gravels. The other two species are cassiduloids which also are reported (Kier, 1962, p. 21) to live in sand.

The echinoids are of no use in determining the depth of the sea during deposition of the Upper Scotland Formation. Species of *Echinocyamus* are found in water from 20 to 1,886 meters deep, and *Fibularia* from littoral to 400 meters. The bathymetrical distribution is not known with certainty for any living species of *Cassidulus*. Vaughan (1945, p. 21) stated that the Foraminifera and corals indicated relatively shallow water not greater than 183 meters and probably as shallow as 73 meters.

STRATIGRAPHIC DATA

Most of the echinoids were collected from the Chalky Mount Member of the Upper Scotland Formation. According to Vaughan (1945), "the foraminifera fauna of the Upper Scotland Formation is obviously middle Eocene, and it may be considered the type middle Eocene larger foraminiferal fauna of America." The lower half (50-100 meters thick) of the Chalky Mount Member (Senn 1940, p. 1554) consists of massive to coarse-bedded gritty sands, alternating with a few well-bedded finer-grained sands. The upper half consists of an alternation of friable, coarse, gritty sands, and medium-grained sands, with a thickness of 20-40 meters.

COLLECTION DATA

The echinoids were collected at the localities listed below. The position of these localities on a map can be found in Vaughan (1945, pl. 1). Detailed lithologic data for each site are also available in Vaughan (1945, pp. 6-18). The holotypes and figured paratypes are in the Naturhistorisches Museum, Basel, Switzerland, and the remainder of the collection is in the U.S. National Museum.

Upper Scotland Formation

Upper Chalky Mount Member

S102a,b	Base of member. Northern slope of Chalky Mount (Parish of St. Andrew).
S168	Northern slope of Chalky Mount, near locality S102
S1114	Northern slope of Chalky Mount, NE of summit (Parish of St. Andrew).

Middle Chalky Mount Member

S58	Left bank of Mount Hillaby River, 46-54 m. E of Murphys-Friendship road (Parish of St. Andrew).
S80	Base of member. Slope between Spa Peak and Canegarden River on western side of cross-fault scarp (Parish of St. Joseph).
S160	Small hill on Lowes Ridge, 100 m. NW of ruin of Lowes windmill, Trechmann's locality "Sunbeam" (Parish of St. Andrew).
S359	Western part of Chalky Mount massif, NE side of flat-topped ridge 80-90 m. south of S375 and 165-180 m. SSW of S360 (Parish of St. Andrew).
S360	Upper part of member. Prominent ridge in western part of Chalky Mount massif, approx. 550 m. WSW of highest summit of Chalky Mount (Parish of St. Andrew).
S361	Ridge directly north of highest peak of Chalky Mount (Parish of St. Andrew).
S375	Upper part of member. Western part of Chalky Mount massif, in small ravine, approx. 100 m. SW of S360 (Parish of St. Andrew).
S378	Upper part of member. East side of ridge between Murphys River Valley and Goggins River Valley.
S1107	North of Chalky Mount (Parish of St. Andrew).

Lower Chalk Mount Member

S152	Top of member. Footpath on northeastern side of Spa Peak (Parish of St. Joseph).
S164, 165	Eastern end of Chalky Mount near Benab (Parish of St. Andrew).

S379 Upper part of member. Chalky Mount West (Parish of St. Andrew).

Chalky Mount Member

S1108 Goggins Hill

Murphys Member

S110 Senn test pit 88, near end of cart track, 330 m. SE of Turner's Hall Estate house (Parish of St. Andrew).

SYSTEMATIC DESCRIPTIONS

FIBULARIA BARBADOSENSIS Kier, new species

(Pl. figs. 1-3; text figs. 1-4, 5A, 6A, 8, 9)

Diagnosis.—Species characterized by short petals.

Material.—One hundred and fifty specimens; most well preserved, but pore-pairs not easily visible in most specimens until adapical surface slightly polished with dental drill, then etched slightly with hydrochloric acid.

Shape.—Elongate, average width 80 percent of length, varying from 65 percent in the narrowest (text figs. 1, 5A) to 93 percent in widest; greatest width anterior to center; in some specimens marginal outline slightly pentagonal, in others oval with smooth marginal outline; height averages 63 percent of length, varying from 50 to 75 percent (text fig. 1).

Apical system.—Plate arrangement not visible, four genital pores, anterior pores closer together than posterior; system anterior; number of hydropores not certain.

Petals.—Petal III slightly longer than other petals, usually with one or two more pore-pairs in each poriferous zone than in poriferous zone of other petals; in holotype (text fig. 4C), 8.9 mm long, 11-12 pore-pairs in poriferous zone of petal III, 9-10 in other petals; petals widely open with greatest width at extremity of petal; petals relatively short, petals III, II, and IV extending two-thirds distance from apical system to margin, petals V and I one-half distance; pore-pairs near extremities of petals same distance apart from adjacent pair as pore-pairs near apical system; pores of pair strongly oblique to each other, outer pore more distant from apical system than inner.

Accessory pores.—Small accessory pores (text fig. 2B) along all sutures except perradial, of ambulacral plates beyond petals.

Peristome.—Central to slightly posterior to center; circular to slightly pentagonal; diameter in adults averaging 10 percent of length of test, varying from 9.3 to 11 percent; one sphaeridium pit behind each pair of buccal pores (pl. fig. 3).

Periproct.—Circular, in adult specimens located nearer to peristome than to posterior margin; distance from peristome very variable averaging 12 percent of length of test, varying in adults from 8 to 17 percent.

Growth.—Because of the presence of very small specimens, the smallest 1.8 mm. long, a growth study was made. The length to width, and length to height ratio (text fig. 1) remain unchanged through the growth of the echinoid. Likewise, the rate of the introduction of new pores (text fig. 6) is unaltered. However, there is a marked change in the relative size of the peristome. In the smallest specimen (text fig. 4A) it is very large relative to the size of the test, having a diameter 23 percent of the length of the test, but in the largest (text fig. 4C) it is only 9 percent of the length. Apparently, as evident from the graph in text fig. 3, the peristome when first formed was initially large. The relative position of the periproct changes with growth. In the smallest specimen (text fig. 4A) it is distant from the peristome with the distance from the two equaling 20 percent of the length of the test, whereas in the largest specimen (text fig. 4C) it is much nearer to the peristome with the distance being only 11 percent of the length. No genital pores are visible in the smallest specimen, 1.8 mm long (text fig. 4A), but they are present on a specimen (text fig. 4B) 3.1 mm long.

Comparison with other species.—Six other species of *Fibularia* are known from the Caribbean and southeastern United States: *Fibularia texana* (Twitchell), *Fibularia alabamensis* Cooke from the Eocene of southeastern United States, *Fibularia minuta* Palmer from the Eocene of Cuba, *Fibularia jacksoni* Hawkins from the Eocene of Jamaica, and *Fibularia farallonensis* Cooke from the Eocene of Trinidad. With the exception of *F. jacksoni,* none of these species have ever been adequately described or illustrated. Because of the great variation in the shape of the test in this genus, it is necessary to measure many specimens before the specific characters can be delineated. Furthermore, because of the small size of the test, photographs do not usually show the position of the petal pores, the most diagnostic feature in the fibularids. Fortunately, many specimens of the American species are available in the U.S. National Museum. These have been measured and drawings of their tests and scatter diagrams of some of their dimensions are included herein. Unfortunately, Palmer's species has never been figured and his description is too brief to be of use. *F. barbadosensis* cannot be compared to it at this time.

Of all these species, *F. barbadosensis* resembles most *F. alabamensis*. It is very similar in shape, having the same length to width ratio as is evident on a scatter diagram (text fig. 1A) in which there is no separation of the points of the two species, but it is slightly lower than *F. alabamensis,* as evident on text fig. 1B. Its peristome is slightly smaller than the Alabama species (text fig. 3), and there are usually one or two less pore-pairs in the poriferous zones of the petals (text fig. 6A). The distance of the periproct from the peristome is approximately the same for each species (text fig. 2A). The most important difference between the two species is that in *F. barbadosensis* the petals do not extend as near to the margin. This difference is clearly shown in text figure 5.

F. barbadosensis is similar to *F. texana* (Twitchell) (text fig. 7A) but differs from it in having shorter petals and more widely separated genital pores. It is easily distinguished from *F. vaughani* (Twitchell) by its smaller peristome (text fig. 7B) and shorter petals (text fig. 7B). Furthermore, in *F. barbadosensis* the distal pore-pairs of each petal are close together, whereas in *F. vaughani* the last one or two pore-pairs are more widely separated from each other than the pore-pairs nearer the apical system.

F. barbadosensis differs from *F. jacksoni* in having a slightly narrower test (text fig. 1A), more pore-pairs in petal III (text fig. 6A), shorter petals with narrower interporiferous zones, and a less pentagonal marginal outline. As can be seen from text figures 1B, 2A, it cannot be distinguished from it by the distance of the periproct from the peristome or by the height of its test.

F. barbadosensis is easily distinguished from *F. farallonensis* (text fig. 6B) by its narrower test, shorter, narrower petals, and more anteriorly situated periproct.

Evolution.—Because specimens of this species occur throughout the Chalky Mount Member (90-200 meters thick) of the Scotland Formation, a search was made for evolutionary trends such as those found by Kier (1957, p. 863; 1964, p. 1123) in other fibularids. The length, width, height, number of pore-pairs in petal III, and distance of the periproct from the peristome is recorded on graphs (text figs. 8, 9), but no distinction is apparent between specimens from the various parts of the Chalky Mount Member. The sands and conglomerates of the Member were probably deposited so rapidly that there was insufficient time for any evolutionary trends to be developed.

Occurrence.—Upper Scotland Formation, Upper Chalky Mount Member: S102a, b, S1114; Middle Chalky Mount Member: S58, S80, S160, S359, S360, S361, S375, S378, S1107; Lower Chalky Mount Member: S152, S164, S165, S379; Chalky Mount Member: S1108; Murphys Member S110.

Types.—Holotype, Basel M6603; figured paratypes M6600, M6601, M6602, M6603.

ECHINOCYAMUS CARIBBEANENSIS Kier, new species

(Pl. figs. 4, 5; text figs. 10-12A-D)

Diagnosis.—Species characterized by long petal III, wide, thick test, and position of periproct near posterior margin.

Material.—Ten specimens, largest 5.9 mm long.

Shape.—Elongate, average width 81 percent of length (text fig. 10B); greatest width slightly posterior to center; height (text fig. 10A) averages 53 percent of length, test slightly protruding at periproct, sunken around peristome.

Apical system.—Plate arrangement not visible, four genital pores, anterior pores closer together than posterior; system central to slightly anterior.

Petals.—Petal III longer than other petals, with approximately three or four more pore-pairs; in holotype, 11 pore-pairs in petal III, 7 in other petals; petals widely open (text fig. 12A), with greatest width in paired petals two-thirds distance from apical system to extremity of petals; in petal III greatest width at extremity; pores of pair oblique from each other, outer pore more distant from apical system than inner.

Accessory pores.—Small accessory pores along suture between ambulacra and interambulacra beyond petals.

Peristome.—Circular, sunken, central or slightly posterior, diameter of opening varying from 17 to 20 percent of length of test; one sphaeridium pit behind each pair of buccal pores.

Periproct.—Circular, located at posterior margin in most specimens, but in largest, 5.9 mm long, periproct more anterior (text fig. 12D), tilting so that opening faces slightly posteriorly.

Comparison with other species.—*E. caribbeanensis* is easily distinguished from *E. macneili* from the late Eocene of Alabama by its wider and thicker test (text fig. 10), more pore-pairs in petal V relative to length (text fig. 11A), and periproct nearer the posterior margin (text fig. 13A). In the holotype and only known specimen of *E. macneili,* the genital pores are much larger than those in *E. carib-*

beanensis, but as suggested by Cooke (1959, p. 33) this specimen may have had larger pores because it may have been a female.

E. caribbeanensis differs from *E. huxleyanus* Meyer from the late middle Eocene Gosport sand in having a wider and higher test (text figs. 10A, B), longer petal III (text fig. 12E), more pore-pairs in petal V relative to length (text fig. 11A), small genital pores (text fig. 12E), and the periproct nearer the posterior margin (text fig. 12E). *E. caribbeanensis* differs from *E. parvus* Emmons from the late middle Eocene Castle Hayne Limestone of North Carolina in having a wider, thicker test (text figs. 10A, B), longer petal III (text figs. 11B, 13B), more pore-pairs in petal V relative to length (text fig. 11A), periproct nearer the posterior margin, and its genital pores closer together (text fig. 13B). It is easily distinguished from *E. meridionalis* Meyer from the Eocene of Alabama and Mississippi by its narrower and higher test (text figs. 10A, B). It is unfortunate that none of the specimens of *E. meridionalis* in the U.S. National Museum shows the petaloid region. Finally, it differs from *E. chipolanus* Cooke from the early Miocene of Florida in having a higher test, but because the holotype and only known specimen of this Florida species has been broken, it cannot be further compared.

Echinocyamus avilensis Lambert from the upper Eocene of Cuba has never been adequately figured, but from Lambert's (1931, p. 298) dimensions of the type it is much larger (16 mm long) and much wider, with the width (15 mm) almost equal to the length.

Occurrence.—Upper Scotland Formation, Upper Chalky Mount Member: S168; Middle Chalky Mount Member: S80, S360, S375, S1107; Lower Chalky Mount Member: S164, S165; Murphys Member: S110.

Types.—Holotype, Basel M6605, figured paratype, M6606.

CASSIDULUS SENNI Kier, new species

(Pl. figs. 6-8; text figs. 14-15)

Diagnosis.—Species characterized by small, broad test, long, broad petals, and slightly developed bourrelets.

Material.—Twenty-four specimens with surfaces poorly preserved due to secondary growth of calcite and partial silicification; details of petals and phyllodes only visible after polishing with dental wheel and etching slightly with hydrochloric acid.

Shape.—Test small, average test 8 mm long, smallest 6.8, largest

12.6 mm; elongate, width averaging 86 percent of length, very little variation in length-width ratio (text fig. 14A); greatest width posterior to center; test low, average height 40 percent of length (text fig. 15D); greatest height anterior (text fig. 15C) at apical system; deep groove leading from periproct to posterior margin; peristome sunken.

Apical system.—Anterior, four genital pores, anterior pair closer together than posterior, madreporic pores extending back between posterior genital pores; probably monobasal, but specimens too poorly preserved to be certain.

Petals.—Broad, anterior petals (text fig. 15A) extending almost to margin, posterior extending two-thirds distance from apical system to margin; petals closing slightly distally, with interporiferous zones equal in width or slightly wider than poriferous zones; posterior petals slightly longer than others with three to five more pore-pairs than in petal III, two to four more than in petals II or IV; in small specimens, 6.9 mm long, 16 pore-pairs in petal II, 16 in IV, 19 in V; in largest specimen, 12.6 mm long, 21 pore-pairs in III, 22 in IV, 26 in V; as apparent from text fig. 14B, rate of production of new pores decreases with growth.

Periproct.—Supramarginal, located slightly more than one-half distance from apical system to posterior margin; deep groove extending from opening to margin.

Peristome.—Slightly anterior of center, wider than high, pentagonal, sunken.

Floscelle.—Bourrelets slightly developed; phyllodes (text fig. 15B) wide, single pores in each plate, with slight crowding of pores, one or two pores occluded in each half-ambulacrum.

Tuberculation.—Owing to poor preservation, details of tuberculation not known.

Comparison with other species.—None of the species of *Cassidulus* known from the Caribbean or America resembles this species. Its broad and long petals, broad test, and slightly developed bourrelets readily distinguish it from all other species of *Cassidulus.*

Occurrence.—Upper Scotland Formation, Upper Chalky Mount Member: S102a, b; Middle Chalky Mount Member: S80, S360, S361, S1107; Lower Chalky Mount Member: S152; Murphys Member: S110.

Types.—Holotype, Basel M6607, figured paratypes M6608, M6609.

CASSIDULUS MESTIERI Kier, new species

(Pl. figs. 9-11; text fig. 16)

Diagnosis.—Species characterized by high test, narrow petals.

Material.—One specimen, well preserved except for erosion at apical area.

Shape.—Holotype 13.4 mm long, 12.0 mm wide, 8.6 mm high, greatest width posterior to center; test high with steep sides, greatest height slightly posterior to apical system; posterior truncated obliquely so that periproct slightly visible from above; margin rounded; adoral surface depressed around peristome.

Apical system.—Missing.

Petals.—Petals narrow (text fig. 16A), slightly widened, open distally; anterior petal shortest, extending only one-half distance from apical system to margin; posterior petals longest, almost twice as long as anterior petal.

Periproct.—Supramarginal, located high on posterior truncation; with slight groove extending from opening to posterior margin; slightly wider than high.

Peristome.—Anterior, large, pentagonal, wider than high, sunken.

Floscelle.—Bourrelets well developed, giving pentagonal outline to opening; phyllodes moderately broad (text fig. 16B), five or six pores in each half ambulacrum with one occluded pore; buccal pores.

Tuberculation.—Most of tubercles eroded.

Comparison with other species.—This species is easily distinguished from *Cassidulus senni* Kier, new species also from the Upper Scotland Formation, by its much higher test, shorter, narrower petals, more posterior periproct, and larger peristome. Of all the species of *Cassidulus* known from the Americas it resembles most *Cassidulus peruvianus* (Brighton) from the Eocene of Peru. Its narrower, shorter petals, less sloping adapical posterior surface, and higher periproct distinguish it from this Peruvian species.

Occurrences.—Upper Scotland Formation, Lower Chalky Mount Member: S164.

Type.—Holotype Basel M6610.

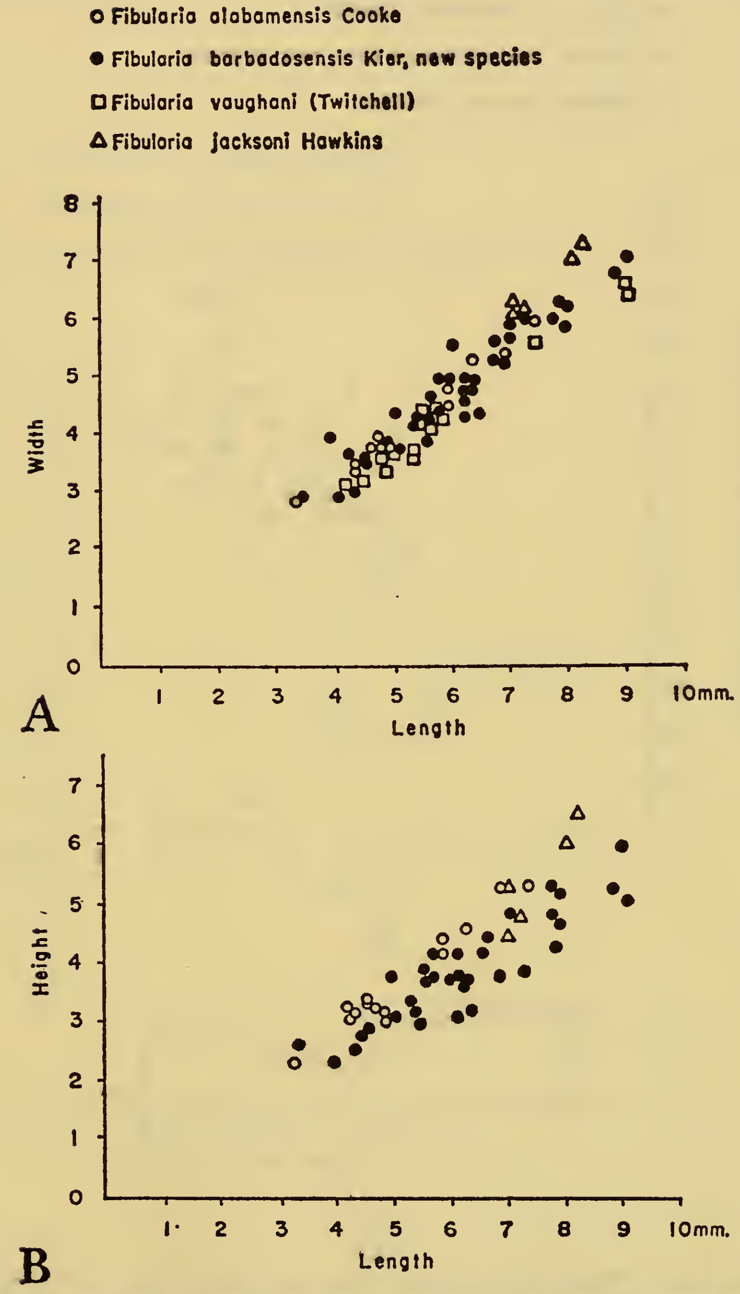


Fig. 1.—**A**, Width relative to length in *Fibularia barbadosensis, F. alabamensis, F. vaughani,* and *F. jacksoni.* **B**, Height relative to length in *F. barbadosensis, F. alabamensis,* and *F. jacksoni.*

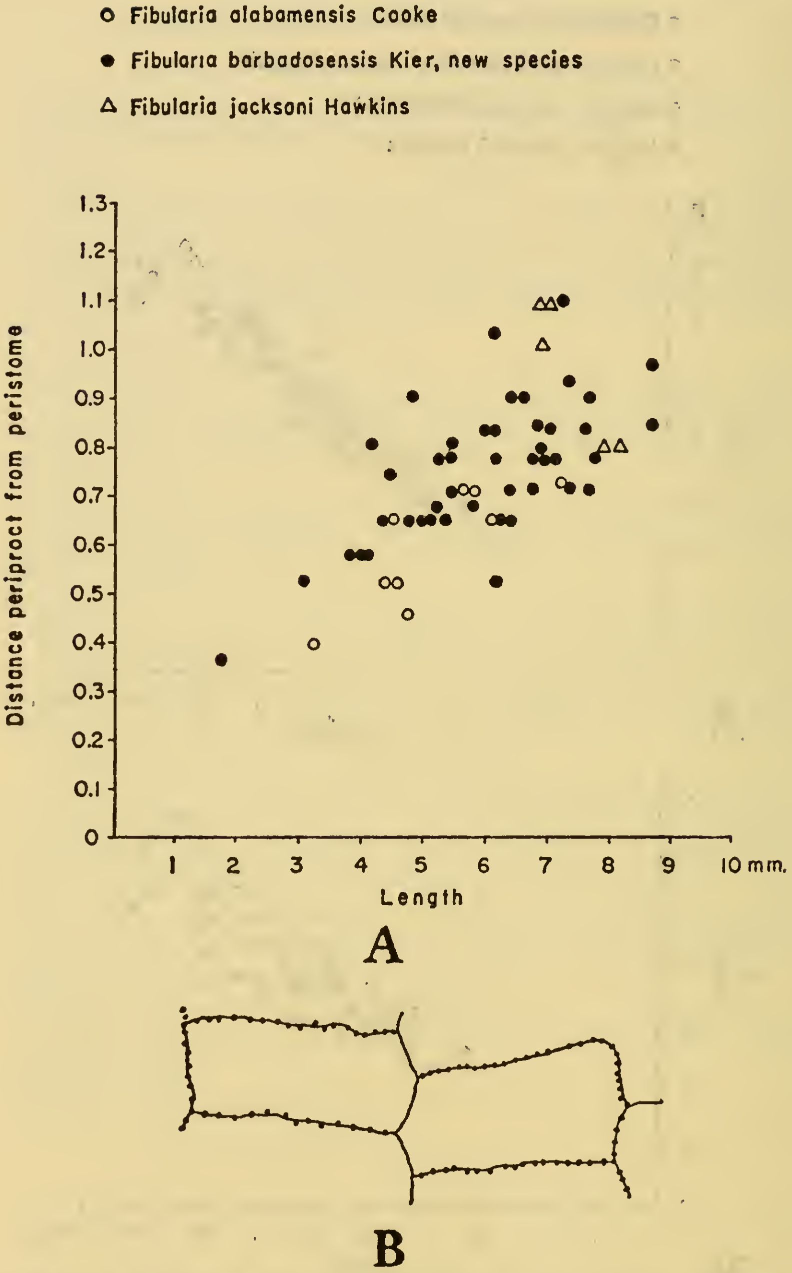


Fig. 2.—A, Distance of the periproct from the peristome relative to the length of the test in *Fibularia barbadosensis, F. alabamensis,* and *F. jacksoni.* B, *Fibularia barbadosensis* Kier, new species: Accessory pores along sutures of ambulacral plates near ambitus; Basel M 6600, loc. S80, × 35.

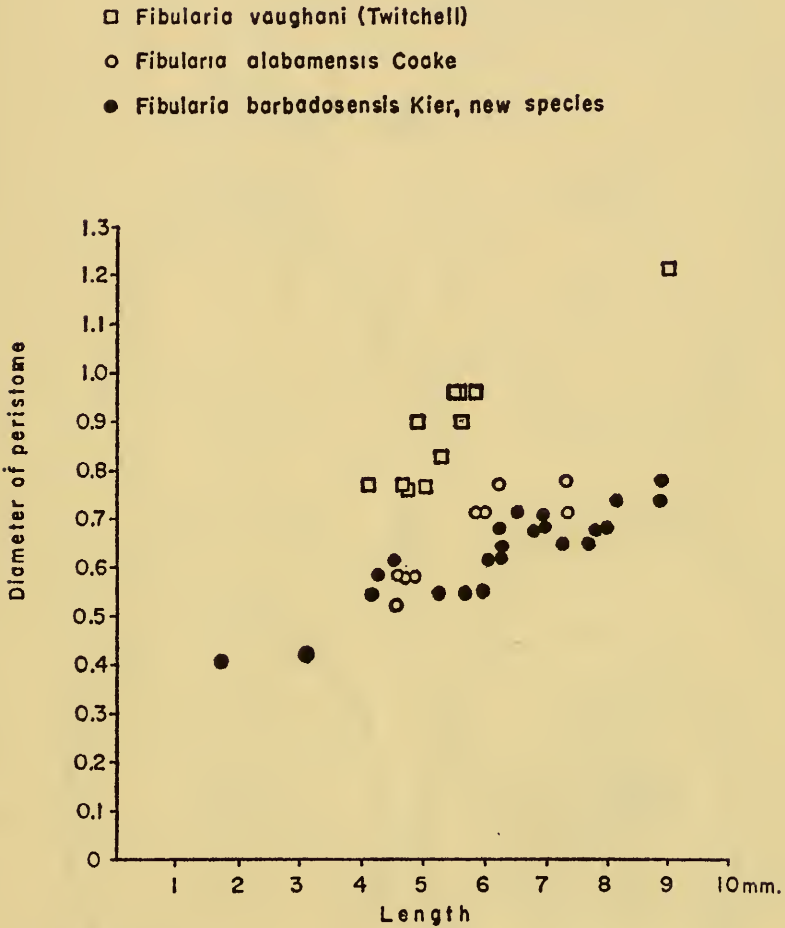


Fig. 3.—Diameter of peristome relative to length of test in *Fibularia barbadosensis, F. vaughani* and *F. alabamensis.*

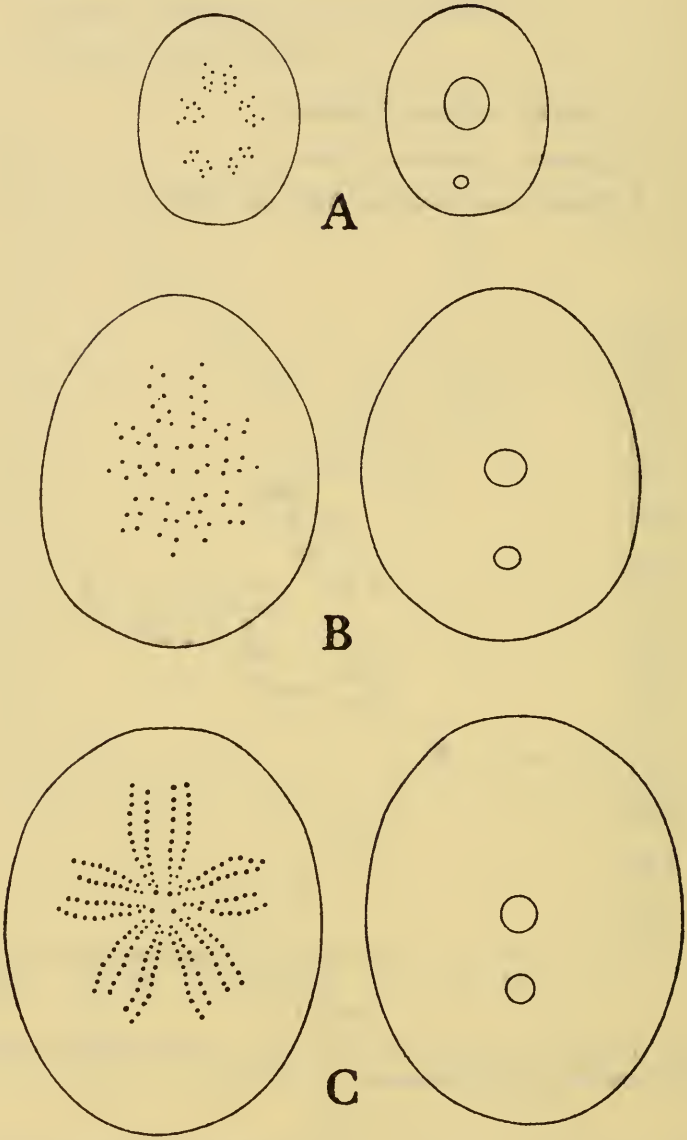


Fig. 4.—*Fibularia barbadosensis* Kier, new species: Growth series. **A**, Smallest specimen in collection, 1.8 mm long, Basel M6601, loc. S375, × 15; **B**, Specimen 3.1 mm long, Basel M6602, loc. S375, × 15; **C**, Holotype, 9.1 mm long, Basel M6603, loc. S1107, × 6.

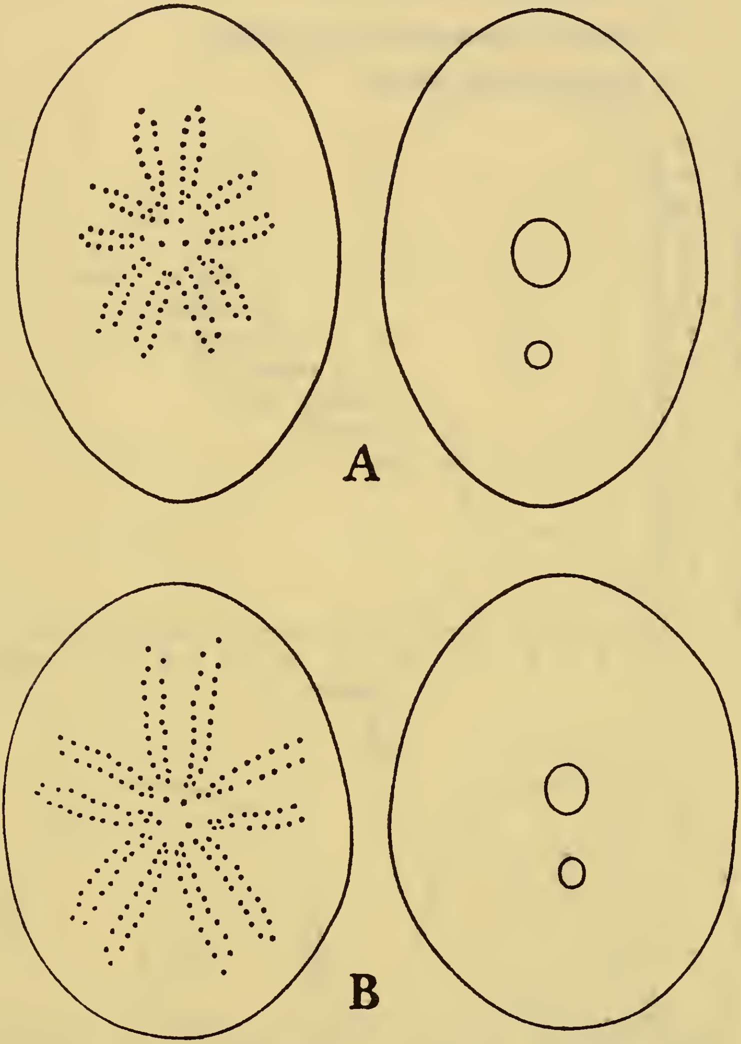
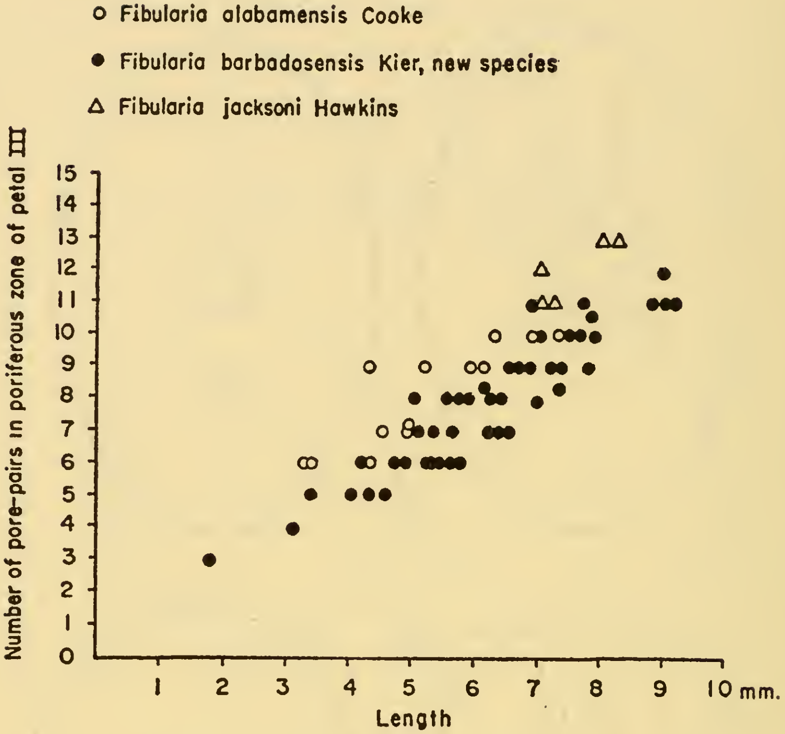
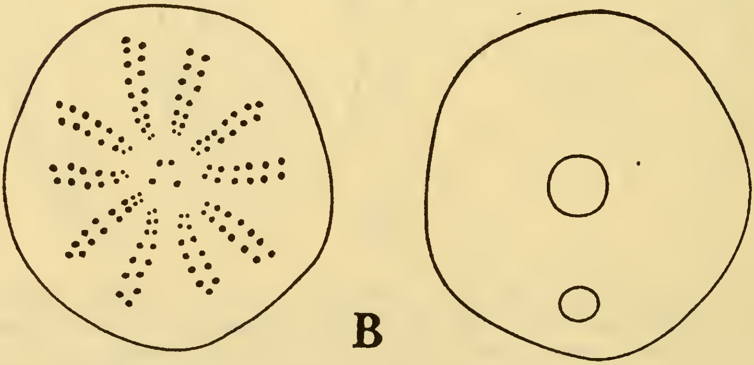


Fig. 5.—**A**, *Fibularia barbadosensis* Kier, new species: Narrow specimen, Basel M6604, loc. S1107, × 10. **B**, *Fibularia alabamensis* Cooke: Holotype, USNM 372887, upper Eocene, probably Moody Branch Formation, at USGS 10014, stream on line between sec. 20 and 29, T. 4 M., R. 15 E., 6 miles west of Andalusia, Covington Co., Alabama, × 8.



A



B

Fig. 6.—A, Relation of the number of pore-pairs in a poriferous zone of petal III to the length of the test in *Fibularia barbadosensis, F. alabamensis,* and *F. jacksoni.* B, *Fibularia farallonensis* Cooke: Holotype, USNM 638629a, middle Eocene, Navet Formation, Farallon Rock, near San Fernando, Trinidad, × 10.

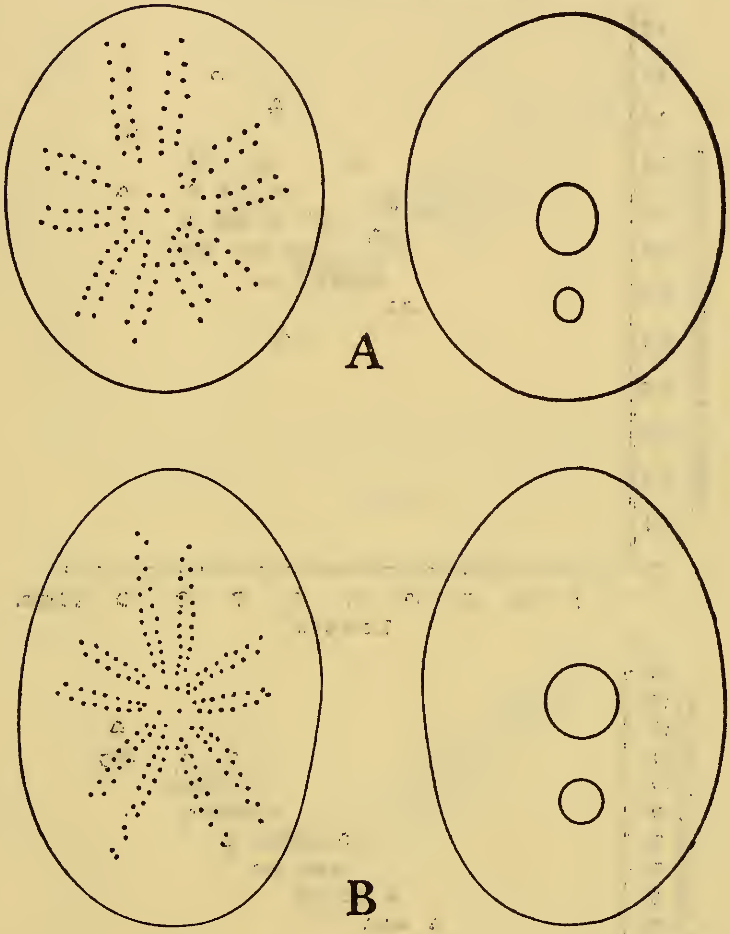


Fig. 7.—**A**, *Fibularia texana* (Twitchell): Holotype, USNM 559480, Lee County, Texas, × 10. **B**, *Fibularia vaughani* (Twitchell): Holotype, USNM 166486, late Eocene, Ocala Limestone, Flint River at Little Horseshoe Bend, 4 miles below Bainbridge, Georgia, × 8.

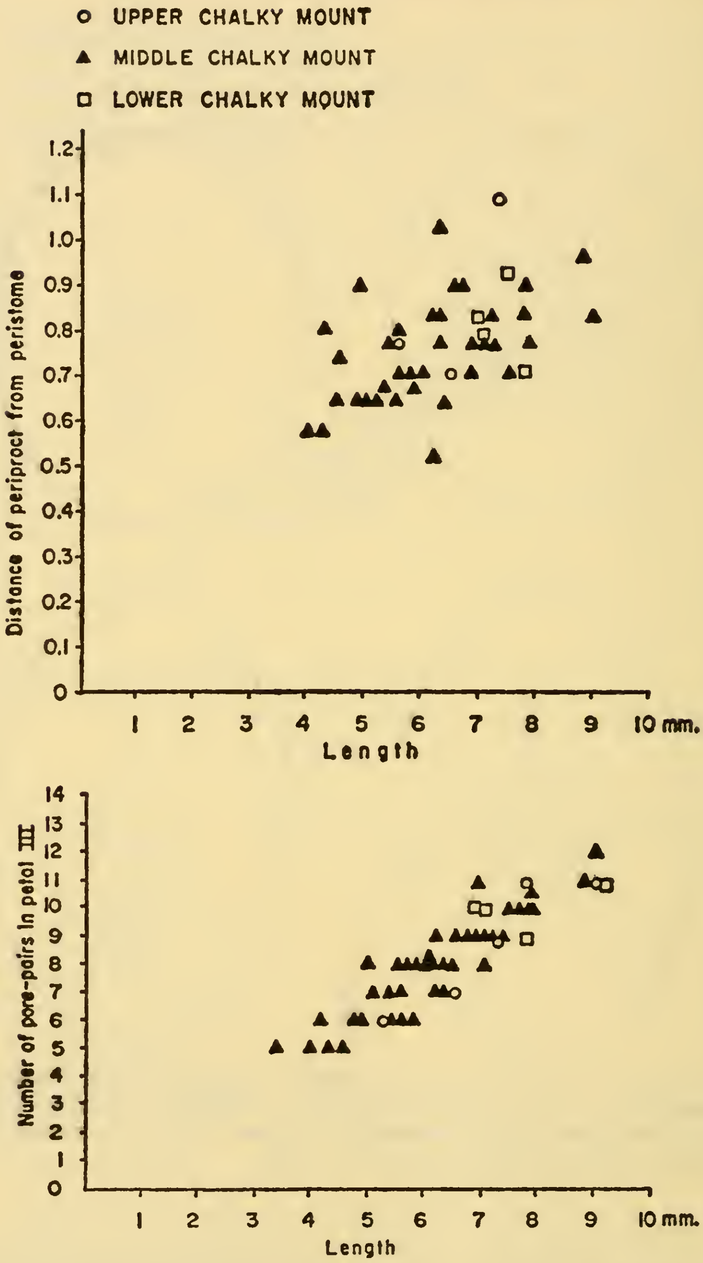


Fig. 8.—*Fibularia barbadosensis* Kier, new species: Relation of the distance of the periproct from the peristome, and the number of pore-pairs in petal III to the length in specimens from the Lower, Middle, and Upper Chalky Mount Members of the New Scotland Formation.

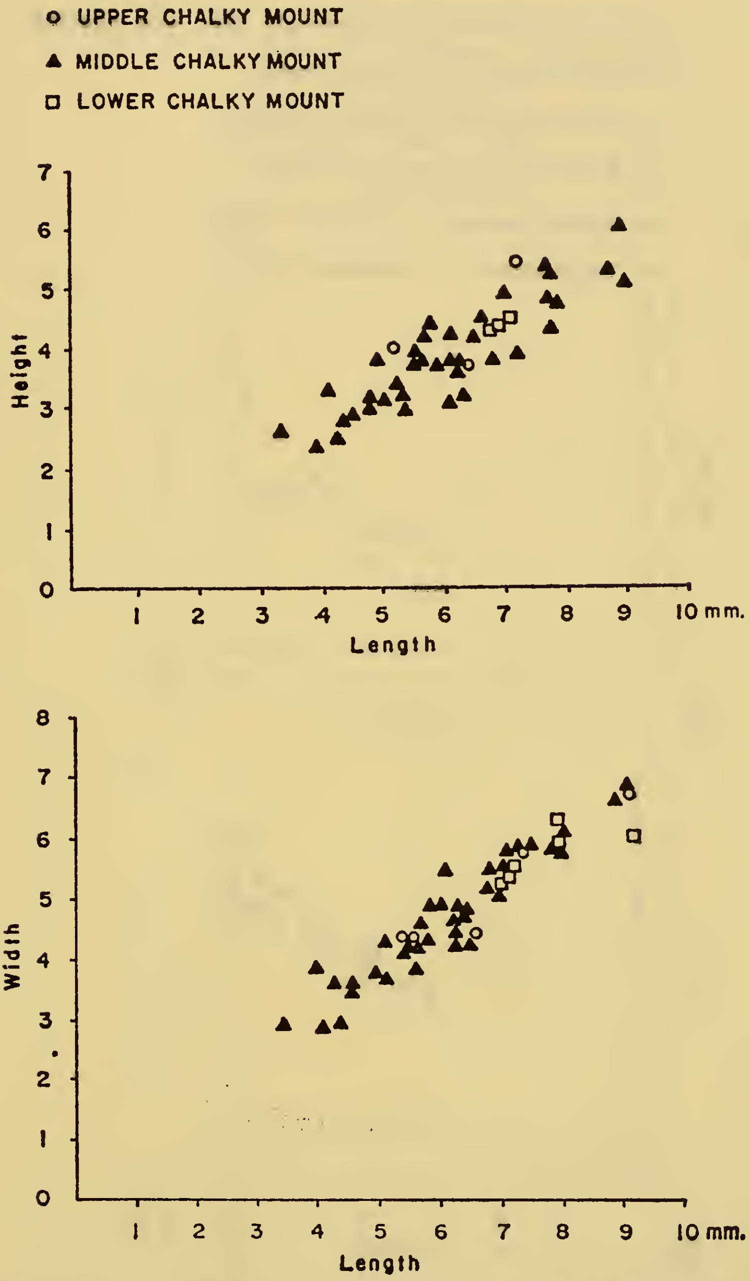


Fig. 9.—*Fibularia barbadosensis* Kier, new species: Relation of the height and width to the length in specimens from the Lower, Middle, and Upper Chalky Mount Members of the New Scotland Formation.

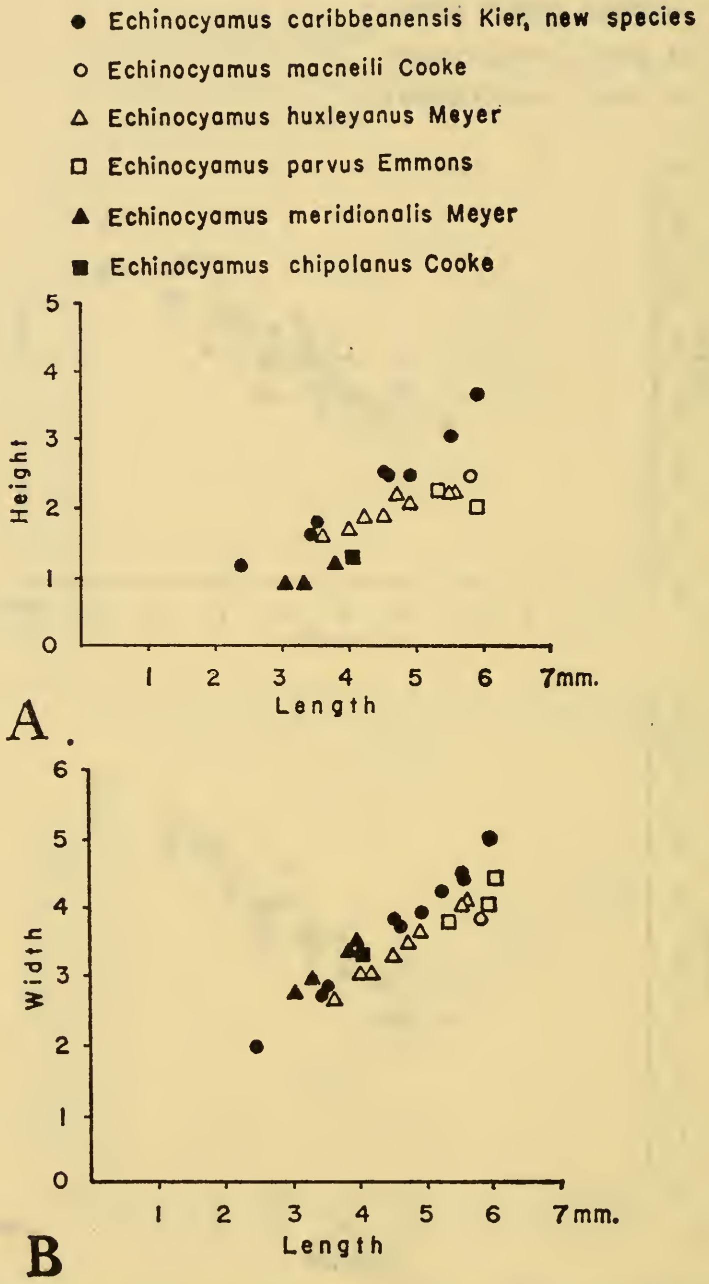


Fig. 10.—A, B, Relation of height and width to length in five species of *Echinocyamus* from eastern America for comparison with *Echinocyamus caribbeanensis* Kier, new species.

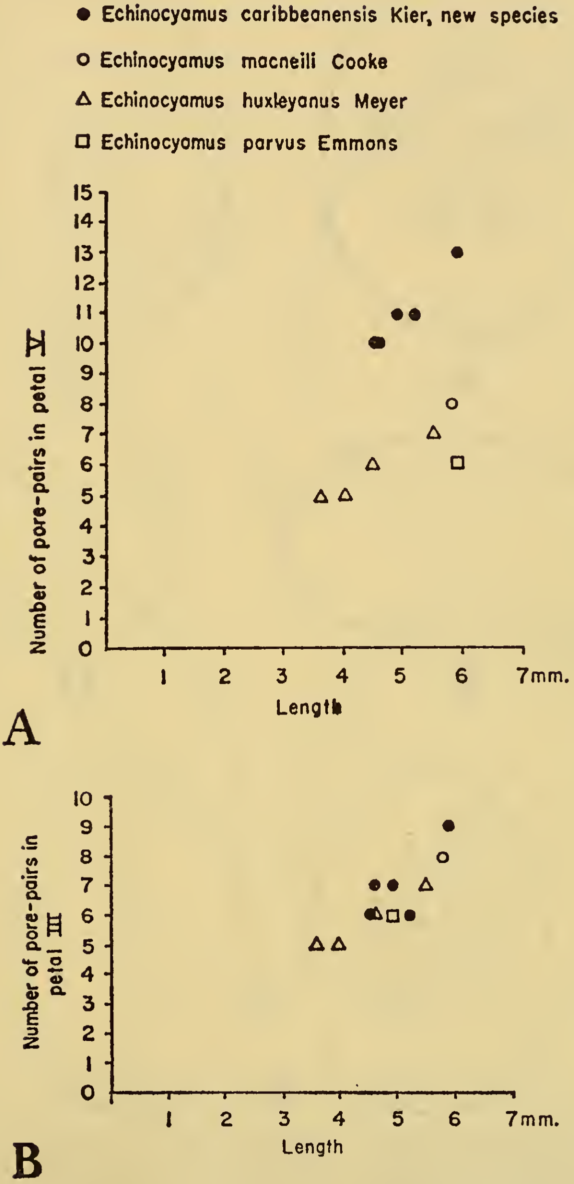


Fig. 11.—A, B, Relation of number of pore-pairs in one poriferous zone in petals V and I to the length of three species of *Echinocyamus* from eastern America for comparison with *Echinocyamus caribbeanensis* Kier, new species.

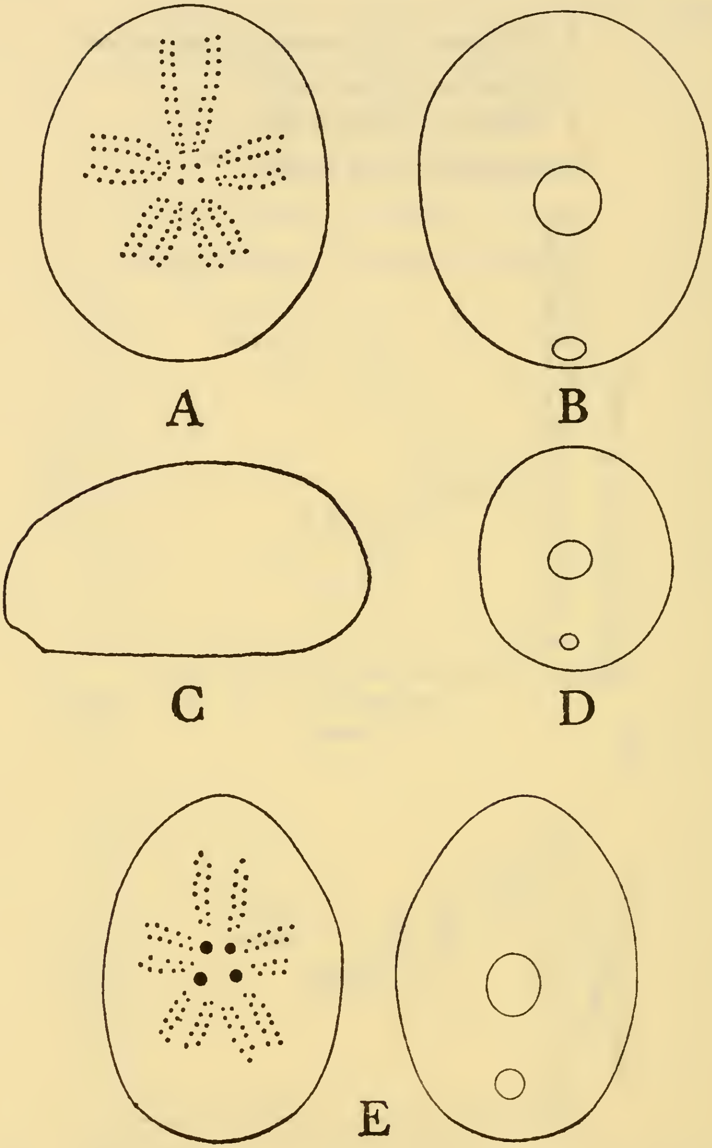


Fig. 12.—**A–D,** *Echinocyamus caribbeanensis* Kier, new species: **A–C,** Adapical, adoral, right side of holotype, Basel M6605, loc. S80, × 10; **D,** Adoral view of Basel M6606, loc. S1107, showing more anterior position of periproct in largest specimen (5.9 mm long), × 5. **E,** *Echinocyamus huxleyanus* Meyer: Adapical and adoral view of USNM 499001, Geneva, Alabama, × 10.

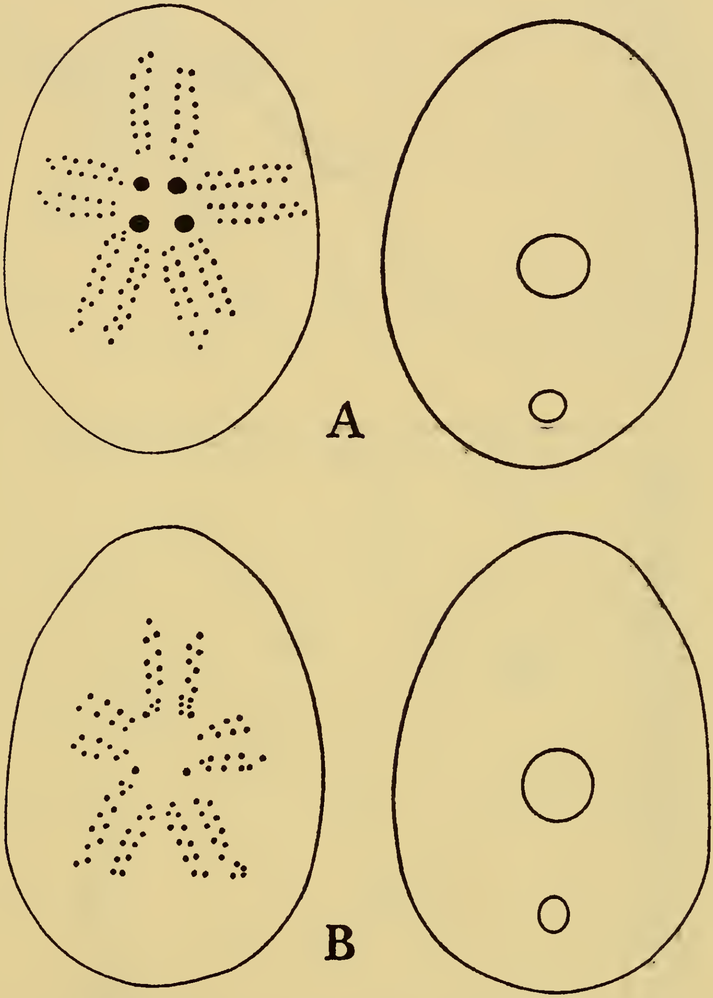


Fig. 13.—**A**, *Echinocyamus macneili* Cooke: Adapical and adoral view of holotype, USNM 562297, from late Eocene equivalent of Moodys Branch Formation at USGS 15562, creek flowing into Conecuh River in the NE ¼ sec. 32, T. 4 N., R. 15 E., Covington County, Alabama, × 10. **B**, *Echinocyamus parvus* (Emmons): Adapical and adoral view of USNM 499002, from middle and late Eocene Castle Hayne Formation at USGS 10363, J. M. Thomas' farm 10 miles north of Jacksonville, Onslow County, North Carolina, × 10.

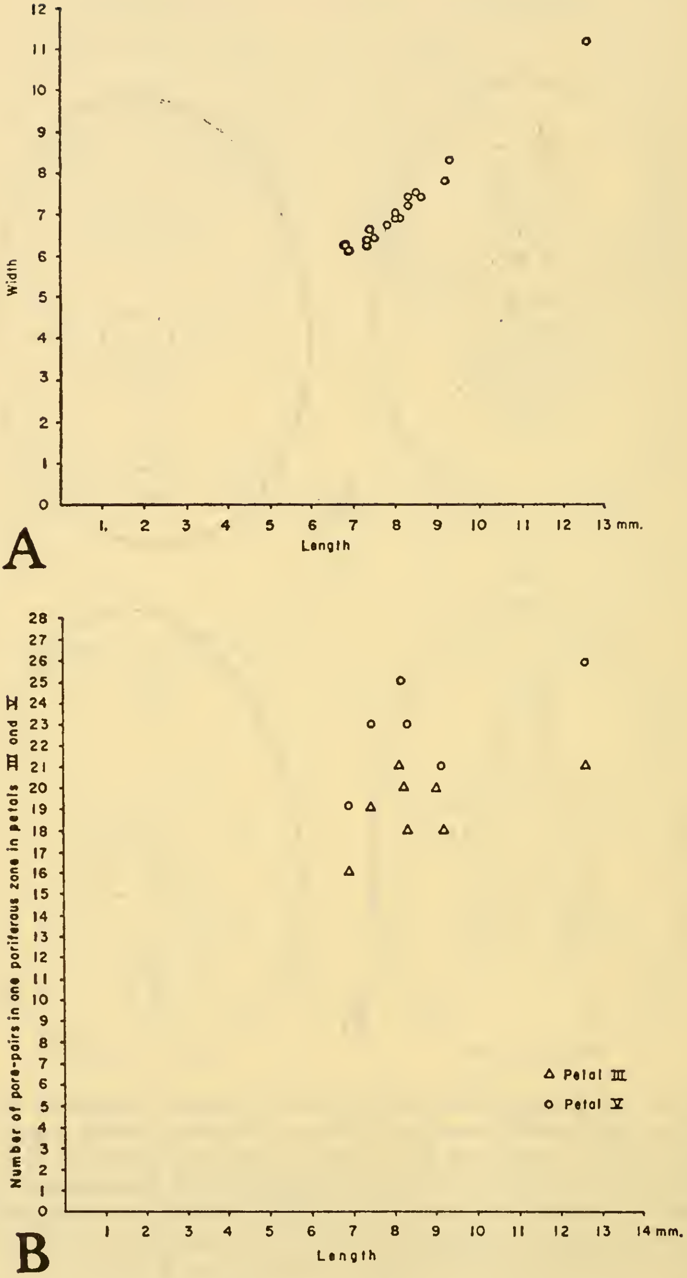


Fig. 14.—*Cassidulus senni* Kier, new species: **A**, Width relative to length; **B**, Number of pore-pairs in one poriferous zone in petals III and V.

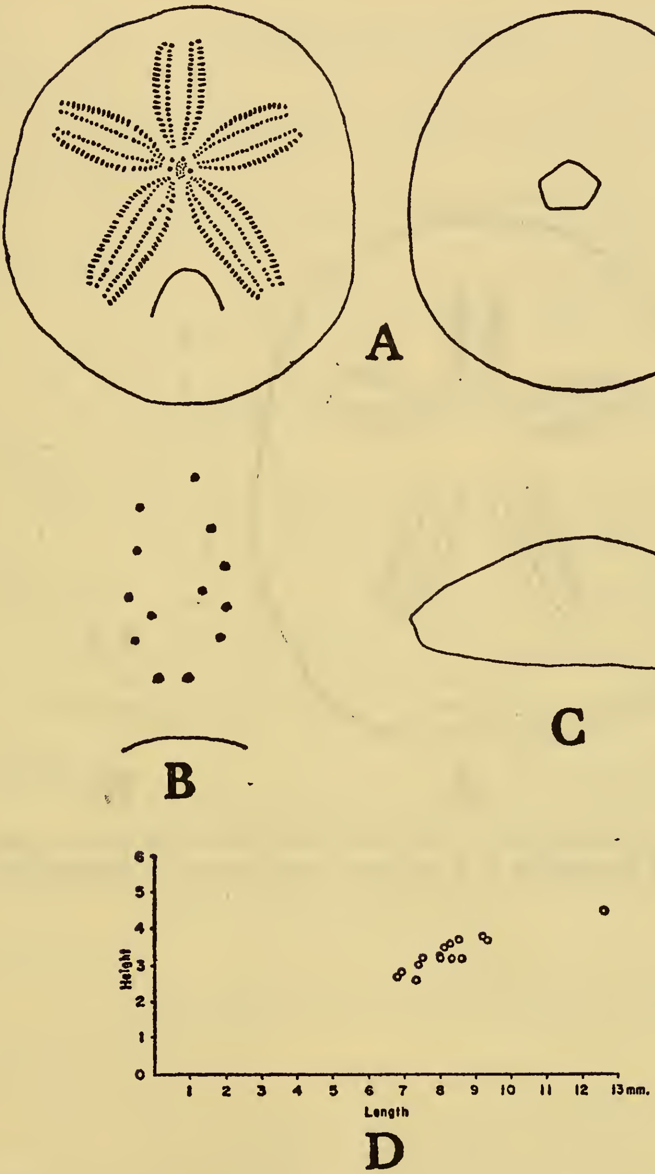


Fig. 15.—*Cassidulus senni* Kier, new species: **A**, Adapical and adoral view of holotype, M6607, loc. S152, × 4; **B**, Phyllode of ambulacrum V of M6608, loc. S80, × 30; **C**, Right side view M6608, loc. S80, × 5; **D**, Relation of height to length.

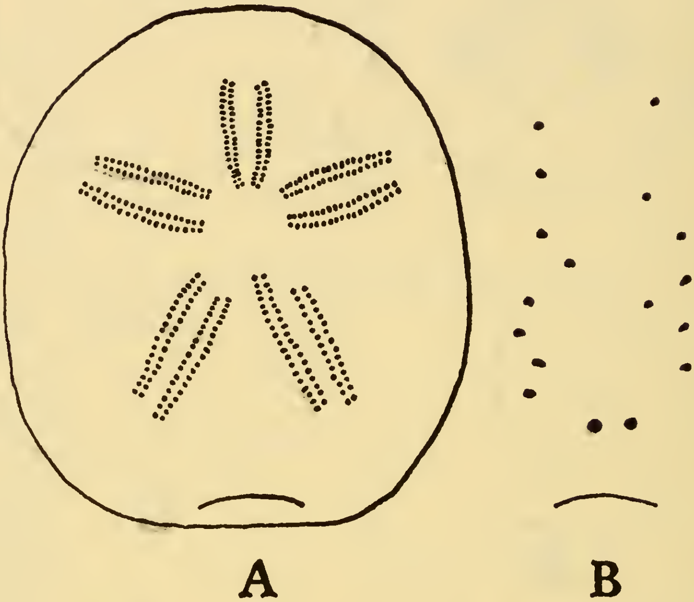


Fig. 16.—*Cassidulus mestieri* Kier, new species: **A**, Adapical view of holotype, M6610, loc. S164, × 5; **B**, Phyllode of ambulacrum II of holotype, × 25.

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EXPLANATION OF PLATE

Fibularia barbadosensis Kier, new species

1, 2, 3, Adapical, right side, and adoral view of holotype, Basel M6603, loc. S1107, × 5.

Echinocyamus caribbeanensis Kier, new species

4, 5, Adapical and adoral view of holotype, Basel M6605, loc. S80, photographed in alcohol, × 9.

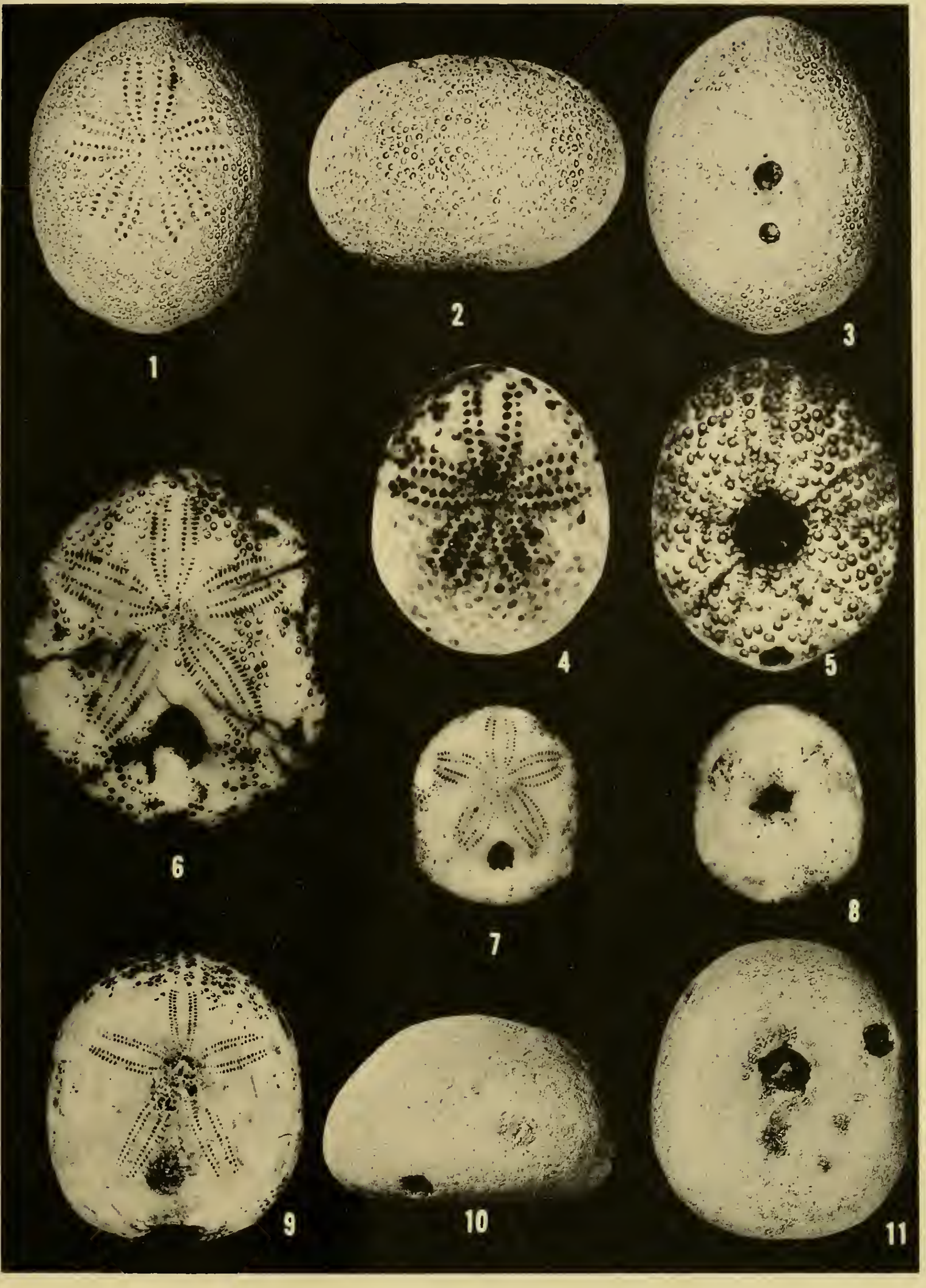
Cassidulus senni Kier, new species

6, Adapical view of holotype M6607, loc. S152, photographed in alcohol, × 4.

7, 8, Adapical and adoral view of M6609, loc. S152, photographed in alcohol, × 4.

Cassidulus mestieri Kier, new species

9, 10, 11, Adapical, left side, adoral view of holotype M6610, loc. S164, adapical view photographed under alcohol, × 3.



1, 2, 3, FIBULARIA BARBADOSENSIS Kier, new species; 4, 5, ECHINOCYAMUS CARIBBEANENSIS Kier, new species; 6, 7, 8, CASSIDULUS SENNI Kier, new species; 9, 10, 11, CASSIDULUS MESTIERI Kier, new species

nstitution.
n Miscellaneous Collection.
1966-67.

ower's Name	Date Returned
	APR 3 1975
	MAR 1 7 [illegible]
	JUN 1 4 1978
Medical Center	OCT 2 9 1980