SMITHSONIAN
MISCELLANEOUS COLLECTIONS

VOL. 117

"EVERY MAN IS A VALUABLE MEMBER OF SOCIETY WHO, BY HIS OBSERVATIONS, RESEARCHES,
AND EXPERIMENTS, PROCURES KNOWLEDGE FOR MEN"—JAMES SMITHSON

(PUBLICATION 4134)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
1953

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

ADVERTISEMENT

The Smithsonian Miscellaneous Collections series contains, since the suspension in 1916 of the Smithsonian Contributions to Knowledge, all the publications issued directly by the Institution except the Annual Report and occasional publications of a special nature. As the name of the series implies, its scope is not limited, and the volumes thus far issued relate to nearly every branch of science. Papers in the fields of biology, geology, anthropology, and astrophysics have predominated.

Leonard Carmichael,
Secretary, Smithsonian Institution.

CONTENTS

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 117, NUMBER 1

Thomas Lincoln Casey Fund

NORTH AMERICAN FIREFLIES OF THE GENUS PHOTURIS

BY
HERBERT SPENCER BARBER
WITH PREFACE AND NOTES BY FRANK A. McDERMOTT

(Publication 4051)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
NOVEMBER 27, 1951

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 117, NUMBER 1

Thomas Lincoln Casey Fund

NORTH AMERICAN FIREFLIES OF THE GENUS PHOTURIS

BY
HERBERT SPENCER BARBER
WITH PREFACE AND NOTES BY FRANK A. McDERMOTT

(Publication 4051)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
NOVEMBER 27, 1951

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

PREFACE

At the time of his death, on June 1, 1950, Herbert Barber had nearly completed the manuscript of a monograph on the North American fireflies of the genus *Photuris*. Subsequently, I was requested by Dr. E. A. Chapin, curator of the division of insects, U. S. National Museum, to review the manuscript with a view toward putting it in shape for publication. I have done this with mixed feelings of wonder at the amount of field work involved (not always in the easiest places for such studies), of admiration for Barber's persistent checking and rechecking of observations, and the logical deductions he has drawn, and of regret that he was not able to complete the work to his own satisfaction. Actually, the monograph as he wrote it is so nearly complete that little more than the correction of a few obvious typographical errors and the change of an occasional word or punctuation mark has been made in the text. His pencil sketch diagramming the flashes of the males of the various species of *Photuris* has been redrawn for reproduction, with the addition of those species he describes but did not include in his sketch.

The beetles of the family Lampyridae are almost unique among insects because of the ability of most species to produce light, a function limited to only a few other insects, although widely distributed among marine forms. As in most other insects, the family has been divided into a large number of genera, one of the most distinctive of which is *Photuris,* limited at present to New World species, and being more or less replaced in the Old World by the genus *Luciola,* of somewhat similar characteristics.

The generic name *Photuris* was first used by Dejean (1833), established by LeConte (1852), and subsequently used by Lacordaire (1857), Olivier (1886), and others, for species presumably falling naturally into this classification. The vagaries introduced by several authors have been sifted by Mr. Barber, and the details are given in the text of this monograph. Barber has done a beautiful piece of work in unraveling the tangled skein of nearly a score of morphologically very similar species, many with adjacent but overlapping habitats, and with distinct mating habits. He says, "All structures, even those of the male genitalia, appear identical in our numerous species." His manuscript refers to sketches of the aedeagus of *Photuris frontalis,* which he uses as typical, but his sketches have not been found, and I have substituted for them sketches of this structure from *Photuris lucicrescens* from Delaware. In Barber's segregated set of 19 species and varieties, 10 show the aedeagus extruded, and except for size there is no observable difference in the different species; the aedeagus of *Photuris jamaicensis,* sketches of which have been kindly lent me by Dr. John B. Buck, is also apparently identical with that of Barber's species.

That Barber was able to recognize his species in dried specimens, when he had not seen the flashing conduct, was demonstrated to me when I submitted to him a series of five vials containing specimens collected around Wilmington, Del., each vial representing a different flash; for four of the vials he told me correctly the type of flash after a few minutes examination with a lens; the fifth contained specimens having a flash with which he was not familiar, and which were probably abnormals.

This work of Mr. Barber may stem ultimately—aside from his general interest in the Lampyridae—from a conversation between him, Dr. E. A. Schwarz, and myself in 1910, when I was studying the relation between light emission and mating habits of the fireflies. *Photuris pensylvanica* was mentioned, and Dr. Schwarz remarked on the enormous numbers in which it occurred in Panama. I asked if it were the same species, and he replied something to the effect that it was the same species from Massachusetts to Panama, and then added that "some day somebody is going to split that thing up." This Mr. Barber has done with infinite care and persistent checking. That portions of the picture are still confusing cannot be denied, but it is very evident that what was long considered to be a single species is undoubtedly a complex of many morphologically closely similar species with quite distinct habits, habitats, and mating behavior. If these have to be considered "physiological species," so be it.

That this condition is not peculiar to *Photuris* is indicated by another case among the Lampyridae described to me by Mr. Barber in June 1947. While collecting specimens of the supposed *Lecontea* (*Pyractomena*) *lucifera* (Melsheimer), near Washington, he encountered a species giving a single bluish flash instead of the twinkling 5-component flash previously ascribed to *lucifera,* but upon inspection of his vials the next day he concluded he had mixed his specimens, as all those he had taken were apparently identical. On his next trip he very carefully segregated the 1-flashers from the 5-flashers, but upon inspection he was again unable to tell one from the other by general appearance. In this case the aedeagi proved to be different, but the question still remains as to which of the two is the one originally called *lucifera* by Melsheimer.

While the original manuscript of this monograph was apparently prepared by Mr. Barber about 1929, his interest in the problem continued unabated, and at least two species were defined after that time. His letters to me from 1926 to 1929 indicate the development of the ideas given in the monograph, and later correspondence gave evidence of the confirmation and extension of his observations, and also recorded his difficulties with cabinet specimens. Mr. Barber had started, about 5 years ago, an extensive review of the taxonomy of the Lampyridae, which work was most regrettably interrupted by his death. His notes show a complete grasp of the difficulties involved, an accurate and broad knowledge of the literature, and the modern concept of a species as a dynamic unit, a breeding population. Perhaps some quotations from his notes made in the course of his work on this revision may not be amiss:

Dated February 14, 1945:

> The writer's belief that each species is an isolated self-perpetuating population, limitless in individuals by past and future generations, and that our taxonomy must correctly interpret these natural species which contrast so hopelessly with the customary "taxonomic" species, has combined with his inability to apply the available names to his samples of "natural" species, to discourage completion of manuscripts.

Undated, probably 1944:

> If, however, a collector seeks the luminous species when they are active, distinguishes the signals of the several species which may be in their nuptial flight, and the peculiar flashes emitted by the opposite sexes of each, and collects individuals which emit a particular type of flash, his samples thus assembled and segregated will more correctly represent the unit species he has observed. If, also, the observer selects convenient undisturbed localities, such as upland fields, woods, river banks, marshes, etc., in which he can repeat his observations in successive seasons and years, he may find that each peculiar habitat has its sequence of species peculiar to it, their larvae present most of the year, the adults active for only a few days at the correct season, except the unpredictable abnormal individuals who leave no progeny. Repeated verification of observations is essential.

As late as September 1949 he wrote to me—

> This problem (the species of *Photuris*) is far more complicated than you think, and we are still far from the truth. Taxonomy from old mummies which fill collections is a misguided concept. It leads to the misidentification of rotten old samples in collections. How these poor fireflies would resent being placed in such diverse company—among specimens of enemy species—if they were alive and intelligent! What contempt they would feel for the "damned taxonomist."

Barber's own field observations covered, for the most part, a rather limited geographical range, roughly within a radius of about 100 miles from Washington, D. C., and to judge from the species from Wisconsin, Cape Breton, and elsewhere it is quite possible that a number of other types of flashing conduct may be found in areas outside of those he covered. Only future work can show how general the distribution of his species may be and how much overlap in range may occur.

The practical mind may ask, "Of what use is such a study?" To which we may reply with Faraday's famous retort to Gladstone: "Of what use is a newborn babe?" Aside from the basic "increase and diffusion of knowledge among men," we can never tell when, where, and how a given observation may be of practical importance. The chance observation of a bacteriologist a quarter of a century ago, that bacteria did not grow in the presence of a mold, is the basis of the multimillion-dollar antibiotics industry of today. The possible importance of the Lampyridae as predators against agricultural pests has barely been touched upon (see p. 2 of this monograph, and the writer's "Common Fireflies of Delaware," Wilmington, 1948). In any event, such a study as this of Mr. Barber's on *Photuris* is, as Emerson says of beauty, "its own excuse for being."

FRANK A. McDERMOTT.

Wilmington, Del.
December 4, 1950.

Thomas Lincoln Casey Fund

NORTH AMERICAN FIREFLIES OF THE GENUS PHOTURIS

By HERBERT SPENCER BARBER[1]

Division of Insect Identification
Bureau of Entomology and Plant Quarantine
United States Department of Agriculture

CONTENTS

INTRODUCTION

Although it has been argued that so-called "physiological species" should not be given distinctive names, inasmuch as they cannot be identified from average cabinet specimens, this attitude is opposed to the objectives of the study of natural history. The demand for visible external characters by which species may be "identified" and the exaltation of this principle as a standard of specific value have already, within the memory of most of us, broken down before the newer standard (useful in many groups but not universally so) based upon internal or reproductive organs. Species being biological units composed of populations reproducing their kind and supposedly isolated from other species by barriers of some kind, it behooves the student to find the characters by which they may be recognized. If these characters are external and "structural" in the old sense, the investigator

---

[1] For a biographical sketch of Mr. Barber, see Proc. Ent. Soc. Washington, vol. 52, pp. 259-269, 1950.—Editor.

is lucky. But if all the customarily used structural characters of shapes, sizes, and colors are variable within all of several allied species which are distinct in ecological habitat, time of maturity, habits, and courtship behavior, the student must find new standards or abandon his study. In the face of general opinion among systematists, which opinion has itself become standardized, the temptation is to take the latter course. But it is a pity that so few systematists realize that the only fundamental object of naming species is, in the ideal, to produce a system by which records of observed facts about species may be indexed so that the students of insect economy, behavior, anatomy, genetics, etc., as well as the systematist, may assemble and sort the desired data. Surely the confusion will be inextricable if only those species that chance to display some "structural" character receive distinctive names.[2]

In some groups specialization in structure seems to have occurred without apparent specialization in habits; in other groups structures remain practically identical but habits have become distinct; and in still others the exoskeletal variation within members of a brood may render ordinarily used characters useless, or plasticity of habits may, by accident, accompany temporary development of a differential habitus. Hybridization may be so common as to unite similar species into a variable or even homogeneous population, or may be so rare that fertile offspring, fit for reabsorption into either of the self-perpetuating species, are as infrequent as in mules.

In the genus *Photuris* individual variation is so common that the following studies have yielded few characters besides certain generalized differences of color, size, and, in a few cases, proportion; but since these are connected with habitat and habit distinctions, they must serve until better diagnostic characters are found. All structures, even those of the male genitalia, appear identical in our numerous species.

Although *Photuris* larvae are general predators on snails and soft-bodied insects and may be of some economic value as enemies of cutworms (Hess, 1920),[3] the specialization of different but hitherto confused species to different and particular types of breeding ground indicates diversity in the preferred prey. Records of observations on

---

[2] Dr. Ferris has published similar views (Ferris, G. F., The principles of systematic entomology, p. 48, Stanford, Calif., 1928). For a further discussion see Mayr, Ernst, Systematics and the origin of species, New York, 1942 (1949), particularly p. 20, "What is a taxonomic character?"—McD.

[3] Names and years in parentheses refer to the Literature Cited at the end of the monograph.—McD.

feeding habits are fragmentary and cannot now be associated with particular species, but it should be obvious that marsh-inhabiting species could have little influence on a cutworm infestation in an adjoining field, whereas an abundant upland form, such as *pyralomimus,* described below, might be an important enemy.

OBSERVATIONS ON ADULT BEHAVIOR

Since the writer's interpretation of our *Photuris* fauna as he has observed it differs from that of students of fireflies who rely upon dried specimens and upon the standards of the older taxonomists, he begs for a moment that readers imagine themselves sharing with him a few selected experiences that have forced great changes in his belief as to what constitutes a species.

1. A hilltop field of grass bordered by woods in Rock Creek Park, D. C., early in June.—*Photuris* have just appeared here in the past few days, and on this evening they are flying in numbers over the field but not in the woods. Many are flashing in the gathering dusk as they fly a few feet above the grass, and only two types of flash are apparent in the air, the commonest being a series of about six very quick flashes in less than a half second, of not great brilliance. These are all males flashing their signals, hoping for answering flashes from prospective mates. Rarely one may see such a response in the short grass—a brief, less brilliant, single glow of about a third of a second duration—and observe the quickened repetition of the male's signals as he approaches in a long oblique descent. This female flash appears seldom in the air. Green leaves and the fingers are held over the bulb of a small flashlamp by the observer, concealed among foliage, and an attempt to mimic the female flash is made immediately following the flash of a nearby male. He comes rapidly to the hand and is caught; other males have seen the mimic of the female's flash and are coming also, so that the collector may catch half a dozen with the hand without moving from the edge of a concealing bush. A steady light does not attract, but frightens the males away. Another type of flash is occasionally seen as we ramble about, but it is the short, frequent, but very irregular flash of disturbed individuals, usually females, whose agitation is visible in abnormal functioning of the light organ.

This species the writer identifies doubtfully as *versicolor* Fabricius, which was described in 1798, without more definite locality than North America, from a specimen received from Mr. Hirschell and has since been incorrectly suppressed as a synonym of an earlier given specific name.

2. A rocky, heavily wooded island in the gorge of the Potomac late in June.—At the downstream end an alluvial deposit subject to freshets supports a dense growth of maples bound together by a canopy of wild grapevines, hiding the stars; underneath, a few sandy freshet channels can serve as paths. The great wood interior is filled with innumerable flashes of greenish-white light, and at first there seems no variation in the flashes. Each firefly appears to give a single short, very bright flash for each second that it flies, and all those flashing are males. An occasional slightly different flash on foliage or ground is investigated and discloses the presence of females, which have presumably mated and are not at all interested in the self-assertive males.

Two or three times during the preceding winter and spring the floods have swept for days, roaring between the trees and among the sandbars, bringing logs and smaller driftwood, which lie in masses where the trees chance to hold them. Other species of fireflies appear discouraged by such abuse of their breeding ground, but before the firefly season comes, the glowworms of this form are abundant in and about these masses of river drift, above and in the immediate vicinity of which the males later fly in numbers. Occasional individual adults are to be seen in every few hundred feet of river forest in June, but these are supposedly strays maturing where they were left as larvae by the water. The spring freshet of 1928 washed out the glade in which the species was watched the two preceding years, but it left an accumulation of drift on some logs 50 feet to one side. Few of this species were seen where formerly abundant, but they later became numerous about the driftwood. This species is herein named *potomaca,* p. 28.

3. Crossing the current to the Virginia shore, we see the same species in fewer numbers in the fringe of trees on the bank, but in the field behind are a few belated males of the flicker-flash species above described (*versicolor* Fabricius?). The path crosses the small neglected field and dips into a damp hollow carrying the drainage from Black Pond and bordered with scattered willows, beyond which the ground rises a few feet to a terrace upon which low alders grow. Then there is another narrow grassy strip and the wooded rocky hillside rises abruptly. The willows and low vegetation along the sluggish stream are glittering with myriads of flashes, of almost the same short duration and interval as the greenish lights we have just left in the river forest, but these are faintly orange instead of greenish, and slightly slower, about three flashes in 4 seconds. The samples caught are all males, but are smaller in size, differently colored, and

have slightly more elongate antennae. This species is herein named *hebes,* p. 34.

4. A few steps farther, the path enters the alders and immediately a very different type of flash confronts us. Poising almost motionless in the air, its light begins dim, grows steadily to great brilliance and dies abruptly, to reappear a quarter or half minute later as the firefly poises a few feet distant and again remains illuminated for from 1 to 2½ seconds. All these are, as before, males, but they are larger, broader, and much paler in color. Their females are found demurely about their business of seeking food, for the female *Photuris* eats other fireflies; but since no courtship is observable they are supposed to be already mated individuals no longer interested in the surrounding lights. This species is herein named *lucicrescens,* p. 33.

5. Drive 15 miles to the tide marsh of the Anacostia River, and even though the hour is midnight *Photuris* of several species are still flashing. The long crescendo flash just described is conspicuous in the bushes bordering the marsh, and in the treetops is a very short, bright flash, almost an explosion of light, at 4- or 5-second intervals. Samples of this species we cannot reach in its normal flight. But over the level tops of the tall, rank grass of the marsh another very different flash greets us—an instantaneous explosion of light followed immediately after an extremely short, dark interruption by a protracted brilliant light lasting 1 to 2 seconds, with the end perceptibly diminished in intensity. We wade into the deep grass and ooze and catch samples. They are not half so large as the crescendo-flash species on shore, and some have wing covers pale except basal remnants of the brown vittae. Certainly it is the only species seen tonight to which the original habit notes and description of *pensylvanica* (original spelling of specific name), published by De Geer more than a century and a half ago, can be applied. While emitting this double flash the male (for no females are visible to us) poises in his flight over the grass tops, dips slightly and rises, describing little U-shaped curves of light, the finish a little higher than the first flash. He must watch for his bride's answer straight beneath, since marsh grass stands vertical at this season and cannot be seen through obliquely. But his behavior is the result of instinct instead of reason and reflects an immensely old specific adaptation to this particular ecologic environment. No females can be found while we walk forward, but if we turn and force our way backward through the grass their annoyed flashes deep in the disturbed grass or on the surface of the ooze permit their capture in numbers. In the vial used to preserve these females I find

a minute fish (*Umbra*). Was a female eating a fish when caught? No other debris is in the vial.

6. Dense *Baccharis* bushes on a sand spit joining a wave-eroded bluff surmounted by oaks and pines, overlooking the brackish water of an arm of the Chesapeake early in July.—A warm evening breeze sways the bushes and low among them, or rising in their lee, fly moderate numbers of a small firefly emitting short, abrupt, faintly orange flashes at intervals of about 3 seconds. Specimens caught resemble the small, willow-swamp form (*hebes,* above), and the long double-flash species of the fresh-water tide marsh (*pensylvanica*), but they seem to have larger eyes and shorter antennae than these others.

Again, a small salt meadow near the mouth of the Potomac estuary, in front of pines, hollies, oaks, *Myrica, Baccharis,* and *Iva* bushes, in successively more frequently inundated tidal shore line than the wetter salt marsh.—Among these bushes and straying among the nearby grass tops appear short, slightly orange flashes at 2- to 3-second intervals, but the insects keep well down where the shore breezes do not blow them away from their native habitat, thus contrasting strongly with the other species visible in the woods.

The small size of the firefly and its feeble flash resemble those of *hebes,* but the preserved samples differ in that this salt-marsh species shows larger eyes, shorter and stouter antennae, a black labrum, and a broad, black, midpronotal vitta. The ancestors of this species having for ages past held their place among the shore bushes against breezes, the generation now under observation flies low among the sheltering bushes undisturbed by a mild wind which scatters and forces down the flight of *hebes.* We shall later (p. 35) name this new form *Photuris salinus.*

7. Varying from year to year with the earliness or lateness of the season, the flicker-flash species (*versicolor*) appears in the above-described field at Black Pond about the middle of May and has become relatively scarce by the second week of June, when it is replaced by a slightly smaller form whose males, when not disturbed, appear to have two distinct types of light signals. This form seems to originate from the swampy ground among the willow and alder clumps some two weeks before the larger species, *lucicrescens,* and the smaller one, *hebes,* above discussed, begin to be seen. The behavior of this intermediate species (if it be but one form with two habits) will be variously interpreted according to preconceived notions, but requires record here.

As the sky colors fade to gray, the first sharp, greenish-white flashes appear in the clumps of bushes and on their darker eastern sides, contrasting strongly with the feebler orange flashes of the few early males of *Photinus scintillans,* which almost immediately cease their activity. As dusk deepens, the *Photuris* become numerous, the very short, sharp flashes being emitted at intervals of from 3 seconds, on a pleasant evening, to perhaps 10 seconds, if it is cool and there is heavy dew. In the latter case they soon cease to fly and their slower flashes emanate from males resting on foliage in slightly more sheltered situations. But from time to time there appear among them males flying slowly over grass or bushes, or even resting on foliage if it has become cool, and emitting long, tremulous flashes, less intense than the commoner sharp flash, consisting of perhaps 10 to 20 pulsations, and lasting about a second. Within a quadrant of perhaps 50 yards' radius from the same point of observation, these long tremulous flashes may appear, followed by others, becoming more and more numerous, the shorter flashes disappearing until for a few minutes the long flashes dominate. This phenomenon suggests either that another species has temporarily become active, as the writer has often observed with certain species of *Photinus,* or that a contagious emotional exuberance has changed the behavior of those males formerly emitting the short flashes. Samples of the producers of each type of flash are not distinguishable, as in the case of *Photinus* above alluded to, and are hereinafter (p. 31) described as but one species, *tremulans.*

8. Late in July the swampy forest bordering the Patuxent River at Priest's Bridge, Md., is visited. As on previous visits during the preceding three weeks, only one species of *Photuris* (*lucicrescens*) seems to be active, displaying its long, crescendo flashes, but the numbers are now much reduced, and the flash appears shorter compared with our half-second pendulum, used for estimating duration of flash and of dark interval. The light appears to last from three-fourths second to about one and one-half seconds. The treetops are watched for the very short flashes seen elsewhere, but none are seen there now, nor were they seen on previous visits. We return along the road to the Capital, stopping when colonies of fireflies are seen. *Photinus pyralis* having ceased its activity at an earlier hour, no flashes are seen except about trees bordering wet spots in the hollows, usually swampy courses of small streams. Two such places show only the crescendo flashes, but about 6 miles west of Priest's Bridge we first see numbers of the very short explosions of light in the air about the tree tops. A gust of wind disturbs the fireflies, and one comes down among the lower branches flashing at about 5-second intervals,

very bright and short, about like the one-tenth-second camera shutter held against a light. When almost within reach the strong spotlight beam is abruptly thrown on him, and the net brings him to hand. No chance this time to have netted the wrong firefly, but he looks no different from those taken in their long crescendo flash. No more come down, and we must give up and go home.

Why were none of these flashes seen at Priest's Bridge or at two other stations? Why do both types of flash occur here and at some other places?

Various answers will satisfy various persons, but no one knows. Envy the bats their wings? With them we might follow single specimens through their evening's activities and see if they change their flashes.

By the first week in August the firefly population of the wooded island, the alluvial field, the willow-lined marshy stream, and the alder bushes near Black Pond has changed. A few belated females and an occasional male of the large crescendo-flash species (*lucicrescens*) are mixed with larger numbers of the short-flashing, smaller form (*hebes*) but are no longer confined to the restricted areas as observed in June. Abnormals appear in all populations, and these late-issuing individuals may have been lacking in some of the factors inducing early transformation or fertilization, and the resulting restless dispersal flights may have carried them far beyond the preferred breeding ground. The whole impression is that of meaningless variation, and doubts of specific significance are inevitable under such conditions. In the tidal marshes the little double-flash species (*pensylvanica*) has vanished, and from the shore forests strays of other species, most of them females, have wandered out over the marsh where they mingle with surviving individuals of a small *Pyractomena* and several small species of *Photinus*. Here again one can see only chaos in their behavior, but next year at the proper time and place the new generations will court their mates in a similar manner. Specific flashes will win specific answers, leading to reproduction. Perhaps we may learn that the manner of flashing is a barrier to possible intermixing of species. Perhaps the late-season abnormals are mixtures. Must we then ignore the differences in the early-season broods?

9. Through the kind interest of friends, observations and well-preserved samples of *Photuris* are available from the vicinity of Winona, Minn., where three apparently distinct species were encoun-

tered on the evenings of July 6 and 8, 1926, by Miss E. Myers and B. Boland. Two localities were examined: The first, which was rather dry land, 10 miles west of Winona on the road to Stockton, yielded 13 males of a form (*versicolor* var.?) whose males emitted five short, greenish flashes as fast as one could count, at perhaps half-minute intervals, while flying 2 or 3 feet above the tips of the tall weeds, and four males (*caerulucens*) that emitted a slow, blue-green flash of about 1 second's duration, whose light was dimly visible after the end of the flash. Flashes of the latter species were seen in much greater numbers in more open pastureland nearby and over trees. This latter species was taken in series (30 specimens) at the second locality in Wisconsin between Dodge and Bluff Siding, 10 miles northeast of Winona, producing the bluish-green, 1-second flashes over damp ground near a tamarack swamp. With it in almost equal numbers (24 specimens preserved) flew a slightly smaller but otherwise similar species (*aureolucens*) that emitted single, short, orange-colored flashes indistinguishable from the flashes of *Photinus castus* (?), which had been abundant at the first locality. Neither the latter species nor the 5-flash species was observed at this second locality.

Thus in one evening in June at Washington one may encounter pure colonies of five or more species of *Photuris,* and the vicinity of Winona yields three species which occur at the same time but are biologically very distinct, although, considered taxonomically, they offer few reliable characters for recognition of cabinet specimens. All these species have been until now commonly identified as *pensylvanica.* If, however, the observer finds localities in which several of these species are mixed, and their several females contribute to the confusion of flashes, and if the observer collects but few samples without noting their flashes, he is readily convinced that it is only variation, and that there is no law of uniformity in the genus *Photuris.*

Variation in motive for flash, in the flash itself, as well as in size and in pigmentation of body, must be admitted, and the writer is far from satisfied on a great many points in this complex problem. The female flash serving as a sex signal in response to a male flash for the same purpose must be rarely visible to us. The flashes we see from females must often be warnings or nervous responses to irritation, but another suggestive phenomenon has been observed too often to be ignored: Sometimes the familiar flashes of a small species of *Photinus* male are observed excitedly courting a female, supposedly of the same species, whose response flashes appear normal to its kind, but when the electric light is thrown upon them one is startled to find the intended bride of the *Photinus* is a large and very alert female *Photuris* facing him with great interest. Does she lure him to serve as her repast? Very often a dim steady light near the ground proves under the flashlamp to be a small, recently killed male *Photinus* being devoured by a nonluminous female *Photuris,* and females of the largest form of *Photuris* (*versicolor*) have been found quietly feeding on dimly glowing males of *Photinus pyralis* that had been wrapped in silk in an orb web from which the spider had departed, the *Photuris* female crawling on the web apparently in no danger of becoming entangled. Cannibalism has often been observed in captivity, male *Photuris* being devoured by their supposed females; but the writer's observations and those of McDermott (1917), as well as those of Williams (1917) and Hess (1920, p. 52), were made when all our familiar *Photuris* were called by one name, and the sexes may not have been conspecific. The accounts of *Photuris pensylvanica* by all three of these writers seem to have been based upon two or more species whose differences were interpreted merely as variation, but as series of rapid flashes are referred to in each it appears that some forms of the possibly composite species here called *versicolor* Fabricius were included in the material for each of these studies.

Mistakes will be made by the most careful observer in his attempt to record what he sees in connection with definite samples for subsequent comparative study. Minor variations occur in the population of a single species. Pure colonies are not often found. No satisfactory timing device has been available. A watch producing half-second ticks worn at the ear might offer sufficiently definite time rhythm for more accurate estimates of flash duration and interval.[4] The half-second swing of a short pendulum on a stick held in the hand is sufficiently accurate in spite of variation due to one's irregular movements. Its beat can be felt without looking away from the observed firefly, and luminous paint on the apparatus has been found unnecessary. After striking at a particular individual, two fireflies, perhaps of different forms, may be found in the net, an unnoticed individual having happened to be within the sweep of the net. Perhaps the desired specimen is missed and an imposter receives the label of careful observation, false when thus attached. But more often the trouble of writing labels for single individuals in separate vials tempts one to trust memory too far and vials become confused.

---

[4] Some cheap watches tick four times to the second and if alternate ticks are of different tone are very useful as a standard rhythm by which flash duration and intervals can be estimated.

Certain typical observations have been contrasted in the above account, and a short statement regarding measurement and interpretation must be made.

It should be obvious that since these phenomena are visible only in the natural environment and represent the normal ways in which undisturbed males seek to satisfy their mating instinct, laboratory methods of exact measurement or controlled experiment are of no use. It is difficult for one observer to contrast, verify, record, and reconstruct all the factors of all the forms in this intricate problem, even in the limited environment of Washington. Imagining the ideal opportunity for observation, we might wish for two adjacent pure colonies which could be observed and contrasted at leisure. In any pure colony we must expect to observe (1) some variation in the normal behavior of the seeking males, and (2) very irregular behavior on the part of the females that have mated.

The courtship flashes of *Photuris* males appear to have become specialized in certain species from the normal short, single flash emitted at rather regular intervals of 5 to 10 seconds, by increased frequency in *hebes* (which flashes at 1- to 3-second intervals according to the warmth or coolness of the evening), and in *potomaca* (which, on a warm evening, may attain a rate of nearly two flashes per second), or the duration of the light emission may be lengthened and interruptions introduced as in the flicker-flash species *versicolor,* the protracted tremulous flash of *tremulans,* the interrupted protracted coruscation of the small marsh-inhabiting species *pensylvanica,* or the long crescendo flash of *lucicrescens.*

The first-mentioned simple flash is given in such diverse colonies, varying so in size, color, localities, and dates of appearance, that no well-defined single species is discernible at this time, and no specific name is here attached to samples. The frequency, pattern, and intensity of the characteristic flashes of the males of several of the species of *Photuris* described herein are diagrammed in figure 1.

NOMENCLATURE

Fears have been entertained that an unfamiliar name must be adopted to replace *Photuris.* This name first appears in the 1833 edition of the Dejean Catalogue (p. 103), where 34 American species are included, all but a few of which (perhaps all but three species) are nomina nuda. *Photuris versicolor* Fabricius and *hectica* Fabricius are valid species therein contained, and were it not for the query after the latter name the designation of this species (*hectica* Fabri-

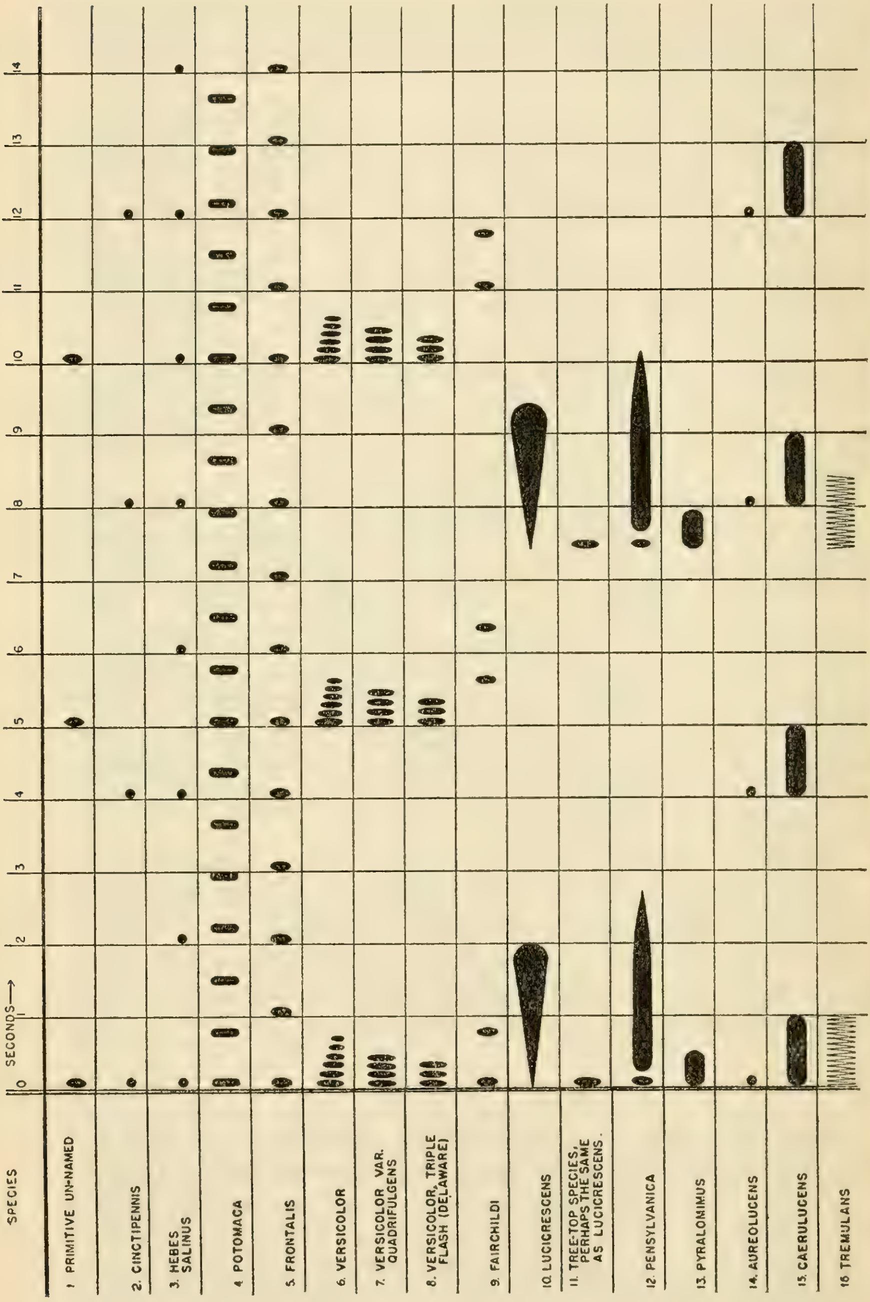


FIG. 1.—Diagram of flashing conduct of males of *Photuris* species. The time scale gives the usual frequency and duration of the flashes; the height and length of the marks indicate the intensity and pattern of the flashes. For further explanation see opposite page.

EXPLANATION OF FIGURE 1

No.	*Species*	*Key No.*	*Duration and intensity of single flash*	*Frequency of flash*	*Color of light*
1	Primitive unnamed	..	Short; single Moderate	1 each 5 secs.	Yellowish?
2	*cinctipennis*	17	Short; single Weak	1 in 4 secs.	Yellowish?
3	*hebes* *salinus*	15 16	Short; single Weak	At 1 to 3 secs.	Almost orange
4	*potomaca*	7	Short; single Bright	Rapid, up to 2 per sec.	Greenish
5	*frontalis*	5	Short; single Moderate	At 1-sec. or less intervals	Greenish
6	*versicolor*	8	Composite of 3 to 5 or 6 very short, bright coruscations	At about 5 secs.	Greenish
7	*versicolor* var. *quadrifulgens*	9	Composite of 4 very short, bright coruscations	do.	do.
8	*versicolor,* triple flash (Delaware)	..	Composite of 3 very short, bright, rapid coruscations	do.	do.
9	*fairchildi*	11	2 short coruscations separated by an interval Moderate	At 5 to 6 secs.	?
10	*lucicrescens*	14	¾ to 2½ secs. Very bright	At 5 to 10 secs.	Greenish
11	Tree-top species, perhaps the same as *lucicrescens*	..	Very short and bright	do.	do.
12	*pensylvanica*	6	Long; double Moderate	do.	do.
13	*pyralomimus*	10	½ sec. Moderate	do.	Yellowish?
14	*aureolucens*	13	Short Weak	1 in 4 secs.	Yellow
15	*caerulucens*	12	1 sec. Moderate	1 in 4 secs.	Bluish green
16	*tremulans*	11a	1 sec. Bright	1 in 5 to 10 secs.	Greenish

cius) as genotype by Motschulsky (1853) would demand recognition. But Laporte's revision (1833) of the genus *Lampyris* proposes a different name, *Telephoroides,* for six valid species, including *pensylvanica,* and LeConte's 1852 rejection of "this uncouth name" claiming that it was printed "as a French word" appears to be an unwarranted action. LeConte's apparent belief that a generic name is invalid unless accompanied by diagnoses also led him to refer to *Photuris* as "the hitherto unpublished name of Dejean." In further subdivision of the group, Motschulsky (1853) adopted both of the above generic names and proposed seven new ones, designating genotypes for all. Lacordaire (1857, p. 338, footnote 1) supports LeConte's attitude and rejects Motschulsky's work, but in spite of the latter's designation of *occidentalis* Olivier as genotype of *Telephoroides* Laporte he credits this genus to Motschulsky and (p. 339, footnote 5) designates *pensylvanica* DeGeer, with *versicolor* Fabricius mentioned as synonym, as genotype. Gorham (1880) follows Lacordaire but designates *pensylvanica* as the type of *Photuris* LeConte. E. Olivier (1886) also ignores Motschulsky's genotype designations but rejects only five of his genera. In his 1907 work E. Olivier does not allude to genotype and suppresses all nine genonyms (credited to Motschulsky) under *Photuris* LeConte, but in 1910 the same author recognizes three genera, again ignores genotype designation, and arbitrarily lists the generic synonyms.

A future study must extricate the tangled nomenclature, but for the present it is enough to claim that Motschulsky's designation of *hectica* Fabricius as type of *Photuris* Dejean is invalid under the second paragraph of Article 30e of the International Code, and since no other genotype designation is known the writer hereby designates *Lampyris versicolor* Fabricius type of *Photuris* Dejean.

The genotype of *Telephoroides, Lampyris occidentalis* Olivier, 1790, designated by Motschulsky (1853), is unknown to me, and Lacordaire's designation of *pensylvanica* is invalid; but since the former is cataloged in the genus *Photinus* by E. Olivier, 1910, our continued use of the name *Photuris* for our North American species may be justified even though the actual publication of the Dejean Catalogue dated 1833 may be subsequent to the Laporte revision, which appeared the same year.

A still more exasperating case is that of *Pyractomena,* in which varied applications and spellings of the name have been incompletely cataloged without application of the genotype principle. Revision of all usages of the name is required, and we may even be forced to suppress its earliest valid form as a synonym of *Photuris,* but the proposal of substitute names is unwise until more complete bibliographical research is done and a better consideration of systematic relationships is possible. It now appears that *Lecontea* E. Olivier, 1899, is the proper genonym for the North American forms, although it differs in only one letter from the pythid genus *Lecontia* Champion, 1889.

Those seeking to apply the law of priority and the genotype principle to lampyrid genera may find the following chronological outline suggestive:

1833. Dejean (p. 102) groups 11 species into a genus that first carries the name "*Pyractomena* Dejean," but, although specific names are listed from Klug, Mannerheim, Latreille, and Dejean, no description of any of these species by these authors has been found. Since all appear to be nomina nuda the writer believes *Pyractomena* must be considered a nomen nudum of this date, although he also believes that the citation of Dejean by authors subsequently adopting his proposed genonym demands (article 19) that evident lapsus calami or typographical errors be corrected. One of the included species, *marginata* Latrielle, may be found to be valid if a mention of *marginata* Linnaeus or Fabricius or Olivier can be found in Latreille's publication, but his only mention of this species that the writer has found (Humboldt and Bonpland, vol. 1, p. 348, 1811) is casual. He uses the French spelling without citation of author, and in the abbreviated German translation of this paper (Germar Mag., vol. 1, part 2, p. 122) the Latin name replaces the French form but without citation of Linnaeus.

1837. Dejean (p. 115) same as in 1833.

1843. Sturm (p. 76) in cataloging his collection adopts "*Pyractomena* Dej.," listing eight forms, all apparently nomina nuda, except the third species, *marginata,* which is accompanied by citations to Linnaeus, Fabricius, and Olivier. The generic name is therefore valid, with *marginata* Linnaeus, 1767, as its type, but this species is cataloged by E. Olivier, 1910, as a Brazilian species of *Photinus* with only two references, the original description and the redescription with figure by Olivier, 1790. This latter figure looks so much like a *Photuris* that *Pyractomena* Sturm may be one of its synonyms or subgenera, but until Linnaeus' and Olivier's types can be identified with adequate modern specimens no certainty can be felt that the figure represents the Linnaeus species.

1845. Melsheimer (Proc. Acad. Nat. Sci. Philadelphia, vol. 2, p. 304) described two Pennsylvanian species using the genonym *Pyratomena* (*c* omitted), but since he cites "Dej. Catal." for the name, "a lapsus calami or a typographical error is evident," and the generic name must be considered a homonym of that used by Sturm, but with *lucifera* Melsheimer, 1845, as its type.

1847. Erichson (Wiegemann's Archiv für Naturg.) adopted *Pyractomena,* citing Dejean, for a new Peruvian species, *interrupta,* which became his monobasic type and is cataloged by E. Olivier, 1910, in *Photinus,* although its bifid claws are more suggestive of certain groups of *Photuris.*

1849. Solier (*in* Gay, Hist. Chile, vol. 4, p. 445) cites Dejean and thought he adopted his invalid generic name, but spelled it *Pyractonema* (transposing the *n* and *m*), for nine new Chilean species which have since stood as a distinct genus under this name. His first species, *compressicorne,* is figured and is here designated genotype, but, as above argued, correction of spelling is required and the name becomes a homonym. The proposal of a new name is postponed pending a better knowledge of the limits of the genus *Lucidota,* of which *Pyractonema* Solier appears to be a part.

1849. LeConte (*in* White's Statistics of Georgia, p. 31, supplement) includes no valid species.

1850. LeConte (*in* Agassiz, Lake Superior, p. 228) lists *Lampyris borealis* Randall under *Pyractomena* Dejean, this being the basis of the below-cited remarks by McDermott, 1917.

1852. LeConte (Proc. Acad. Nat. Sci. Philadelphia, vol. 5, p. 336) includes five species under *Pyractomena* Dejean, *borealis* Randall being the fifth species. A generic diagnosis being given, many authors have held this as the first valid publication of the name.

1853. Motschulsky (Etud. Ent., 1852, p. 37) uses an *e* instead of an *a* in "*Pyrectomena* Dejean" for which he designates "*Pyractomena vitticollis* Mannerheim" of Santo Domingo as genotype, but since this species appears previously undescribed, although originally included (nomen nudum) by Dejean, the generic description is held to be the first validation of the specific name.

1857. Lacordaire (Gen. Coleopt., vol. 4, p. 321) suppresses *Pyrectomena* (Dejean) LeConte as synonym of *Photinus* but later (p. 324, footnote 5) applies it to one of the subgeneric groups, containing six species.

1880. Gorham (Trans. Ent. Soc. London, 1880, p. 32) treats *Pyrectomena* (Dejean) Motschulsky, LeConte, citing *vitticollis* as type and recognizing six species.

1899. E. Olivier (Bull. Mus. Hist. Nat. Paris, vol. 5, p. 371), not knowing of the use of *Lecontia* Champion, 1889, for a genus of Pythidae, proposed *Lecontea* as a new name for *Pyractomena* LeConte, 1851 (1852) (into which he merged *Pyrectomena* Motschulsky, 1852) on the ground that *Pyractonema* Solier, 1849, has priority. *Lecontea* E. Olivier is therefore isogenotypic with LeConte's genus.

1917. McDermott (Can. Ent., vol. 49, p. 53) adopted the present writer's opinion (now reversed) and, holding the Solier and LeConte genonyms not homonyms, designates *Lampyris borealis* Randall type of the latter.

From these facts it appears necessary to regard *Pyractomena* Sturm as a possible subgenus or relative of *Photuris* and to discontinue the use of the former name in the sense so long accepted.

A much more perplexing case also demands consideration but seems to affect only the indexing of synonyms. To state that *Pyrectosoma* Motschulsky, 1854 (p. 39) is an isogenotypic synonym of *Photuris* Dejean when its description was apparently drawn from a species of *Lecontea* (*Pyractomena*) cannot but offend those who regard genera as groups of species displaying the diagnosed characteristics; yet the fact remains that *versicolor* Fabricius was originally designated as its genotype, and Motschulsky's subsequent "corrections" (1855, p. 72) after seeing Fabricius' type of *versicolor* cannot change its generic nomenclatorial status. But to catalog his taxonomic opinions it is still necessary to list *Pyrectosoma versicolor* Motschulsky, 1853, 1854, and 1855 [not Fabricius] in the synonymy of *Lecontea,* indicating that it is a pure primary homonym of the synonym of *Photuris* and nomenclatorially not available for use as the name of any species. In Opinion 14, the International Commission on Zoological Nomenclature, 1910, has considered most of the principles involved in this case, and in Opinion 65, 1914, a hypothetical case almost identical in principle is treated, but these deal only with the question of availability of the names.

These genonyms and genotypes, excluding the *Pyractomena* series already discussed, may be listed:

Photuris Dejean, 1833, p. 103.
  hectica Fabricius, genotype designated by Motschulsky, 1853, is not available because doubtfully included by Dejean (Article 30e of International Code).
  versicolor Fabricius, type by present designation. (This species is also the originally designated genotype of *Pyrectosoma* Motschulsky, 1853.)
Photuris LeConte, 1852, p. 337.
  pensylvanica DeGeer, designated by Gorham, 1880 (species not originally included in Dejean).
Telephoroides Laporte, 1833, pp. 127 and 144.
  occidentalis Olivier designated genotype by Motschulsky, 1853, p. 55 (cataloged in *Photinus* by E. Olivier, 1910).
  pensylvanica DeGeer (*versicolor* Fabricius), genotype designation by Lacordaire, 1857, p. 339, footnote 5, is invalid because subsequent to that by Motschulsky.
Pyrectosoma Motschulsky, 1853, p. 38.
  versicolor Fabricius, genotype by original designation (therefore isogenotypic with *Photuris* Dejean, but characterization was drawn from misdetermined specimens supposed to belong in *Pyractomena* of LeConte, *Lecontea* Olivier).

Generic characters of *Photuris* are amply diagnosed by LeConte, 1852, but our more recent papers on fireflies appear to have considered the lunate last joint of the labial palpi and the cleft external claw of all tarsi as unworthy of notice. In habitus all *Photuris* in our fauna differ from other genera of fireflies in their more oval and much less depressed form, which permits their sturdy, agile movements to be so characteristically distinct. Supporting these peculiarities in adults, their larvae are of such distinctive form and are so adapted to free movement upon the surface of the soil that E. Olivier's

1907 and 1910 elevation of the group to subfamily rank distinct from the Luciolinae is readily acceptable.

SPECIES OF PHOTURIS

The easy taxonomy of previous studies is reflected by Leng (1920) in cataloging only three species of North American *Photuris* and listing five supposed synonyms. Only two mild protests against this simple concept of our forms are known to me, Wenzel (1896) having remarked on "two forms of *Photuris frontalis*" taken by him at Anglesea, N. J., and Blatchley (1924) having sought to recognize *lineaticollis* LeConte, 1852 (name omitted in LeConte, 1881), as a distinguishable variety. Whether the better-described *Telephoroides lineaticollis* Motschulsky, 1854, is identical with the form to which LeConte had previously applied the name is immaterial at present, and since the writer does not know the LeConte type of this species the name is tentatively applied in the following table to a conspicuous southern form displaying the character originally stated.

Two of the other species named by LeConte, 1852, *congener* and *frontalis,* were confused by that author prior to his 1881 revision and have ever since been misdetermined in all collections, the latter name always being applied to the former species, and *frontalis* proper being unrepresented by specimens. But in the Leng list *congener* appears erroneously placed as synonym of *divisa.*

Of the four much older names hitherto considered conspecific with *pensylvanica, marginata* Panzer, 1789, type locality "America meridionale," may be deleted from our lists since it is almost certainly a South American species of *Photuris* not identical with any form in our fauna, but since Panzer's name is preoccupied by *Lampyris marginata* Linnaeus, 1767,[5] some other name must be used for his species when it is reidentified. *Photuris versicolor* Fabricius, 1798, is not a synonym of *pensylvanica* and must be recognized as one of our species, but the writer's observations would indicate a need of much more critical study than has here been possible since his notes record different behavior at different stations. The brief description of *vittigera* by Motschulsky, 1854, appears applicable to the majority of

---

[5] The source of Professor Brunniche's sample which Linnaeus described cannot be known and the type locality is America. This habitat was restated as southern America by G. A. Olivier, 1790, whose figure shows long legs and antennae suggesting *Photuris,* and was further restricted to Brazil by E. Olivier, 1910, who listed the species in *Photinus.* But as stated elsewhere in this paper (see p. 15) *marginata* Linnaeus is genotype of *Pyractomena* Sturm.

individuals inhabiting local fresh-water tide marshes, but this little species is believed to be the original *pensylvanica* DeGeer, 1774, and seems not to be elsewhere treated in literature unless it is one of the two forms mentioned by Wenzel (1896) as *frontalis.*

SPECIES HERE DISTINGUISHED

Unsatisfactory as are many of the distinctions used in the accompanying table and in the appended comments, it is believed best thus to emphasize the inadequacy of preserved specimens for specific identification. The variation of characters customarily used for taxonomic distinction is so obvious in the large series before me that, had the specimens not been carefully collected to represent species distinguishable on behavioristic peculiarities, no attempt at division would have been made. Failure of such species to exhibit sufficiently well-marked differential characters is probably not an uncommon phenomenon, but owing to the existing dominance of taxonomy over biology such species are too frequently ignored. A number of other species of *Photuris,* believed to be new, are before me, but the formality of naming them without the support of a definite knowledge of their habits would be objectionable. It is believed that many more biological units must be recognized and that many observers must contribute opposing opinions before an agreement as to method of taxonomic treatment is possible; but the long-accepted simplicity of this genus is an example of our ignorance of one of the commonest, most conspicuous, and supposedly best-known groups of insects.

PHOTURIS MALE GENITALIA

Since no specific distinctions in the male genital structures have been observed, although abundant prepared material has been examined, we must give added emphasis to the supposed specific barriers indicated in the courtship behavior, the ecological adaptations, and the nuptial seasons of the different forms.

The male genitalia are unlike those of other lampyrids I have examined, as well as the four genera considered by Sharp and Muir, 1912, in that the sides of the "basal piece" are produced into long, slender, clubbed, lateral processes extending beyond the apex of a slender median lobe. A well-developed but very slender flagellum or internal sac, often 4 mm. in length, armed with minute, flattened, spinelike scales, is invaginated from the median orifice through the median foramen and extends well into the coiled tube (stenazygos), which passes through the basal orifice of the aedeagus and attaches to the base of the median lobe. This flagellum appears capable of being evaginated and probably is inserted to the spermatheca during copulation; but except in length no distinctions were observed in the different forms of which preparations were made. In no prepared material has this flagellum been evaginated, and no duct attached to its apex (probably the functional orifice) has been seen.

[The sketches (figs. 2, 3) are of the aedeagus of *Photuris lucicrescens* from specimens taken in Delaware, Mr. Barber's drawings from *Photuris frontalis* not having been found. Figure 2 shows dorsal, ventral, and lateral views of a cleared specimen, indicating some of the internal structure, and figure 3 the dorsal and lateral views on a larger scale of another specimen with the lateral processes spread. The lateral lobes fuse with the dorsal surface of the median lobe at about basal third, and are armed internally opposite this point with a strong transverse ridge, which is sharply angulate at inner third.—McD.]

TABLE OF SPECIES OF PHOTURIS

1. Pronotum with or without infuscate area but always without a pair of oval, red discal spots.. 2

Infuscate median vitta of pronotum narrowed (sometimes interrupted) in middle third by two conspicuous oval red or orange spots (*pensylvanica* group comprising numerous similar species, of vaguely dissimilar habitus but distinctive habits and habitats).............. 6

2. Pronotum entirely pale yellow.................................. 3

Pronotum with discal infuscation.................................. 4

3. Elytra entirely black; metasternum concolorous with the yellow head and thoracic sclerites above and below; fourth visible sternite with apical margin pale, the lutescent area broad at middle, narrower toward but not reaching the sides; apical infuscation of femora gradual and hardly noticeable, but knees, including base of tibiae, pale; length 8.4-11.5 mm. Type locality, Alpine, Tex. (*flavicollis* Fall, 1927, not E. Olivier, 1886)................1. *brunnipennis* var. *falli,* new name

Elytra black with narrow sutural and broader lateral yellow margins which are not continuous around apex; head, prothorax and mesothorax yellow above and below; the metasternum piceus; coxae and basal five-sixths of femora yellow, the knees, tibiae, tarsi, antennae, and four abdominal sternites black; length 11 mm. Type locality, Paradise Key, Fla................2. *brunnipennis* var. *floridana,* new var.

4. Pronotal infuscate area median; front flavous........................ 5

Pronotal infuscation longitudinally divided by narrow median pale line; front infuscate; emargination of penultimate sternite, size, sculpture, etc., as in *floridana* except front broader in male, more than twice as wide as one eye in same aspect. Type locality, "Missouri Territory."
3. *divisa* LeConte

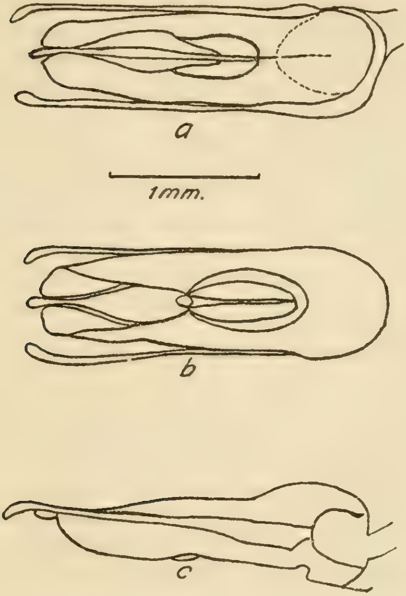


Fig. 2.—Aedeagus of *Photuris lucicrescens* Barber. Cleared specimen showing part of the internal structure. *a,* dorsal view; *b,* ventral; *c,* lateral.

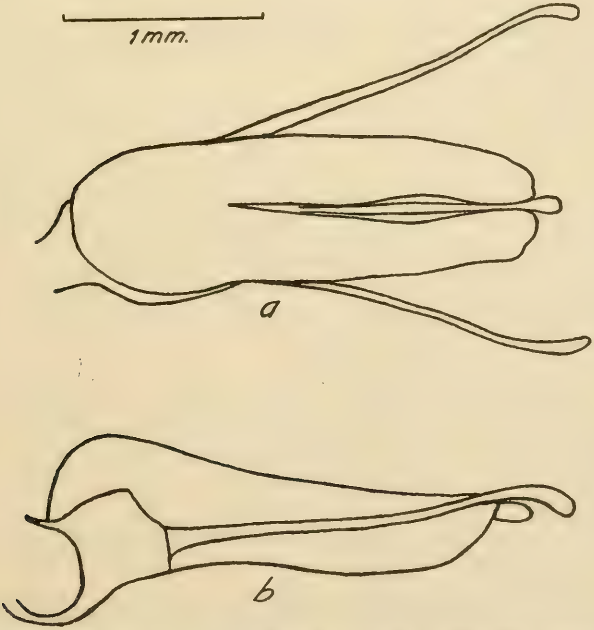


Fig. 3.—Aedeagus of *Photuris lucicrescens* Barber. Specimen showing lateral processes spread. *a,* dorsal view; *b,* lateral.

5. Pronotal infuscate area large, oval, not constricted and shading imperceptibly into yellowish border; size, color, sculpture, and front as in *floridana* but emargination of second luminous sternite less deep and more broadly arcuate. Georgia (type locality), Florida, and Texas ....4. *congener* LeConte

Pronotal infuscate area abruptly limited, usually twice as long as wide and constricted at basal third; size larger (12 to 14 mm.), more robust; coloration similar to *congener* but infuscation darker, pale elytral margins continuous around apex, and femoral infuscation reaching middle; front narrower, not wider than radius of eye. Georgia (type locality), Maryland. Males emit short, slightly yellowish flashes at less than 1-second intervals........5. *frontalis* LeConte

6. Coxae infuscate 7

Coxae pale (except posterior pair in *lineaticollis*)..................... 14

7. Size larger (10 to 17 mm.).. 8

Size small (8 to 10 mm.), pronotal infuscation usually broad with smaller pair of reddish spots; color variable, the elytra usually with short or moderate oblique pale vittae which are sometimes absent, sometimes subentire, or the usually well-marked elytral infuscation occasionally reduced to basal region by the increase of marginal and sutural lutescence toward apex; femora infuscate in apical third; tarsal joints pale with short apical infuscation; fourth visible sternite infuscate, sometimes with posterior margin narrowly pale. Inhabits fresh-water tidal marshes of Chesapeake estuaries, June and July; males fly at top of marsh vegetation, poising to emit a protracted double flash of greenish-white color, the first part very short and immediately followed by a longer light emission lasting 1 to 2 seconds, while making slight dip and rise; females remain deep in vegetation (?*vittigera* Motschulsky)......................6. *pensylvanica* DeGeer

8. Fourth visible ventral segment mostly black, usually with narrow white posterior margin (more variable in *fairchildi*); knees and usually basal third of femora, as well as pale elytral markings, ochreous..... 9

Fourth visible sternite mostly white, the basal margin narrowly infuscate, broadly so laterally; femora cream white with ante-apical infuscation; first joint of hind tarsi white with apical fifth infuscate; length 12 to 14 mm. Abundant late in June in thick woods on alluvial banks of Potomac River above Washington, D. C., the males emitting short, greenish-white, very bright flashes at intervals of about 1 second while flying through foliage................7. *potomaca,* new species

9. Infuscation darker; oblique elytral vitta usually shorter; male coruscations flickering or composed of three or more quick flashes. Chesapeake region and Minnesota, in latter region paler in color.......... 10

Infuscation more brownish; elytral vitta usually longer; male coruscations, single flashes except in *fairchildi* which emits a double flash; Minnesota, New York, Nova Scotia, and Virginia................. 11

10. Elytral vitta usually well-marked but short; tarsal and antennal joints strongly flavous basally; male coruscations of several types, three, four, or several quick flashes differing in locality and brood, perhaps indicating distinct forms. District of Columbia, Maryland, Delaware, and Minnesota..........................8. ?*versicolor* Fabricius

Elytral vitta obsolescent; tarsal and antennal joints almost wholly black; male coruscations consisting of four slow flashes. Cape Henry, Va. ....9. (*versicolor?*) *quadrifulgens,* new var.

11. Form slightly more robust; hind tarsal and antennal joints a little more slender, the fourth to eighth inclusive measuring 4½ mm.; subhumeral pale band usually broader than epipleural infuscation; length 12 to 13 mm.; males flying slowly at top of tall grass and over lawns, dipping and flashing at about 5-second intervals, much like *Photinus pyralis* but beginning its flash on downward flight. Selkirk, N. Y., July 3, 1924..............................10. *pyralomimus,* new species

Form slightly more slender; hind tarsal joints a little broader; antennal joints shorter, the fourth to eighth inclusive measuring 3½ or 3 mm... 12

12. Antennal joints 4 to 8 inclusive measuring about 3½ mm.; male coruscations single; habitat near Winona, Minn.......................... 13

Antennal joints 4 to 8 inclusive measuring about 3 mm.; male coruscations double; habitat Cape Breton Island.......11. *fairchildi,* new species

Generally similar in appearance to *fairchildi,* differing chiefly in having shorter and narrower elytral vittae and somewhat darker coloration. The antennae and posterior legs are proportionately somewhat longer, the elytra a little wider, and the pronotum longer relatively to the width than in *fairchildi;* the characteristic flash of the male is unique, a 1-second long, vibrating, tremulous coruscation. Habitat, low land below Black Pond, Va..............11a. *tremulans,* new species

13. Size of *pyralomimus* (about 13 mm.); males emitting a slow, bluish-green flash of about 1-second duration. Winona, Minn.
12. *caerulucens,* new species

Size slightly smaller (about 12 mm.; abnormals measuring 10.5 mm. and 13 mm.); males emitting a short, yellowish flash. Near Winona, Minn....................................13. *aureolucens,* new species

14. Elytra with well-developed oblique vitta; infuscation pale brown....... 15

Oblique elytral vitta obsolete, infuscation very dark.................. 17

15. Size small (10 to 12 mm.); labrum entirely pale or infuscate......... 16

Size larger (about 15 mm.); labrum pale at base, black at apex; more robust, pronotal infuscation normal, oblique elytral vitta long; males flying in abundance in July in swampy woods, poising in flight to emit a long crescendo flash of greenish-white light of from 1 to 2½ seconds' duration, and of sufficient brilliance to illuminate foliage several feet distant. Type locality, Priest's Bridge, Patuxent River, Md......................................14. *lucicrescens,* new species

16. Labrum wholly pale (rarely slightly clouded); antennae long (7 to 8 mm.), slender; eyes smaller (2.0 to 2.2 mm. across); median pronotal infuscation very narrow, often interrupted at middle; oblique elytral vitta sometimes short, rarely evanescent; males flying in abundance about bushes in July, emitting short, rather feeble, slightly orange flashes at about 1-second intervals. Inhabits willow-covered fresh-water lowlands. Type locality, outlet of Black Pond, Va.
15. *hebes,* new species

Labrum black; antennae shorter and stouter; eyes larger (about 2.5 mm. across); median pronotal black area broad; male flash much like that of *hebes* (*supra*); inhabits salt-water marshes along Chesapeake Bay. Type locality, a *Baccharis* thicket on sand spit at Sherwood Forest, 7 miles northwest of Annapolis, Md. (July 7 and 9, 1928.) ....16. *salinus,* new species

17. Size small (11 to 12 mm.), pronotal vitta normal, coxae and legs white except ante-apical infuscate cloud on inner edge of front femora and often some apical infuscation on tibiae and tarsal joints; pale margin of elytra continuous around apices; first four visible sternites with pale hind margins. Type locality, Sherwood Forest, near Annapolis, Md. ....17. *cinctipennis,* new species

Size large (15 to 17 mm.); pronotal vitta usually interrupted; basal half of femora and the coxae, except posterior pair, ochreous, the latter partly or wholly infuscate; 4 black sternites without pale border. Habits unknown. Florida and Louisiana......18. *?lineaticollis* LeConte?

1. PHOTURIS BRUNNIPENNIS var. FALLI, new name

Photuris flavicollis FALL, 1927, not Olivier, 1886.

This conspicuous form was named after the present paper was virtually complete, and its practical identity with *brunnipennis* was not suspected until a specimen from Alpine, Tex., the type locality, was obtained from Mr. Schaeffer and compared (January 1927) with the Cuban specimens mentioned under the following variety. Such close relationship between two striking forms, one inhabiting a tropical swampy region, and the other almost the summit of the Continental Divide in western Texas, should be supported by intermediate colonies. Fall's original description mentions the triangulate labial margin, which is obscured by regurgitated material in my unique specimen, but the divergence in this structure between Cuban specimens of *brunnipennis* and the type set of *floridana,* mentioned below, is noteworthy.

2. PHOTURIS BRUNNIPENNIS FLORIDANA, new variety

Eleven males taken by the writer on February 19 and 23, 1919, at Paradise Key (Royal Palm State Park) about 40 miles southwest of Miami, and four specimens (two males, two females) labeled Miami, Fla., March 1920, P. Laurent, received from George M. Greene, differ from the Cuban form, *brunnipennis* J. DuVal, in that the yellow margins of the elytra are much broader, the metasternum is wholly piceous, and the fourth visible sternite of abdomen is piceous, except, rarely, faintly paler at middle, but never with the broad white posterior margin as in the Cuban samples. The latter consist of a male and female from Cayamas and Habana, determined by E. Olivier in 1911, and by Leng and Mutchler in 1922, supported by a series of 4 males and 12 females from Sanitago de las Vegas, Cuba. A better knowledge of peculiarities of different colonies of *brunnipennis* in Cuba may show these differences to be insignificant. The writer failed to make notes on the behavior of the specimens he collected but believes they were flying low in the dense "hammock" forest at dusk and emitting short single flashes. The type locality is Paradise Key.

Type and 14 paratypes, U.S.N.M. No. 61001.

In *floridana* the labium is small, oval, slightly infuscate, and rarely shows more than a feeble median tooth, while in Cuban *brunnipennis* the infuscation is darker, the integument stronger, and the anterior margin prominently tridentate, the teeth being formed by four equal emarginations.

3. PHOTURIS DIVISA LeConte, 1852

Twelve specimens in National collection, with data as follows: Topeka, Kans. (Popenoe), four specimens, one of them dated July 19; Riley County, Kans. (Popenoe), four specimens, June 1, 4, and 19; Kansas (Snow), two specimens; Baldwin, Kans. (Bridwell), one specimen, and Lincoln, Nebr., July, collected at electric light, one specimen. The type locality is "Missouri Territory," and there are three specimens in the LeConte collection bearing green discs, which, according to that author's labeling system, indicate "Nebraska, etc." All specimens have the third antennal joint longer than the second, as noted by LeConte, and all are males. The manner of flashing appears to be unrecorded.

4. PHOTURIS CONGENER LeConte, 1852

The type stands as the seventh specimen of the series labeled *frontalis* LeConte in the LeConte collection, apparently where that author placed it when preparing his 1881 synopsis. Type locality is Georgia. Nineteen specimens in National collection from Florida (Daytona, March 1907, P. Laurent, one specimen received from George M. Greene; Haulover (near Allenhurst), March 10 and 14; Crescent City, May 25, and Lake Harney, Hubbard and Schwarz, thirteen examples) and Texas (Columbus, July 3, Schwarz, one example, and, without definite locality, from Belfrage collection, four examples). One female from Texas shows no pronotal infuscation and one each from Crescent City and Lake Harney have this infuscation broken into a narrow prescutellar spot and a broader spot over the head, but in the other specimens it is a large, ill-defined, elongate, discal infuscation. Habits unrecorded. Length 9 to 11 mm.

5. PHOTURIS FRONTALIS LeConte, 1852

This species appears not to have been recognized since its description more than 75 years ago, all students having followed LeConte, 1881, in applying the name to another species, *congener,* from which it differs conspicuously in its larger size and more robust form. It occurs in abundance in ravines and along the foot of a wooded bluff facing Breton Bay, 2 miles from Leonardtown, Md., in July, the males flying rapidly through the foliage but not going high among the branches. They emit very regular, quick, bright flashes of yellowish color at intervals of about three-fourths of a second, abruptly discontinuing the flashes when they alight on foliage. Only two females have been seen in several evenings spent in watching this species, one, which was glowing faintly, in the grasp of a large phalangid on the ground and more than half eaten, July 8, 1923, and one which produced a fine streak of light as it descended to alight upon a leaf some 8 feet above the ground, July 4, 1927.

The species was observed abundantly in the locality on July 13, 1923, June 19, 1925, and July 4, 1927; but was sought vainly on June 18, 1926, and June 7, 1927. One male was caught at Sherwood Forest, near Annapolis, Md., July 13, 1927 (P. G. Russell), and another on St. George Creek, in St. Marys County, Md., July 1, 1931.

6. PHOTURIS PENSYLVANICA (DeGeer, 1774)

?*Telephoroides vittigera* MOTSCHULSKY, 1854, p. 60.

If the original types can be studied the above synonymy may need revision, but of the species observed and collected by the present writer only one appears referable to either of the descriptions originally accompanying the above specific names. This is the diminutive species appearing in great abundance over the tall grass of the Potomac and Patuxent tide marshes. The majority of the specimens fit Motschulsky's description, but only a few have the brown tint of the elytra confined to the base as described by DeGeer, who records the size as equivalent to 10 mm. His figure (pl. 17, fig. 8) is 14 mm. in length but other familiar species are equally enlarged. His indirect quotation from Acrelius informs us that they particularly inhabit the prairies of Pennsylvania all summer, flying and shining like thousands of sparks. Information about Acrelius has since come to notice in the very interesting comment by Jones (Ent. News, vol. 41, p. 305, 1930), and it appears most likely that the type locality is within the present city of Wilmington, Del., the southern part of which was until a few years ago a fresh-water marsh and might then have been called prairie. Ecologically it must have been practically identical with the marshes near Washington, over which vast numbers of this little firefly may be observed. Samples studied consist of about 90 specimens preserved by the writer on numerous visits to their restricted habitat, and supported by two specimens from the collection of George M. Greene, labeled Riverton, N. J., June 17 and July 3, 1899, which may be regarded as practically topotypes.

In many of them the oblique, pale elytral vitta is obsolete or evanescent and in some the confluent infuscate area is narrowed by widening of the lateral and sutural pale borders. In mid-April, 1927, larvae were found by means of their lights to be very abundant in the drier part of the marsh near the Shaw Lily Ponds, Kenilworth, D. C., and when taken indoors they prepared their cells, pupated, and issued as adults within a few days. Six weeks later (June 1) the first adults were seen in the same locality, and 10 days later they had become very numerous. By mid-July the numbers were considerably reduced.

This species first attracted my attention on June 24, 1924, in the Patuxent River marsh at Hills Bridge, Md., 20 miles east of Washington, and since it occurs in pure colony unmixed with other species of *Photuris,* and flies at about the height of one's head as he wades in the marsh grass, it offers a very convenient contrast with the treetop-frequenting forms that have hitherto been identified as *pensylvanica.* Its very distinct behavior is so striking that it is strange no observers have described it. Its habits have been noted often by the writer, both in the Patuxent and Potomac marshes, and the following composite account may better represent the species than scattered detailed records.

One arrives after sunset, intending to watch. The dusk is settling down over the marsh, and no firefly lights have yet been seen. Then, in the darker, eastern side of an isolated alder bush comes the first flash. Inspection discloses a male of this species rapidly ascending a stem from the now very dark interior of the bush. Numbers of others are thus appearing, but as yet they do not take flight, colors of foliage being still visible. They flash at intervals in the darker places, each flash being a very short, bright explosion of light succeeded by an equally short and abrupt interruption, followed immediately by the protracted second flash, the whole lasting 1 to some 3 seconds. When dusk has sufficiently advanced they fly, and others appear all over the marsh. While producing the light they poise in one place, with only a slight fall and rise in height, or perhaps while ascending they make a slight spiral movement. No females can be found, except by accident, until their presence near the roots of the grass is understood, when the explanation of the peculiar stationary coruscation of the male manifests itself. The grass standing vertical, the response flash of the female could not be seen by the male unless he poised directly over her and waited long enough for her to answer his signal. Can such a high degree of adaptation of courtship behavior to the peculiar structure of marsh plant growth be other than an indication of long-established specific distinction? As one cannot thus imitate the male and cannot expect the female to respond after the rude commotion made by one's close approach, flashlight mimics are abandoned. Females confined in a screen-covered pan on the bow of the skiff, which has been placed in the stream, partly concealed in the wildrice, apparently answer flashes of males, but the latter are too distant and the cloud of mosquitoes, as well as the belief that males recognize and avoid abnormal environment, discourages perseverance.

7. PHOTURIS POTOMACA, new species

No other characters than those given in the key have been noticed, and variation is found even in these. Five of the 24 males show greater extent of the basal infuscation of the fourth visible sternite, approaching the condition in *versicolor*. In two of the same series the apical infuscation of the tarsal joint is diffused basally and in the eight females taken with these males the fourth sternite is black or only narrowly bordered with white. Abundant and conspicuous as this species is in the shore woods of the Potomac above Washington, the writer has failed to preserve an adequate series, as only two lots are available: 19 males and 4 females from Offutt Island (type locality) in the Potomac, 2½ miles below Great Falls, Md., June 23 and 24, 1926, and 9 specimens, 3 of them females, taken June 30, 1926, on the Virginia shore at Stubblefield Falls, near Plummers Island, Md. Another male was taken July 1, 1926, by the river near Black Pond, Va. As already stated, the males emit very short, greenish flashes at regular intervals of about 1 second, while flying in woods along the river banks.

Type and 32 paratypes, U.S.N.M. No. 61002.

8. PHOTURIS VERSICOLOR (Fabricius), 1798

The type locality is recorded as "Habitat in America Borealis Dom. Hirschell," but a record of the residence of, or places visited by, Mr.

Hirschell in this country has not been found by the writer. The useful characters of the original description are: large size; black antennae with the articles a little pale at base; black elytra with margin, suture, and a short vitta yellow; black legs with knees yellow.

About 100 recently collected specimens from the Chesapeake region display this combination, but, although they are not believed to represent one homogeneous species, the writer's notes on behavior are insufficient for their separation. All notes refer to flickering coruscations, but unfortunately no timing device other than the experience from timing photographic exposures was used in making observations on any of them. The discrepancies in my records are, however, too great to ascribe merely to varying judgment. Although possibility of errors cannot be denied and temperature alters behavior to some extent, the following notes on observed flashes are offered as perhaps of help in future observations.

An early form was found in a field in Rock Creek Park (June 19, 1924, and June 2, 1925) and along the Virginia shore of the Potomac River near Stubblefield Falls (June 20, 1924), males flying slowly 5 to 15 feet above ground, emitting a rapid series of five or six short flashes of moderate intensity and greenish hue in less than one-half second and at short intervals. Numerous males were attracted excitedly to the mimic of the female light by a flashlight dimmed with green leaves and fingers, while the writer stood concealed in foliage at edge of field. Basal third to half of first joint of hind tarsi is yellow in preserved samples, except in two specimens (June 2, 1925) in which yellow extends to apical fourth. Elytral vitta varies from short basal vestige to two-thirds entire.

In a field near Cabin John Postoffice, Md. (June 7, 1927), males emitted three or four short flashes in about a second, followed by a long rest, but when observed the temperature was falling rapidly after a warm afternoon and we may suppose that persistent males were acting abnormally.

In the field below Black Pond (10:30 p. m., August 2, 1927) among the few females and very rare males of *hebes* and *lucicrescens* then surviving, a single male *versicolor*(?) flew swiftly along the edge of the woods, 15 to 30 feet above the ground, emitting greenish flashes in series of four in about three-fourths of a second and at 6- to 8-second intervals, the fourth of each series being much less brilliant than the first two. This individual was observed to fly 300 yards or more before descending within reach of the net, and since it displays no characters by which it can be separated from the above series it is regarded as a stray from the earlier brood, belated, perhaps, by having transformed in a place chilled by a flow of cold spring water. Its elytral vitta is a mere vestige, and the antennal joints are not pale at base, but this may also be the result of a cold environment.

Among confusion of flashes by several species two specimens emitting only three flashes were taken June 8, 1927, at Breton Bay near Leonardtown, Md., one resting on foliage and leisurely producing three flashes in about 1½ seconds at rather long intervals, the other flying and emitting three flashes in one-half second at about 5-second intervals. In these the first joint of the hind tarsi is about three-fourths yellow.

Mr. McDermott observed a form at Claymont, Del., on June 11, 1927, which flew 3 to 10 feet above the grass, emitting three rapid successively brighter flashes at 2- or 3-second intervals.

Among what seemed to be five species of *Photuris* active at the mouth of a sharp ravine in Sherwood Forest on the Severn River near Annapolis, Md., June 29, 1927, were a few swift-flying males emitting a very rapid and brilliant flickering flash with perhaps eight or more vibrations too fast to count, in about one-half a second, at intervals of about 3 or 4 seconds, and at distances between flashes of from 10 to 20 feet. Attempts to distinguish the series of seven males and five females preserved from this locality have failed.

Near Winona, Minn., July 6, 1926, a series of 13 males was preserved by Miss E. Myers and Mr. Boland, who noted that they flew 2 or 3 feet above the tall weeds, emitting usually five greenish flashes as fast as one could count at intervals of perhaps 30 seconds. These specimens average a little smaller in size and are paler in color but otherwise appear not separable from the above forms.

9. PHOTURIS VERSICOLOR QUADRIFULGENS, new variety

Three specimens captured out of a score observed May 21, 1927, near Cape Henry, Va., are darker colored, with scarcely a trace of the basal paleness on antennal or tarsal joints, the elytral vitta wholly absent in one specimen, an obsolescent vestige in another, and very short in the third, and the elytral apices black in two specimens, while the pale margin is very narrowly continued around apex in the third. They were emitting greenish, bright, perhaps one-half-second flashes in series of four, with short intervals of about a second and longer intervals of a quarter to a half minute, but the evening was not cold, and mosquitoes were very aggressive. The specimens were found flying among scattered pines on the old sand dunes bordering a small fresh-water marshy area near the south end of the bridge over Long Creek about a mile east of Lynhaven Inlet. Length 13 to 14 mm.

Type and 2 paratypes, U.S.N.M. No. 61003.

10. PHOTURIS PYRALOMIMUS, new species

Size and habitus of *versicolor* but a little more robust and less deeply infuscate. Individuals vary from pale brown with ill-defined pale marks to dark brown with sharply defined yellow markings. The lutescence of hind tarsal and antennal joints varies greatly, that of the former occupying one-third to five-sixths of the first joint. In about one-fifth of the specimens the epiplural infuscation is enlarged. The species was observed by the writer in vast numbers July 3, 1924, near Selkirk, N. Y., flying slowly about the lawns and hayfields, the males dipping, flashing, and poising at tips of tall grass very much like *Photinus pyralis,* but emitting their half-second flash during the descent as well as the ascent. Thirty-three males and three females preserved.

Type and 35 paratypes, U.S.N.M. No. 61004.

11. PHOTURIS FAIRCHILDI, new species

Varies from pale elytra with basal infuscation (three specimens) through darker shades of brown on infuscate areas of elytra to the normal dark-brown infuscation (two specimens) more common in the genus. Fourth visible sternite is narrowly bordered with white in three specimens, the white more extended in others, until in three specimens the infuscation is only conspicuous at sides. The slightly shorter antennal joints and the uniform size of about 12 mm. are practically the only differences observed to support the distinct behavior and remote habitat. Ten specimens, one a female, were received from Graham Fairchild, with the information that they were caught over marshy ground at Baddeck, Nova Scotia (Cape Breton Island), about 9:30 p.m. on July 14, 1927; that they fly rapidly and emit two medium flashes separated by an interval about twice as long as one flash, but that the flashing is not very regular.

Type and 9 paratypes, U.S.N.M. No. 61005.

11a. PHOTURIS TREMULANS, new species

This species has been taken in low ground below Black Pond, Va. It resembles the type specimen of *Photuris fairchildi* but is somewhat darker and has short and narrow elytral vittae; the antennae and posterior legs are proportionately longer, the elytra somewhat wider, and the pronotum tends to be longer relative to the width. The very characteristic male flash, a long tremulous coruscation lasting one-half second to a second, differentiates this species clearly from others of similar appearance.

Type and 4 paratypes, U.S.N.M. No. 61006.

12. **PHOTURIS CAERULUCENS**, new species

Form and colors as in the paler variety of *versicolor* from vicinity of Winona and hardly distinguishable from it in the cabinet. The shorter antennal joints, slightly broader first joint of hind tarsi, and very slightly smaller average size help in the recognition of preserved specimens of the present species, whose lights were observed as very different from the *versicolor* also present there. According to the collectors, who called this species the "slow blue," the normal male flash is a steady bluish-green light of about a second's duration, dimly visible for some time after the flash. Twenty-six males and four females were collected by Miss E. Myers and Mr. Boland on July 8, 1926, over damp ground close to a tamarack swamp near Bluff Siding (type locality) in Wisconsin, 10 miles east of Winona, Minn., in company with another species (*aureolucens*), and four males and two females were preserved two days earlier near Stockton, Minn. (10 miles east of Winona), where they were less abundant among the pale variety of *versicolor*.

Type and 35 paratypes, U.S.N.M. No. 61007.

13. **PHOTURIS AUREOLUCENS**, new species

Form and coloration of *caerulucens*, from which it is almost indistinguishable in cabinet specimens. The smaller size and slightly more slender antennal and hind tarsal joints are inadequate recognition marks, but the information kindly supplied by the collectors states that this species emits a single, short yellowish flash not to be distinguished from that of *Photinus castus*, and flies about the tops of tall weeds in marshy ground, appearing in the dusk before *caerulucens*, with which it occurred but from which it is conspicuously different in the color and the duration of the flash. Twenty-three males and one female collected near a tamarack swamp in Wisconsin, near Bluff Siding, 10 miles east of Winona, Minn., July 8, 1926, by Miss E. Myers and Mr. B. Boland.

Type and 23 paratypes, U.S.NM. No. 61008.

14. PHOTURIS LUCICRESCENS, new species

This is the largest, palest-colored, and most brilliantly luminous of the species encountered by the writer in the Chesapeake region, but much remains to be learned of its behavior. It may be the species figured by G. A. Olivier, 1790, as *pensylvanicus* DeGeer. Cabinet specimens may be recognized by their pale coxae, brownish color of infuscate areas, usually strong development of the lutescent borders and oblique vitta of elytra, and the irregularly lutescent areas in the first three or four visible sternites. The series from the densely wooded low shores of the Patuxent River at Priest's Bridge, Md., 20 miles east and slightly north of Washington, D. C., has been chosen as typical because in this locality no other species was observed during July, and especially because the puzzling short flashes in the treetops, mentioned below, appeared to be absent. Here the myriads of flashing males usually flew lower in the forest, and emitted lights of greenish-white color, which began dim, grew brighter, became very brilliant, illuminating foliage for several feet around, and ended abruptly, having lasted from about three-fourths second to 2½ seconds, as timed by a pendulum of one-half-second beat. The type, allotype, and 11 paratypes were taken from this colony on June 29, July 1, and July 22, 1927, and the behavior of the numerous population of the species was also watched on the evenings of July 5 and 12. On the latter date special attention was given to the presence with *lucicrescens,* in woods of adjacent valleys, of a similar or identical form flying about the upper branches of the trees and emitting extremely short (perhaps one-tenth second) and bright flashes at intervals of 3 to 5 seconds. Satisfactory samples of those thus flashing could not be obtained, but on July 22 a male observed to be emitting these instantaneous flashes was caught by a wind eddy and descended, still flashing, within reach, where it was illuminated by the flashlight beam and taken. No characters have yet been found by which it can be differentiated from typical *lucicrescens.* Among a series of males from Sherwood Forest, Severn River, near Annapolis, Md., July 5, three specimens were thought to be giving these very short flashes, but not having been illuminated by flashlight before netting it was feared that a nonflashing *lucicrescens* might have been taken.

In some localities, or under some conditions, this species appears to poise for its long flash. At other times and places what may be this species flies a zigzag course over the bushes, coruscating only while on a short sidewise flight at nearly right angles to the general direction of its advance, and in some localities the size averages a little smaller and the flash shorter. At times a definite vibration to the light can be seen. F. A. McDermott, at Claymont, Del., July 19, 1927, describes in a letter the strong crescendo flash as "unquestionably vibrating" and recounts his attraction and capture of males by producing short flashes with a small pocket flashlamp covered by two layers of plantain leaves. The writer's success in similar attempts has been variable and leads to the belief that the searching males have extremely good vision and readily perceive an enemy unless the observer stands concealed in foliage. His most striking success, however, was not with a flashlight but by the use of the light of the fireflies dying and glowing brightly in the cyanide bottle. The latter was held concealed, its light being exposed for very short periods by quickly opening and closing the hands, and several males were observed to alter their course and approach as if for courtship.

Although the dates on preserved specimens range from June 21 to August 29, the period of chief abundance usually covers about 3 weeks in early July, after which males are less in evidence and through August most of the individuals encountered are females. The 136 specimens are from the following localities: Maryland—Priest's Bridge (type locality), Plummers Island and vicinity, Lanham, Berwyn, Sherwood Forest, and Breton Bay; Washington, D. C.; Virginia—Hunting Creek (1 mile south of Alexandria), Black Pond, near Great Falls; Delaware—Claymont. (One specimen seen at Louisville, Ky., June 1945.—McD.)

Type and 135 paratypes, U.S.N.M. No. 61009.

15. PHOTURIS HEBES, new species

Forty-two specimens are preserved from the type locality, Black Pond, Va. (Potomac River, 2 miles below Great Falls), collected June 28, 1925, July 21 and 26, 1926, July 3 and 28, and August 2, 1927. These are of small size (about 11 mm. long) and have relatively long antennae, and pale (sometimes slightly infuscate) labrum, but exhibit considerable variation in the extent of the elytral vitta, which usually passes the middle, although it is sometimes evanescent, or may be broader and attain the apical fourth of elytra. The pronotal infuscation is rarely interrupted by medium coalescence of the orange spots, but may sometimes attain a width approaching that of one of the orange spots. Fourteen specimens from Chalk Point (7 miles south of Annapolis, Md.) were preserved July 13, 1926, out of many seen flying about *Baccharis* bushes and over the intervening tall grass bordering the salt water. The flying males emitted short, sharp, yellow flashes at about 1-second intervals, in strong contrast with the much brighter, greenish flashes of another species occupying adjacent trees. On searching for the females they were found in numbers in the bushes and grass. At this place the impression of the yellowish character of the light was very strong, while in the type locality the impression of contrast was less marked.

Four other specimens seem referable to this species and are from Plummers Island, Md., July 9 and 24, 1902 (H. S. Barber), the Virginia shore near the same island, July 21, 1923 (H. S. Barber), and Lakeland, Md., July 5, 1909 (F. Knab). Preserved samples of *hebes* resemble the average specimen of *pensylvanica* in their small size and dorsal coloration, but the intermediate joints of the antennae are longer and the coxae are pallid. The very similar specimens found by Wenzel in the sea-water meadows at Anglesea, N. J., have much shorter antennal joints and are here referred to *salinus;* they are probably one of the "two forms of *Photuris frontalis*" taken there and mentioned by Wenzel, 1896. A closely related form inhabiting the Florida Everglades is omitted, the writer having failed to make sufficiently definite observations upon its habits.

Type and 59 paratypes, U.S.N.M. No. 61010.

16. PHOTURIS SALINUS, new species

Similar in size, form, and flashing habits to *hebes* but peculiar to the drier margins of salt marshes near Chesapeake Bay, and differing in having the labrum black, the antennae shorter and slightly stouter, the eyes larger, and the infuscation of the mesopleurae more pronounced.

Type locality, a *Baccharis* thicket on sand spit at Sherwood Forest, 7 miles northwest of Annapolis, Md. (July 7 and 9, 1928). Other localities: a *Baccharis*-bordered salt-grass area on St. George Creek, St. Marys County, Md. (July 1, 1931).

Specimens doubtfully referred to this species were collected near Lloyds, Dorchester County, Md., on July 10, 1907, by the writer, and at Anglesea, N. J., by H. W. Wenzel, probably being one of the two forms mentioned by him (1896) as *Photuris frontalis.*

Type and 43 paratypes, U.S.N.M. No. 61011.

17. PHOTURIS CINCTIPENNIS, new species

There is a possibility that the small (11 to 12 mm.) species for which this name is proposed may be identical with either *Photuris lineaticollis* LeConte, 1852, or *Telephoroides lineaticollis* Motschulsky,

1854. The small size, almost wholly white legs, white elytral epipleura, deep black elytral disc, broad pale elytral margins, and usually total absence of oblique median pale vitta make this form conspicuously distinct in collections. Unfortunately its distinctness was not recognized at time of collection, when attention was concentrated upon other species, and its lights were not particularly noted. Among the flashes observed on that occasion, and not ascribed specifically to individual fireflies, were, however, only the more ordinary short and regular flashes commonly given by restless females of most *Photuris* species and by searching males of a few species. Two females were collected at Breton Bay, Md., July 8 and 13, 1923, and a series of three males and six females at Sherwood Forest (type locality) on the Severn River near Annapolis, Md., June 28 and 29, and July 5, 1927, only females being taken on the last date.

Type and 10 paratypes, U.S.N.M. No. 61012.

18. PHOTURIS LINEATICOLLIS LeConte, 1852

?*Telephoroides lineaticollis* Motschulsky, 1854.

Under this name are placed six very large, dark-colored female specimens from Florida and Louisiana, as listed below. There is, however, considerable doubt about their identity, since the writer failed to notice a specimen in the LeConte collection which might be the type of that author's short remark of 1852 validating the nomen nudum of the Dejean Catalogues. The identification of *lineaticollis* Motschulsky by Gorham, 1880 (p. 110), from Quebec, requires reexamination. Blatchley (Can. Ent., vol. 56, p. 165, 1924) has quoted this remark and added some discussion, but states the length as 14 mm., agreeing in this respect with the form described by Motschulsky, 1854. In only two of the specimens, all of which are larger than the length just stated, is the median infuscation of pronotum of linear form, the other four having this dark line interrupted broadly at middle, forming a larger rounded anterior spot and a narrow prescutellar spot.

This is probably our largest North American firefly, and if the large area of the urate reflector in the lumious segments is an indication of its light, it may be our brightest-flashing species as well. No notes on its habits are now available, however. The six specimens are labeled as from Archer, Fla., March 1882 (Koebele); Hillsboro County, Fla., May (Hubbard and Schwarz); Lakeland, Fla., April 1912 (G. G. Ainsley); Duval County, Fla., and Covington, La., May 28 (Soltau).

ADDENDUM

NOTES ON SOME GENERAL CHARACTERS OF NORTH AMERICAN PHOTURIS

By Frank A. McDermott

A somewhat detailed examination has been made of 28 specimens representing 19 species and varieties of *Photuris* which Mr. Barber had assembled as representing most of the species discussed in the foregoing monograph, and also of type specimens of *tremulans* and *salinus*. Measurements and points of particular difference or interest are given later in this section.

Certain characters are in general very similar in all the species, these being of some generic importance. There is, of course, some variability between different specimens of the same species in all characters; such phenotypic differences are to be expected, and there are instances where the variation may overlap between species, for example in over-all length or width. It is difficult to describe accurately in words, or even to illustrate properly, the shape of some of the appendages—e.g., the labial palpi—though an attempt has been made to make them recognizable. Some of these general features are discussed in detail below, and in some instances may be compared with the generic characters as given by LeConte, Olivier, and others. For the sake of reference, the generic descriptions by LeConte, Lacordaire, and Olivier are also given.

Pronotum.—Unlike the conditions in the commoner species of the genera *Photinus* and *Lecontea,* the carapacelike pronotum does not completely cover the head, so that, as viewed from above, a portion of the eyes and frons is visible. The shape of this structure is generally roughly scutate, or perhaps more accurately, rounded ogival, broader than long, and with rounded angles at the posterior lateral corners. In most species there is a median pigmented area, usually consisting of a central dark-brown or black figure, between two orange or pink areas; in some species this pigmented area is absent, being represented by a merely shaded or dusky spot in the otherwise uniform chitin. Outside of this pigmented area, the remainder of the pronotum may be opaque yellow or white, translucent, or even transparent. The shape of the dark pigmentation is at least somewhat characteristic of the species, though somewhat variable in different specimens. The characteristic form, as represented by *Ph. versicolor,* is a T on a triangular base, the apex of the latter coinciding with the median line at the anterior edge of the pronotum, and the cross bar of the T lying along the posterior edge; this T-form is subject to several specific modifications, as given in the descriptions of the species. There may or may not be a median sulcus in the pronotum, and there would seem to be some doubt as to whether, when present, it is a natural character or an artifact resulting from distortion in drying.

In the specimens examined the ratio of width to length of the pronotum varied from 1.2 to 1.5; no relation was evident between this ratio and the over-all size of the insects. The proportion of the total length (pronotum plus elytra) represented by the pronotum varied from 18 to 21 percent, averaging about 19.7 percent.

Scutellum.—This small structure is roughly kite- or coffin-shaped, and varies in coloration more or less, and to some extent in outline, with the species; again, it is difficult to express the exact shape in words. Anteriorly to the scutellum, the two mesonotal plates may usually be seen sufficiently to note the color, which is frequently the same as that of the scutellum.

Elytra.—Since the elytra represent about 80 percent or more of the total area of the insects as seen from above, differences in them are the most easily recognized characters. In general, two types of elytral outlines are found in these species: (1) Those in which there is no marked widening or outward curvature of the lateral edges, and which are therefore described as parallel or practically parallel; (2) those in which such a widening is definitely noticeable, usually as the result of the presence of a distinct margin, and where the resulting outline is at least subparallel and approaches a long oval. This condition results in a considerable range of variation in the ratio of length to width, the figures found for the species embraced here varying from 2.3 to 3.81.

The base or ground color of the elytra varies from a very dark brown—nearly black in some specimens—to a pale grayish tan. Perhaps it is in the base color that the greatest amount of individual variation will be found. For instance, three specimens of *Ph. lucicrescens* in Barber's collection, dated 1927, are all light, although there is some difference between them; two taken by the writer in Wilmington in 1948 are both much darker than Barber's specimens, although otherwise very similar. Of course the expression of such color tones in words may convey to another reader a different shade from that intended, and hence an attempt to give a very definite color classification is not justified. Another difficulty is the darkening of the specimens with age; the originally practically pure white of the luminous segments becomes eventually a brownish yellow, and other light areas undergo a similar darkening; presumably the darker portions also deepen in tone. Still a third factor is that in examination under a binocular microscope with intense illumination, all colors appear lighter and brighter than under general illumination; hence the appearance under the latter condition may really be more significant than under the microscope.

In the majority of the species, a rather definite lighter border or margin is present on both the lateral and sutural edges of the elytra, and these margins may be continuous by meeting around the tips of the elytra. In some, the lateral margins are relatively quite wide for a considerable part of the elytral length, and are associated with an increase in the maximal width. The sutural margin is usually rather narrow, not much more than a line. A further feature characteristic of many species is a light-colored stripe, called a vitta by LeConte and Barber, beginning at or near the shoulder (humerus) and extending lengthwise of the elytron, and obliquely so as to approach the suture; this stripe may vary in length from one-fourth to seven-eighths of the elytral length, a variation of some diagnostic value. It is usually fairly wide at the anterior end, narrowing rapidly at first, and then gradually for the greater part of its length, eventually becoming indefinite and no longer traceable. Usually each elytron has one or more ridges or costae, which appear to be lines along which there is an exaggeration of the general tuberculation. These costae usually begin at or near the humerus, and may extend for almost the entire length of the elytron, but more frequently end indefinitely at one-half to two-thirds the length. They tend to diverge, and when oblique stripes or vittae are present, the most prominent ridges may mark the middle of these stripes. However, it has been noted that the number of such costae is not necessarily constant in all specimens of a species, and although not infrequently given in the description of a species, they appear to be unreliable as a specific character. This is also true of the hair, which is a prominent feature of most species; occasionally this may be locally developed in a manner requiring mention, but usually it is a general condition and rather variable.

Head.—Viewed from the front the head appears to be composed mainly of the two large eyes and the frons—the area between the eyes and bearing the antennal sockets. The width of the frons, its color, unusual details of the antennal sockets, the slope or divergence of the interocular margins, etc., may be of diagnostic importance, but for most species the measurements do not provide means of identification. The ratio of the frontal width across the eyes to the total length varies from 0.18 to 0.24 for the specimens examined, without parallelism to the total length. In these species, the frons is usually depressed medially.

The terminal joint of the maxillary palpi is the portion of this structure most easily observed; this joint is usually long-conoidal in outline, flattened and lighter on the inner surface, and frequently the tip is flattened or bent to give a finger-tip appearance; usually this tip is rounded, sometimes nearly straight across, and may appear as a sharp point by lateral view. The labial palpi, described as lunate by LeConte, is rarely even approximately crescentic in these species—at least it is a very asymmetric crescent. Perhaps it is best described as being of a long, narrow mitten shape, with the "thumb" projecting at a right angle; this thumb may be curved at the end, and may have a low protuberance at its base. For most of the species, the variations in outline are slight.

The labrum (perhaps more properly the clypeus) shows some variation; the edge may have one or more small projections, and the whole structure may be short, not completely covering the closed mandibles. The mandibles are curved, sickle-shaped rather than semicircular, and under the microscope may appear to be hollow; they are brown, lighter in the proximal portion, and although appearing rather thick (0.05-0.1 mm.) for insects of the size of these, are sharp-pointed.

Antennae.—Perhaps next to the elytra and the pronotum, the antennae are the most conspicuous features in *Photuris*. They are longer than in many lampyrids, but are simple, 11-jointed, and slightly tapering. Their length, expressed as a fraction of the total length of the insects, varies from 0.455 in *pensylvanica* to 0.69 in *hebes,* the majority being between 0.5 and 0.6. The third joint is little if any longer than the second; the first joint is usually the longest, and any one of joints 4 to 10 is usually as long as or longer than the sum of the second and third; the eleventh is usually somewhat shorter.

Sternites.—The first four visible sternites are of about the same length, and usually mainly some shade of brown, the posterior one frequently being one-third to one-half white; the posterior edges are but little sinuate, being nearly straight. The sixth and seventh sternites are completely white and represent the main luminous area; the eighth is usually much smaller and white, but not apparently luminous, and in a number of species it bears a long (0.25 mm.) median projection, with a base which may be broad or narrow. The posterior edges of the sixth and seventh sternites are usually more or less emarginate or "notched," sometimes deeply; usually both are 1.3 to 1.5 times the length of any of the first four sternites. The "foveae" (points of muscle attachment), noticeable on the ventral side of the luminous segments in *Photinus* and *Lecontea*, are rarely observable.

The aedeagus was extruded in 10 of the 28 specimens examined; in all cases it was of exactly the same type as far as could be determined without dissection; it varied from 1.75 to 3.0 mm. in length, representing 17 to 21 percent of the total body length, and tending to be longer in the larger species. The same type has been found in dissections of *Ph. versicolor* and *Ph. lucicrescens* collected in Delaware by the writer, and in Marthas Vineyard, Mass., by Dr. Frank M. Jones, and is very similar to that of *Ph. jamaicensis* collected in Jamaica by Dr. John B. Buck.

Legs.—The legs of *Photuris* are proportionately much longer than those of *Photinus* and *Lecontea*, and in occasional specimens impress one as being unusually long, especially the posterior pair. Measurements show that these posterior legs vary in length from about 0.65 to 0.85 of the total length of the insects, averaging about 0.75. The outer claws are bifid on all legs, and sometimes there is a small protuberance at the base of one or both claws. Pronounced tibial spurs are present on the two posterior pairs of legs. Claws and spurs are usually a clear brown. The lobes of the fourth tarsal joint usually extend well toward the claws, covering most of the fifth joint. Each lobe has a furry pad on the under surface, which may be gray or black, instead of yellow or brown.

The generic descriptions referred to above are given here.

LeConte, J. L. Proc. Acad. Nat. Sci. Philadelphia, vol. 5, pp. 331-347, 1852. *Photuris* Dejean, p. 337:

> Antennae 11-jointed, slender, elongated, joints 2 and 3 short, last joint of maxillary palpi acutely triangular, last joint of labial transversely lunate; 4th joint of tarsi long lobate, claws externally divided, internally simple; three last abdominal segments phosphorescent; last superior segment with rounded apex.

Lacordaire, Th. Histoire naturelle des insectes, Genera des Coléoptères, vol. 4. *Lampyres*, pp. 307-340, 1857. *Photuris*, pp. 338-340:

> Head moderately elongated or short; eyes of at least ordinary size; antennae fairly long, most frequently very slender and bristle-like, of 11 joints, the first a reversed cone, the 2nd and 3d of relatively variable length, the 4th often longer than those following, these sub-equal. Prothorax transversal or not, semi-

circular in front, widely edged except at the base, the angles more or less prominent. Elytra soft, sub-parallel for the most part, more rarely oval. Legs long and slender, posterior femora very prominent on the inner edge, 1st joint of the posterior tarsi at least as long as the two following together, the 4th very long, deeply divided into two slender lobes, the 5th long, in part free; claws simple or bifid at the end. Abdomen not lobed on the sides. Body elongated, parallel or oval, flat.

LeConte, J. L. Trans. Amer. Ent. Soc., vol. 9, 1881. *Luciolae,* p. 37:

The eyes are large, convex and widely separated above and beneath in both sexes, not conspicuously larger in ♂; the head is rounded, narrowed behind, and not retractile; it is but partially covered by the prothorax, which is, however, of the usual hood-like form and rounded in front. The antennae are longer than one-half of the body, filiform, slender, not compressed, inserted near the anterior margin of the front, and moderately approximate; the second and third joints are about equal, and together are as long as each of the following joints.

The sexes are similar in form, with long elytra and well developed wings; the light organs occupy the whole of the fifth and following segments; stigma-like pores are not obvious, being situated at the base of the fifth and sixth segments and less strongly marked than in *Pyractomena* and *Photinus* ♂. The seventh ventral in ♀ is obtusely triangular; in ♂ the fifth and sixth are broadly emarginate, and seventh is smaller than in ♀, sinuate at the sides and prolonged at the middle, the eighth is a little wider and longer than the prolongation of the seventh. In our species the outer (or anterior) claw is cleft at the tip. The prothorax and elytra are densely rugosely punctured, the former is yellow with a black stripe or spot, each side of which the disc is red; the latter have the whole margin and frequently a discoidal stripe pale. A single genus occurs in our fauna with limited representation.

Olivier, Ernst. Wytsman's Genera insectorum, fasc. 53, p. 57, 1907:

Body elongated, parallel or oblong-oval, having a soft tegument; head hardly visible, attenuated, on a sort of collar projecting from the prothorax; labrum wanting or indistinct because of the proportions of the epistome; antennae long, very slender, the second joint of variable size but always fairly long; prothorax rounded or ogival in front, with the posterior angles sometimes obtuse and scarcely projecting, sometimes very sharp and prolonged posteriorly; legs long and slender; 4th joint of the tarsi bilobed, claws entire or divided . . . ; abdomen composed of 7 segments, the last ones containing the luminous apparatus, which is much more developed in the males. Both sexes have wings and elytra.

. . . the sexual differences consist in the integrity or division of the claws, and particularly in the ♂ the last ventral segment is short, laterally sinuate, and terminated by a linear lobe more or less enlarged; in the ♀ it is large, triangular, with an obtuse point, or slightly incised. As generally among the Lampyridae, the eyes of the ♂ are very large and prominent, and the head appears deeply concave.

Olivier, Ernst. Ann. Soc. Ent. France, ser. 6, vol. 6, pp. 201-240, 1886, is essentially the same as the above. He criticizes Motschulsky's splitting of *Photuris* into several new genera, saying that it would put the two sexes of some species into separate genera.

Bradley, J. C. Manual of the genera of beetles of North America, p. 98, 1930, follows LeConte (1881) and Olivier.

RESULTS OF THE EXAMINATION OF BARBER'S SPECIMENS

2.[1] *brunnipennis* var. *floridana.*

General: A small (9.5 × 3.5 mm.) lampyrid, dark brown, without dark pronotal spot or elytral stripes.

Pronotum: Opaque white with central yellowish area; no black or orange spots, and no sulcus. 1.8 × 2.6 mm.[2]

Scutellum: Yellow anteriorly, white posteriorly; rather narrower posterior point than in most species; mesonotal plates yellow, rather large.

Elytra: 7.75 × 1.75 mm.; rather wide lateral, and narrow sutural margins yellow; margins continuous around tips; no stripes or vittae.

Head: Width across eyes 1.95 mm.; eye length 0.6 mm.

Frons yellow, 0.4 mm. wide above antennal sockets, 0.75 mm. above eyes; interocular margins rather divergent; inner edges of antennal sockets 0.05 mm. apart.

Maxillary palpi light brown; labial palpi almost white. Labrum short, light brown, with very narrow darker edge, and no protuberances.

Antennae: 5.1 mm. long, brown; white visible in joint sockets.

Sternites: 2 to 5 brown; 6 and 7 luminous; 8 white, with rather wide-angled posterior point.

Legs: Coxae yellow, third pair slightly infuscate; femora yellow with brown knees; tibiae and tarsi brown; outer claws bifid, but the inner prong distinctly shorter than the outer one. Posterior legs 7.05 mm. long, 0.74 of the total length.

3. *divisa* (two specimens differing in color and slightly in size).

General: A small lampyrid (9.5-10.0 × 3.1 mm.) brown to dark brown, with a trapezoidal median pronotal pigmentation divided longitudinally by a narrow light streak partially in a narrow sulcus; elytra with distinct white margins, but no stripe.

Pronotum: 1.75-2.0 × 2.25-2.6 mm.; central trapezoidal brown area divided longitudinally by a narrow light line or streak, part of which is in a narrow sulcus; in one specimen the angles are definitely produced posteriorly, in the other they are not.

Scutellum: Light brown or yellow; mesonotal plates dull brown or yellow.

---

[1] Numbers are those given the species in Barber's table.

[2] Length and width, respectively.

Elytra: 7.75-8.2 × 1.55 mm.; brown or dark brown; distinct lateral and sutural margins white, continuous around tips; no stripes or vittae; humeri distinctly inclined inward and backward toward scutellum (different from other species).

Head: Width across eyes 1.85-2.0 mm.; eye length 1.0 mm.

Frons brown, very wide, 0.75 mm. above antennal sockets, 0.85-0.9 mm. above eyes; interocular margins very slightly divergent (different from most species).

Maxillary palpi brown, labial palpi white or light brown; labrum short, light brown.

Antennae: 4.5-5.35 mm. long, brown, unmarked, although joint sockets may be white.

Sternites: 2 to 5 brown, 5 may be darker with narrow white posterior edge; 6 and 7 luminous; 8 white, with a rather sharp central point about 0.25 mm. long.

Aedeagus: 2.0 mm. long.

Legs: Coxae and femora brownish yellow, knees darker; tibiae and tarsi brown; lobes of fourth tarsal joint relatively short. Posterior legs 6.3-6.6 mm. long, 0.65-0.665 of total length.

4. *congener* (old specimen, 1914).

General: A small lampyrid (9.7 × 4.0 mm.) with parallel dark-brown elytra without stripes, and pronotum with central yellow spot, no black area.

Pronotum: 1.85 × 2.6 mm.; central yellow area bearing 2 indefinite longitudinal brown streaks; sharp sulcus in anterior half.

Scutellum: Light brown; mesonotal plates yellow.

Elytra: 7.85 × 2.0 mm., brown without stripes or vittae; practically parallel; 0.45-mm. lateral and narrow sutural margins yellow, continuous around tips.

Head: Width across eyes 2.05 mm.; eye length 1.25 mm.

Frons yellow, 0.5 mm. wide above antennal sockets, 0.95 mm. above eyes; interocular margins more divergent than in most species; inner edges of antennal sockets very close together, 0.05 mm.

Maxillary palpi brown, finger-tipped; labial palpi light brown, more nearly symmetrically crescentic than in most of the species—more like the securiform usual in *Photinus*.

Labrum brown, with a visible point.

Antennae: 4.95 mm. long, proportionately rather short; brown, with white joint sockets.

Tergites: Brown, last 3 with lighter edges.

Sternites: 2 to 5 brown, posterior edge of 5 lighter; 6 and 7 luminous, probably originally white, now yellow brown; 8 has a median posterior point.

Legs: Coxae light brown; femora proximally light brown, shading to dark brown at knees; tibiae and tarsi dark brown; fifth tarsal joint appears shorter than in most species. Posterior legs 7.5 mm. long, 0.775 of total length.

5. *frontalis* (2 specimens which differ mainly in size).

General: A medium-sized lampyrid (12.0-13.5 × 4.2-5.2 mm.), dark, with wide lateral elytral margins and rather short pronotum having an indefinite brown spot.

Pronotum: 2.25-2.75 × 3.25-4.0 mm.; very short, almost semicircular; large central triangular ivory area, base posterior, having an indefinite brown area; angles large and produced posteriorly about 0.25 mm. beyond median line.

Scutellum: White; mesonotal plates dull white.

Elytra: 9.0-10.6 × 2.1-2.6 mm.; brown, distinctly widened by the 0.55-mm. lateral margins, giving a somewhat oval appearance; margins not quite continuous around tips; no stripes or vittae.

Head (larger specimen): Width across eyes 3.2 mm.; eye length 1.55 mm.

Frons ivory white, 0.7 mm. wide above antennae sockets, 1.25 mm. above eyes; antennal sockets 0.1 mm. apart.

Maxillary palpi large, dark brown; labial palpi yellow. Labrum short, dark brown, with 3 points or denticles.

Antennae: 7.65 mm. long in larger specimen; dark brown to practically black; joint sockets white.

Sternites: 2 to 5 brown; 6 and 7 luminous, and apparently not as much longer than the fifth as in most species; 8 yellow, with posterior point.

Aedeagus: 2.0 mm. long.

Legs: Coxae light brown; femora light brown proximally, darker distally; tibia and tarsi dark brown. Posterior legs of larger specimen 10.15 mm. long, 0.76 of total length.

6. *pensylvanica.*

General: A small lampyrid (9.0-10.0 × 3.0-3.5 mm.) with medium brown, white-margined elytra, and pronotal black and orange pigmentation.

Pronotum: 1.75 × 2.25 mm.; median black or very dark brown T-shaped area with large orange spot on each side; no sulcus.

Scutellum: Brown anteriorly, to nearly white at posterior point.

Elytra: 7.5 × 1.6 mm.; base color brown; 0.45-mm. wide lateral and 0.3-mm. sutural margins yellow, continuous around tips; outline nearly oval; oblique stripe from humerus about 5.0 mm. long, about 0.1 mm. wide at humerus, narrowing to end.

Head: Width across eyes 1.85 mm.; eye length 1.0 mm.

Frons ivory, 0.5 mm. wide above antennal sockets, 0.9 mm. above eyes.

Maxillary palpi light brown; labial pale brown.

Labrum short, dark brown, with dull median point.

Antennae: 4.2 mm. long, rather short, brown; joint sockets white.

Tergites: Brown to eighth, latter ivory.

Sternites: 2 to 5 mainly light brown, posterior one-third of fifth, white; 6 and 7 luminous; 8 ivory with median point 0.25 mm. long.

Aedeagus: 1.75 mm. long.

Legs: Coxae light and darker brown; femora mostly light or yellowish brown, darker distally; tibiae and tarsi dark brown. Posterior legs 6.8 mm. long, 0.736 of total length.

7. *potomaca* (two specimens, varying principally in size).

General: A small to medium-sized lampyrid (9.35-12.0 × 3.2-4.5 mm.), light brown, subparallel, white margins and oblique stripes; black and orange spot on pronotum.

Pronotum: 1.85-2.5 × 2.5-3.0 mm.; angles not produced posteriorly; median long-triangular brown mark with apex anterior, and short triangle from this apex to anterior edge of pronotum; large orange area on each side of brown triangle.

Scutellum: White; mesonotal plates dull dark brown.

Elytra: 7.5-9.5 × 1.6-2.25 mm.; light brown with 0.5-mm. lateral and 0.25-mm. sutural margins white; white oblique stripe 0.2 mm. wide at humerus, narrowing to become indefinite at a length of about 5.0 mm.

Head: Width across eyes 2.25 mm.; eye length 1.2 mm.

Frons ivory white, 0.7 mm. wide above antennal sockets, 1.0 mm. above eyes—perhaps less divergent than usual.

Maxillary palpi brown; labial light brown.

Labrum dark brown, with three dull points.

Antennae: 6.0-6.6 mm. long, brown with white rings at joint sockets; seventh joint somewhat the longest.

Tergites: Posterior two mainly white; others brown.

Sternites: 2, 3, and 4 brown, 5 mostly white medially; 6 and 7 luminous; 8 white with median point 0.25 mm. long.

Legs: Coxae brown; femora one-half to two-thirds yellow-brown, distally infuscate; tibiae and tarsi darker brown; lobes of fourth tarsal segment appear longer than usual. Posterior legs of larger specimen 9.15 mm. long, 0.762 of total length.

8. *versicolor.*

General: A fairly large lampyrid (13.0-14.0 × 4.5-5.0 mm.), brown elytra with yellow margins and yellow oblique stripe; black T and orange pigmentation on pronotum.

Pronotum: 2.75 × 3.55 mm.; a median black or dark-brown area having the form of a T with the cross bar lying along the posterior edge of the pronotum; the area between the bar and foot of the T is orange; the foot of the T connects with the slightly wider base of a triangle, the apex of which coincides with the anterior median line of the pronotum. Angles rounded, not produced posteriorly; a row of long yellow hairs on the posterior edge of the pronotum.

Scutellum: Brown; mesonotal plates brown.

Elytra: 11.5 × 2.5 mm., subparallel; base color brown; 0.5-mm. lateral and narrow sutural margins yellow, continuous around tips; yellow oblique stripe 0.25 mm. wide, not appreciably wider at humerus, 7.5 mm. long.

Head: Width across eyes 2.6 mm.; eye length 0.8 mm.

Frons yellow, 0.7 mm. wide above antennal sockets, 1.25 mm. above eyes; inner edges of antennal sockets 0.1 mm. apart.

Maxillary palpi and labial palpi brown.

Labrum brown; appears truncate-triangular with nearly straight edge.

Antennae: 9.2 mm. long (rather long); black, each joint with lighter base; joint 3 rather longer than 2, joints 4 to 10 longer than first joint (exceptional).

Tergite 8 appears to overlap sternite 8.

Sternites: 2, 3, and 4 brown, becoming darker in this order; 5 brown, posterior one-third white; 6 and 7 luminous; 8 white with posterior point.

Aedeagus: About 2.5 mm. long.

Legs: Coxae dark brown; femora light or yellowish brown for proximal two-thirds, distally darker; tibiae and tarsi of anterior two pairs of legs dark brown, of posterior pair lighter. Posterior legs 10.5 mm. long, 0.763 of total length.

9. *versicolor* var. *quadrifulgens.*

General: Much like *versicolor* but darker and narrower; short, indistinct elytral stripe.

Pronotum: 2.6 × 3.25 mm.; pigmentation like *versicolor* except that the upright of the T widens at the base to meet the base of the terminal triangle; shallow sulcus in posterior half of the T.

Scutellum: Dark brown with lighter posterior tip; mesonotal plates dark and light brown.

Elytra: 11.2 × 1.8 mm., dark brown, subparallel; 0.4-mm. lateral and 0.13-mm. sutural margins ivory, continuous around tips; oblique light stripe and ridge from humerus to one-half elytral length.

Head: Width across eyes 2.5 mm.; eye length 1.5 mm.

Frons nearly white, 0.75 mm. wide above antennal sockets, 1.25 mm. above eyes.

Maxillary palpi dark brown, labial dark and light brown.

Labrum short, dark brown, front edge almost straight, except for distinct median protuberance and an indistinct one at each side.

Mandibles large and thick.

Antennae: 8.35 mm. long, practically black; proximal ends of joints a little lighter, and joint sockets white.

Sternites: 2, 3, and 4 brown, 5 mainly brown, posterior one-third white; 6 and 7 luminous, posterior edge of 6 nearly straight; 8 white with posterior point.

Aedeagus: 3.0 mm. long.

Legs: Coxae brown; femora yellow-brown proximally, distal two-thirds dark brown; tibiae and tarsi dark brown. Posterior legs 9.6 mm. long, 0.703 of total length.

10. *pyralomimus* (two specimens, one somewhat lighter than the one described).

General: Much like *versicolor,* but darker, somewhat more oval, and with pronounced oblique stripes on elytra.

Pronotum: 2.55 × 3.8 mm.; pigmentation like *versicolor;* angles much produced posteriorly; no sulcus.

Scutellum: Brown, fading to nearly white at the posterior point; mesonotal plates dull brown.

Elytra: 10.5 × 2.45 mm., distinctly widened by the 0.5-mm. yellow lateral margins; sutural margins 0.35 mm.; margins continuous around tips; outline nearly oval. Oblique stripe 0.5 mm. wide at humerus, becoming narrower, and extending almost to ends of elytra.

Head: Width across eyes 2.5 mm.; eye length 1.2 mm.

Frons ivory, 0.9 mm. wide above antennal sockets, 1.25 mm. above eyes.

Maxillary and labial palpi brown, latter with a low point on the base of the thumb; tips of maxillary palpi rather wide and flat, square-ended rather than round as usual.

Labrum dark brown with median dull point.

Antennae: 7.8 mm. long, practically black, joint sockets white.

Tergites: 3 posterior tergites white.

Sternites: 2, 3, and 4 light brown, 5 white on posterior one-third; 6 and 7 luminous; 8 white with rather sharp posterior point.

Legs: Coxae brown; femora brown for distal one-half to two-thirds, proximally lighter; tibiae and tarsi dark brown. Posterior legs 10.35 mm. long, 0.797 of total length.

11. *fairchildi.*

General: A medium-sized lampyrid (12.0 × 4.0 mm.), light-brown, narrow elytral margins and oblique stripes; pronotal pigmentation similar to *versicolor,* but lacks the cross bar on the T.

Pronotum: 2.15 × 2.85 mm.; median black mark and orange areas much as in *versicolor,* but lacks the cross bar on the T; orange area extends nearly to the posterior margin.

Scutellum: Light brown; mesonotal plates brown.

Elytra: 9.8 × 2.0 mm., light brown; very narrow light-colored lateral and sutural margins; narrow oblique stripe extending to within 2.0 mm. of elytral tip.

Head: Width across eye 2.15 mm.; eye length 1.3 mm.

Frons practically white, brownish under pronotum; 0.55 mm. wide above antennal sockets, 1.0 mm. above eyes; antennal sockets 0.05 mm. apart.

Maxillary palpi brown; labial, dark and light brown.

Labrum brown, filling the mandibular circle.

Antennae: 6.1 mm. long, brown, proximal ends of joints lighter.

Sternites: 2, 3, and 4 brown, 5 about one-half white; 6 and 7 luminous; 8 white with posterior point.

Aedeagus: 2.3 mm. long.

Legs: Coxae light brown; femora yellowish brown; tibiae and tarsi mostly dark brown. Posterior legs 8.2 mm. long, 0.686 of total length.

11a. *tremulans* (description prepared from two selected from a series of very similar specimens).

General: A medium-sized lampyrid (10.25-12.5 × 4.2-4.6 mm.); brown elytra with wide margins, and a short, narrow, oblique vitta on each; pronotal pigmentation similar to that of *Ph. fairchildi,* but brown area less definite. Form slightly oval.

Pronotum: 2.0-2.5 × 2.55-3.0 mm., rounded ogival, posterior edge straight but depressed just adjacent to the angles; a row of long yellow hairs at the median posterior edge. A median long, narrow, brown triangle, extending as a line to the median point of the anterior edge, separates two large orange areas, and may have a short transverse extension along the posterior edge. A 0.1-mm. white margin, lateral and anterior, between which and the orange area the pronotum is dense ivory-colored. No sulcus.

Scutellum: Kite-shaped, with a rather sharp posterior apex, and angular rather than rounded anteriorly; brown, fading to yellow at the apex. Mesonotal plates dull darker brown.

Elytra: 8.25-10.0 × 2.1-2.3 mm.; base color medium brown; lateral margins yellow and 0.5-0.6 mm. wide; sutural margins 0.2-0.25 mm. wide; margins continuous around elytral tips. On each elytron a very narrow (0.1 mm. or less) pale oblique vitta from the humerus to 0.25 to 0.4 of the elytral length. No pronounced costae.

Head: Width across eyes 2.05-2.35 mm.; eye length 1.15-1.25 mm.

Frons ivory, 0.55-0.75 mm. wide above antennal sockets, 1.0-1.1 mm. above eyes.

Maxillary palpi rather large, brown.

Labial palpi ivory to light brown, usual mitten-shape.

Labrum short, dark brown, sinuate to give three low dull protuberances.

Mandibles large, brown.

Antennal sockets white-ringed, 0.05 mm. between inner edges.

Antennae: 6.45-7.4 mm. long, practically black; yellow rings at both proximal and distal ends of each joint; joint sockets white; first joint longest, second shortest, third slightly longer than second, fourth to tenth each of the same length, eleventh slightly shorter than tenth.

Thorax: Ventrally dark brown.

Tergites: Dark brown except eighth, which is white.

Sternites: 2 to 5 mainly brown, 5 has a narrow white posterior margin; posterior edges practically straight. 6 and 7 luminous, 6 shallowly and 7 more deeply notched medially, and 1.3-1.5 times as long as 5. 8 ivory white with median point 0.25 mm. long. 9 small, ogival, ivory white. No foveae evident.

Legs: Coxae of the first two pairs light brown, of posterior pair dark brown; femora mainly yellow, but brownish infuscation may extend to nearly one-half length; tibia dark brown; tarsi somewhat lighter; lobes of fourth tarsal joint extend three-fourths length to claws; tibial spurs large, 0-2-2. Posterior legs long, 8.6-9.5 mm.

12. *caerulucens* (a second specimen slightly lighter than the one described).

General: A medium-sized lampyrid (about 12.0 × 4.0 mm.), dark brown; elytra rather widely margined and with long oblique stripe; pronotal markings like *versicolor.*

Pronotum: 2.5 × 3.15 mm., marked like versicolor; no sulcus.

Scutellum: Brown with white posterior tip; mesonotal plates dull brown.

Elytra: 9.25 × 2.05 mm.; base color dark brown; 0.5-mm. wide lateral and 0.2-mm. sutural margins white and continuous around tips; oblique white stripe distinct for 5.0 mm. from humerus, becoming indefinite.

Head: Width across eyes 2.4 mm.; eye length 1.25 mm.

Frons ivory, 0.85 mm. wide above antennal sockets, 1.05 mm. above eyes, rather less divergent than usual.

Maxillary palpi dark brown, labial light brown; thumb of latter pointed and curved slightly downward.

Labrum dark brown, apparently with 3 dull points.

Antennae: 6.3 mm. long, dark brown, joint sockets white.

Tergites: Brown, except 8th which is white.

Sternites: 2, 3, and 4, dark brown, 5 white on posterior one-third; 6 and 7 luminous; 8 white with rounded posterior point rather wide-angled.

Legs: Coxae dark brown; femora and tibiae yellow brown for proximal half, distally dark brown; tarsi darker. Posterior legs 8.95 mm. long, 0.761 of total length.

13. *aureolucens* (a second specimen darker, and somewhat smaller, 10.75 × 3.9 mm., than the one described).

General: A medium-sized lampyrid (12.8 × 4.0 mm.), light brown with yellow elytral margins and oblique stripe; pronotal pigmentation as in *versicolor,* but cross bar on T narrower and basal triangle relatively larger.

Pronotum: 2.5 × 3.0 mm.; pigmentation as in *versicolor,* but the cross bar on T narrower, and the triangle at the foot of the T relatively larger. Angles slightly produced posteriorly.

Scutellum: Brown, tip white; mesonotal plates brown.

Elytra: 10.3 × 2.0 mm., base color light brown; 0.5-mm. lateral and 0.1-mm. sutural margins yellow; oblique yellow stripe covers outer corner of humerus, narrowing rapidly to 0.2-0.25 mm., and becoming indistinct at a length of 7.5 mm.

Head: Width across eyes 2.25 mm.; eye length 1.3 mm.

Frons ivory, 0.8 mm. wide above antennal sockets, 1.1 mm. above eyes.

Maxillary palpi dark brown, labial brown.

Labrum dark brown, sinuate rather than toothed, to show three protuberances.

Antennae: 6.45 mm. long, practically black, with bases of joints paler, and sockets white.

Tergites: Brown except last, which is white.

Sternites: 2, 3, 4, and 5 brown, a little white on posterior edge of 5; 6 and 7 luminous; 8 white with median point 0.25 mm. long.

Legs: Coxae brown; femora light yellowish brown, infuscate toward knees; tibiae and tarsi dark brown. Posterior legs 8.85 mm. long, 0.692 of total length.

14. *lucicrescens* (three specimens, all light-colored, though slightly different, and of nearly the same size and proportions).

General: A fairly large lampyrid (12.5-13.5 × 4.9-5.2 mm.), practically parallel, with margined and striped elytra and pronotal pigmentation resembling *versicolor.*

Pronotum: 2.5-2.6 × 3.5-3.6 mm.; pigmentation similar to that of *versicolor* but cross bar on the T very short, and orange areas somewhat smaller.

Scutellum: White, and proportionately rather long; mesonotal plates yellow.

Elytra: 10.25-10.8 × 2.45-2.6 mm.; base color light grayish brown, becoming paler toward tips; practically parallel; 0.3-0.5-mm. lateral and 0.1-0.15-mm. sutural margins continuous around tips but indistinct because of pale color of elytra; oblique stripe 7.5 mm. long from humerus.

Head: Width across eyes 2.6 mm.; eye length 1.4 mm.

Frons white, 0.85 mm. wide above antennal sockets, 1.25 mm. above eyes.

Maxillary palpi dark brown, labial light brown.

Labrum short, white with dark brown distal edge, and an indefinite median protuberance.

Mandibles appear large for the other proportions.

Antennae: 8.0-8.25 mm. long, very dark brown with proximal ends of joints white, giving a beaded appearance; tenth and eleventh joints shorter than fourth to ninth.

Tergites: Last tergite white, the two penultimate ones medially white; remainder brown.

Sternites: 2, 3, and 4 light brown; 5 mostly white; 6 and 7 luminous; 8 ivory with triangular median point 0.35 mm. long—not as sharp as in most species.

Aedeagus: 2.6-2.75 mm. long.

Legs: Coxae light brown to yellow; femora, tibiae, and tarsi proximally yellow, distally brown. Posterior legs 10.1 mm. long, 0.76 of total length.

(Specimens of this species collected in northern Delaware in 1947-48 agree with the above except in color, being darker throughout.)

15. *hebes* (a second specimen is very similar).

General: A small lampyrid (10.5 × 2.8 mm.), light brown, practically parallel, wide lateral margins, and pronotal pigmentation somewhat resembling *versicolor.*

Pronotum: 2.2 × 2.7 mm., with median brown area resembling *versicolor,* but lighter and less definite; orange areas similar to *versicolor.*

Scutellum: White; mesonotal plates dull white.

Elytra: 8.3 × 1.4 mm., light brown; 0.5-mm. lateral and narrow sutural margins white; margins barely continuous around tips; a very narrow oblique white stripe on each elytron ending at about three-fourths of the elytral length.

Head: Width across eyes 2.15 mm.; eye length 1.125 mm.

Frons ivory white, 0.6 mm. wide above antennal sockets, 1.0 mm. above eyes; inner edges of antennal sockets 0.1 mm. apart.

Maxillary palpi brown, appearing large for this insect; labial palpi brown.

Labrum short, brown, sinuate.

Antennae: 7.25 mm. long, dark brown with proximal ends of joints lighter; tenth and eleventh joints shorter than fourth to ninth.

Tergites: 6, 7, and 8 white, almost transparent; others brown.

Sternites: 2 yellow, 3 light brown, 4 darker, 5 mostly mottled white; 6 and 7 luminous; 8 white with long posterior point.

Aedeagus: 2.25 mm. long.

Legs: Coxae yellow; femora yellow-brown, knees somewhat infuscate; tibiae and tarsi mostly dark brown, lighter proximally. Posterior legs 8.5 mm. long, 0.81 of total length.

16. *salinus* (44 specimens, including ♀♀, available, of which 10 ♂♂ were selected as covering the range of variation. The ♀♀ tend to be larger and darker, and have smaller eyes and shorter antennae).

General: A medium-sized lampyrid (9-12 × 3.2-4.1 mm.), grayish to yellowish brown under general illumination, with fairly wide, light lateral elytral margins, narrow sutural margins, and a narrow but distinct oblique yellow or white vitta past the midlength of each elytron; pronotum broadly rounded to scutate with a median brown vitta between large orange-colored areas.

Pronotum: 1.9-2.5 × 2.5-3.0 mm.; edges transparent yellow, mottled; scutate to broadly rounded, posterior edge sinuate, but angles not produced beyond median; a row of long yellow hairs along the median half of the posterior edge. The pigmentation consists of a median brown area, hourglass-shaped, 0.2 to 0.6 mm. wide at the constriction, extending from the posterior edge nearly to the anterior edge, sometimes narrowing to a line completely to the anterior edge; occasionally the brown area may widen to a short transverse bar at the posterior edge; large orange-colored areas on each side of the brown area.

Scutellum: Transparent yellow to brown, with lighter posterior apex; mesonotal plates the same color as the scutellum in each specimen.

Elytra: 7.5-9.25 × 1.65-2.05 mm.; base color brown to light brown, appearing grayish or yellowish under general illumination. Distinct lateral margins about 0.5 mm. wide, slightly widening the elytra, giving a slightly oval outline. A narrow white to yellow oblique vitta from the humerus to past the midlength of each elytron. Margins continuous around the tips of the elytra, but indistinct in lighter specimens.

Head: Width across eyes 2.1-2.4 mm.; eye length 0.9-1.35 mm.

Frons yellow, smooth or but little hairy; medially brown toward tops of eyes. Interocular margins constricted over antennal sockets, and divergent toward tops of eyes, intermediate edges nearly parallel.

Maxillary palpi brown; labial palpi light brown, of the usual mitten shape.

Labrum dark brown—practically black; distinctly tridentate in some specimens, obscurely so in others.

Mandibles large.

Antennae: 5.55-6.35 mm. long, brown to light brown, distal ends of joints paler, and proximal ends with a narrow light ring, giving a distinct jointed appearance even by general illumination. Third joint but little longer than the second.

Thorax: Ventrally light to dark brown.

Tergites: 6, 7, and 8 white; the anterior ones may be white or light brown; eighth usually rounded, but truncate-triangular in some specimens.

Sternites: 2 to 5 light to dark brown; 5 may have a white posterior margin; 6 and 7 luminous, white or yellow; 8 white, with a hairy median point; 9 white, ogival.

Aedeagus: Where extruded, of the same type as in the other species.

Legs: Femora yellow, tibia and tarsi brown; tarsal spurs large, 0-2-2. Lobes of fourth tarsal segment fairly long. Posterior pair of legs 7.0-7.9 mm. long.

17. *cinctipennis* (a second specimen a little longer than the one described; otherwise similar).

General: A rather small lampyrid (10.75 × 3.5), dark brown elytra, margined, and with narrow and short oblique stripes; pronotal marking somewhat like *versicolor.*

Pronotum: 2.25 × 2.75 mm., brown pigmentation similar to *versicolor,* but upright of the T very narrow and cross bar short; distinct sulcus, widening posteriorly to include most of the short cross bar on the T; orange area similar to *versicolor.*

Scutellum: Ivory white with central brown spot; mesonotal plates dull pale brown.

Elytra: 8.5 × 1.75 mm., apparently a uniform dark brown except for 0.45-mm. wide lateral and 0.2-mm. sutural margins, which join at the rather unusually pointed tips. A very narrow light-brown oblique stripe extends from the humerus about half the elytral length.

Head: Width across eyes 2.1 mm.; eye length 1.2 mm.

Frons white, 0.7 mm. wide above antennal sockets, 1.0 mm. above eyes.

Maxillary palpi light brown; labial palpi ivory, with a low protuberance on the thumb.

Labrum dull white, edge brown, with a definite median tooth, and a duller one on each side.

Antennae: 6.65 mm. long, mostly dark brown; joints with white proximal ends and white rings at the sockets.

Tergites: Dark brown.

Sternites: 2 to 5 mainly brown, irregularly white in posterior one-third to one-half; 6 and 7 luminous, 6 only very slightly notched, and 7 but little more—both less than in most species; 8 white.

Aedeagus: 2.0 mm. long.

Legs: Nearly all white, hairs brown. Posterior legs 9.1 mm. long, 0.845 of total length.

18. *lineaticollis* (an old specimen, 1882).

General: A large lampyrid (14.5 × 5.2 mm.), very dark, margined elytra, with pronotal pigmentation similar to *versicolor,* but no cross bar on the T.

Pronotum: 2.75 × 3.6 mm., with pigmentation similar to that of *versicolor,* but no cross bar on the T along the posterior edge.

Scutellum: Yellow, nearly translucent in posterior half; mesonotal plates yellow.

Elytra: 11.8 × 2.6 mm., appear dark brown except for rather narrow (0.35-mm.) lateral margin and (0.25-mm.) sutural margin; margins yellow, and not continuous around the tips. There is an obscure lighter-brown oblique stripe from the humerus.
Head: Width across eyes 2.85 mm.; eye length 1.25 mm.
Frons yellow, 1.2 mm. wide above antennal sockets, 1.5 mm. above eyes, rather wider and less divergent than usual; inner edges of antennal sockets 0.2 mm. apart.
Maxillary palpi dark brown, labial light brown.
Labrum dark brown; a dull median tooth or protuberance, and a sharper one on each side.
Antennae: 7.65 mm. long, mainly almost black, proximal ends of joints lighter; ninth to eleventh joints shorter than fourth to eighth.
Tergites: Brown.
Sternites: 2 to 5 dark brown, 5 lighter on posterior edge; 6 and 7 luminous, yellow; 8 triangular, yellow.
Legs: Coxae of first two pair light brown, of third pair very dark brown; femora mostly dark brown, lighter proximally; tibiae and tarsi dark brown; lobes of fourth tarsal joint rather long. Posterior legs 10.6 mm. long, 0.73 of total length.

In the writer's semipopular "Common Fireflies of Delaware" he expressed the idea that the species giving three to five rapid coruscations per flash and flashing at 5- to 10-second intervals is the one which was sent to DeGeer by Acrelius from Wilmington and described by the former in 1774 as (*Photuris*) *pensylvanica*. The reason for this opinion was that this is by far the commonest type of *Photuris* flash now seen in the vicinity of Wilmington, although both the sharp and crescendo flashes of *lucicrescens* and some of the other types described by Barber are also present. This is a dry-land species and has been taken in copula by the writer in a nearby wheatfield where hundreds of the insects were flying over the wheat, around the border growth, and among the trees across an adjacent road. Barber, however, calls this species *Photuris versicolor* Fabricius, 1798, and restricts the specific name *pensylvanica* to a marsh species giving a two-component flash, the first component of which is short and sharp and the second long, basing his opinion on the probable character of the land surface around Wilmington about 1750. He is doubtless correct in his conjecture as to the marshes at this locality at that time; there is still plenty of marsh land along the Delaware River and the estuary of Christiana Creek, though most of that along the Brandywine has been filled in. Mr. Barber did not, so far as I remember, ever tell me that he had arrived at this conclusion, although he did write to me about DeGeer's use of the word "prairies" in connection with his description of the locale of the specimens sent by Acrelius. From the translation of Hesselius' Journal (Delaware History, vol. 2, No. 1, p. 83, 1947), flying over meadows might be interpreted as "fields," and the "sparkling" might be more like the three- to five-flasher than the double coruscation of Barber's *pensylvanica*. I have been unable to find out what Swedish word in Acrelius' letters to DeGeer was translated as "prairie" by the latter. Observations in both northern Delaware and on the opposite New Jersey shore of the Delaware River have so far failed to reveal the presence of a species giving the double flash of Barber's *Photuris pensylvanica* DeGeer, but conditions here have undoubtedly changed materially in the last 200 years, and it is not impossible that industrial wastes have exterminated a once-plentiful species.

Free translations of the descriptions given by DeGeer and by Fabricius are given below:

DeGeer, Hist. Ins., vol. 4, pp. 52-53, 1774:

Lampyrid elongated, elytra of a pale yellowish-gray, and thorax black in the middle with two red spots.

Lampyris pensylvanica oblong, elytra pale grayish brick-colored, thorax black between the margins with two red spots.

The lampyrids of this species are found in Pennsylvania. Mr. Acrelius, who sent me them from this country, says that they are found particularly on the prairies during the whole summer, where they glitter and appear to the eyes of the observers as a multitude of sparks; but they sparkle even more when they fly. One can distinguish them easily from the other species.

In size and shape they resemble the three preceding species (of lampyrids), but the head is larger and less hidden in the thorax, which is smaller than in the other species; there is also a greater distance between the two large black eyes, and the antennae, which almost equal the length of the abdomen, are slender and a little hairy. On the thorax and elytra there are many small hairs.

The disc of the thorax is pale yellow, with a large oval black spot in the middle, beside which there are two small round red spots near the edges; the elytra are yellowish gray, with brown shading near the anterior ends. The abdomen is brown below, but the last three segments are sulfur yellow. The wings are dark brown, the antennae lighter brown, and the legs ochre yellow with some small brown spots.

Fabricius, Suppl. Entomol. Syst., p. 125, Hafnia, 1798:

L(ampyris) black, thorax spotted, elytral margins and median vitta yellowish, apex of abdomen very light. Habitat in North America. Dom. Hirschell.

Body large; antennae black, bases of joints yellowish. Head yellowish or black. Thorax rotund, black spot in the middle, large red spots on both sides, and broad yellowish margin. Elytra smooth, margined with black becoming yellowish, with abbreviated vitta. Abdomen broad, white. Legs black, knees yellowish.

DeGeer's description of the pronotal pigmentation sounds more like a *Photinus* than a *Photuris,* but his mention of the partially exposed head and the long antennae would seem to leave no doubt of the genus of the species described. Fabricius' description of the pronotal pigmentation is more correct for Barber's specimens of both *pensylvanica* and *versicolor.* DeGeer fails to mention the oblique elytral stripe or vitta; this is quite definite in Barber's specimen of *pensylvanica,* and rather shorter in his *versicolor,* agreeing with Fabricius' description. DeGeer's drawing is unconvincing.

Just which is *pensylvanica* and which *versicolor,* must perhaps remain in some doubt for the present, since neither DeGeer nor Fabricius record definitely the flashes of the species they describe. Unless further data become available, it seems well to accept Barber's decision.

LITERATURE CITED

BLATCHLEY, W. S.
1924. New Coleoptera from southern Florida with notes on other interesting species. Can. Ent., vol. 56, No. 7, pp. 164-170.
DEGEER, C.
1774. Mémoires pour servir à l'histoire des insectes, vol. 4, 456 pp.
DEJEAN, PIERRE F. M. A.
1833. Catalogue de la collection des coléoptères, 3d ed.
1837. Idem, reprint, 3d ed.
ERICHSON, G. F.
1847. Conspectus insectorum coleopterorum, que in Republica Peruana observa sunt. Wiegemann's Arch. Naturg., vol. 13, pt. 1, pp. 67-185.
FABRICIUS, J. C.
1798. Entomologia systematica, supplementum, 572 pp.
FALL, H. C.
1927. New Lampyridae. Bull. Brooklyn Ent. Soc., n.s., vol. 22, No. 4, pp. 208-211.
GORHAM, H. S.
1880. Materials for a revision of the Lampyridae. Trans. Ent. Soc. London for 1880, Mem. 8, pp. 1-37.
HESS, WALTER N.
1920. Notes on the biology of some common Lampyridae. Biol. Bull., vol. 38, No. 2, pp. 39-76.
INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE.
1910. Opinions rendered by. Opinions 1 to 25. Smithsonian Inst. Publ. 1938, pp. 1-61.
1914. Ibid. Opinions 57 to 65. Smithsonian Inst. Publ. 2256, pp. 131-169.
INTERNATIONAL RULES OF ZOOLOGICAL NOMENCLATURE.
1926. *In* Proc. Biol. Soc. Washington, vol. 39, pp. 75-103.
LACORDAIRE, J. TH.
1857. Histoire naturelle des insectes. Genera des Coléoptères, vol. 4.
LAPORTE, F. L. DE.
1833. Essai d'une révision du genera Lampyre. Ann. Soc. Ent. France, vol. 2, pp. 122-153.

LeConte, J. L.
1849. Coleopterous insects. *In* White's Statistics of Georgia, supplement (Catalogue of the fauna and flora of the State of Georgia), pp. 25-36.
1850. General remarks upon the Coleoptera of Lake Superior. *In* Agassiz, Lake Superior, p. 228.
1852. Synopsis of the lampyrides of temperate North America. Proc. Acad. Nat. Sci. Philadelphia, vol. 5, pp. 331-347. (Usually incorrectly dated 1851.)
1881. Synopsis of the Lampyridae of the United States. Trans. Amer. Ent. Soc., vol. 9, pp. 15-272.

Leng, C. W.
1920. Catalogue of the Coleoptera of America, north of Mexico. x + 470 pp.

Leng, Charles W., and Mutchler, Andrew J.
1922. The Lycidae, Lampyridae and Cantharidae (Telephoridae) of the West Indies. Bull. Amer. Mus. Nat. Hist., vol. 46, art. 8, pp. 413-499.

Linnaeus, C.
1767. Systema naturae, 12th ed., vol. 1, pt. 2, pp. 533-1327.

McDermott, F. A.
1917. Observations on the light-emission of American Lampyridae. Can. Ent., vol. 49, No. 2, pp. 53-61.

Melsheimer, F. E.
1845-1846. Descriptions of new species of Coleoptera of the United States. Proc. Acad. Nat. Sci. Philadelphia, vol. 2, No. 12, pp. 302-318.

Motschulsky, V.
1853. Études entomologiques, Ann. 1, 1852.
1854. Idem, Ann. 2 and Ann. 3.
1855. Idem, Ann. 4.

Mutchler, Andrew J.
1923. Notes on West Indian Lampyridae and Cantharidae (Coleoptera) with descriptions of new forms. Amer. Mus. Nov., No. 63, pp. 1-9.

Olivier, E.
1886. Études sur les Lampyrides. Ann. Soc. Ent. France, ser. 6, vol. 6, pp. 201-246.
1899. Les Lampyrides typiques du muséum. Bull. Mus. Hist. Nat., Paris, vol. 5, pp. 371-373.
1907. Family Lampyridae. Wytsman's Genera insectorum, fasc. 53, Coleoptera, 74 pp.
1910. Lampyridae. Junk-Schenkling, Coleopterorum catalogus, pt. 9, pp. 1-68.

Olivier, G. A.
1790. Entomologie, ou Histoire naturelle des insectes . . . Coléoptères, vol. 2, pt. 28.

Panzer, G. W. F.
1789. Einige seltene Insecten. Naturforscher, vol. 24, pp. 1-35.

Sharp, D., and Muir, F.
1912. The comparative anatomy of the male genital tube in Coleoptera. Trans. Ent. Soc. London, 1912, pp. 477-642, pls. 42-78.

Solier, A. J. J.
1849. *In* Gay, Historia física y política de Chile, vol. 4, p. 445.
Sturm, J.
1843. Catalog der Käfer-Sammlung, xii + 386 pp.
Wenzel, H. W.
1896. Notes on Lampyridae, with the description of a female and larva. Ent. News, vol. 7, No. 10, pp. 294-296.
Williams, F. X.
1917. Notes on the life-history of some North American Lampyridae. Journ. New York Ent. Soc., vol. 25, No. 1, pp. 11-33.

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 117, NUMBER 2

ADDITIONAL FORMS OF BIRDS FROM COLOMBIA AND PANAMÁ

BY

ALEXANDER WETMORE

Secretary, Smithsonian Institution

(Publication 4052)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
SEPTEMBER 25, 1951

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

ADDITIONAL FORMS OF BIRDS FROM COLOMBIA AND PANAMÁ

By ALEXANDER WETMORE
Secretary, Smithsonian Institution

As work on our ornithological collections from Colombia and Panamá has proceeded, several additional forms new to science have been found and are described in the following pages. There are included with these a few other reports for kinds of birds only partly or not previously known from the two republics concerned, to place this information on record for the benefit of others.

Family ARDEIDAE: Herons

BUBULCUS IBIS IBIS (Linnaeus)

Ardea Ibis Linnaeus, Syst. Nat., ed. 10, vol. 1, 1758, p. 144 (Egypt).

A female cattle egret was taken by M. A. Carriker, Jr., at Punto Muchimbo, Valle, on the lower Río San Juan about 3 kilometers below Palestina, and on the opposite side of the river, on January 3, 1951. The bird is in immature dress, with only a small amount of buff on the crown. This apparently is the first record for Colombia and is indication that this Old World species is now spreading widely over northern South America. It is now recorded from Dutch Guiana, British Guiana, Venezuela, and Colombia. Observers should watch for small white herons, in general like the snowy heron, but with yellow bill. In adults the bill is described as reddish at the base, but these would stand out otherwise because of the strong buff markings on crown and breast.

Family COCHLEARIIDAE: Boat-billed Herons

COCHLEARIUS COCHLEARIUS COCHLEARIUS (Linnaeus)

Cancroma cochlearius Linnaeus, Syst. Nat., ed. 12, vol. 1, 1766, p. 233 (Cayenne).

A boat-billed heron that I shot at the mouth of Río Imamadó on the upper Río Jaqué, Darién, on April 16, 1947, is a specimen of the pale-colored, typical form, not reported previously in Panamá.

COCHLEARIUS COCHLEARIUS PANAMENSIS Griscom

Cochlearius zeledoni panamensis Griscom, Amer. Mus. Nov., No. 235, November 11, 1926, p. 11 (Corozal, Canal Zone).

A female collected by M. A. Carriker, Jr., at Acandí, Chocó, on the western shore of the Golfo de Urabá, January 17, 1950, is representative of this dark-plumaged form of Panamá, here recorded for the first time from Colombia. It will be interesting to determine if this subspecies extends into the lower Atrato Basin, particularly in view of the record of the typical race given above in extreme southwestern Darién.

Family CAPRIMULGIDAE: Goatsuckers

CHORDEILES ACUTIPENNIS MICROMERIS Oberholser

Chordeiles acutipennis micromeris Oberholser, U. S. Nat. Mus. Bull. 86, April 6, 1914, pp. 24 (in key), 100 (Xbac, Yucatán).

In a series of nighthawks collected January 17, 1947, at El Dificil, Magdalena, in the level country to the east of the lower Río Magdalena I find six specimens of this form, previously unrecorded in Colombia. Another was taken at Camp Costa Rica, not far distant, January 26. Others were shot at Norosí, March 14, 1947, and at La Raya, January 22, 1948, both localities being in Bolívar. These birds are wholly typical of this form of Central America, which is common in migration in Panamá and apparently also in northern Colombia.

Family APODIDAE: Swifts

CHAETURA SPINICAUDA AETHERODROMA, new subspecies

Characters.—Similar to *Chaetura spinicauda fumosa*[1] but smaller.

Description.—U.S.N.M. No. 409438, male, Chepo, from 500 feet elevation on Cerro Carbunco, Provincia de Panamá, Panamá, collected April 14, 1949, by A. Wetmore and W. M. Perrygo (orig. No. 14808). Crown, back, wings, tail, and upper tail coverts dull black, with a very faint greenish cast; rump pale smoke gray, shading to smoke gray on lower back; sides of head and of neck hair brown; an indistinct spot of smoke gray in front of eye; throat somewhat whiter than pale smoke gray; upper breast mouse gray, shading to deep mouse gray on abdomen and to dark mouse gray on sides, flanks, and

---

[1] *Chaetura fumosa* Salvin, Proc. Zool. Soc. London, 1870, p. 204 (Bugabá, Chiriquí).

under tail coverts; under wing coverts dark mouse gray. Bill black; tarsus chaetura black; claws chaetura drab (from dried skin).

Measurements.—Males, 13 specimens, wing 100.2-105.2 (103.0), tail 36.8-40.5 (38.7), culmen from base 4.8-5.8 (5.2), tarsus 10.0-11.6 (10.6) mm.

Females, 4 specimens, wing 100.3-107.8 (104.0), tail 37.7-42.7 (40.6), culmen from base 5.0-5.7 (5.2), tarsus 11.0-11.5 (11.1) mm.

Type.—Male, wing 101.3, tail 40.0, culmen from base 5.8, tarsus 10.0 mm.

Range.—Panamá, from the Provincia de Panamá (Chepo, Charco del Toro on Río Majé) through the Comarca de San Blas (Permé) and Darién (Cana, Jaqué) to Colombia, in Antioquia (Puerto Valdivia, Novita, El Real), Cauca (Juntas de Tamaná, Río San Juan), and northeastern Magdalena (Cacagualito).

Remarks.—Small swifts of the species *Chaetura spinicauda* are common in many localities but are so difficult to obtain that it has taken several seasons in the field to secure a sufficient series to determine the identity of those found in Panamá and northern Colombia. When enough had been collected it became apparent that two groups differing in size were included in the range currently assigned to the race *fumosa,* a larger one in Costa Rica and Chiriquí, and a smaller one in eastern Panamá and Colombia. As the form was described by Salvin from two specimens from Bugabá, western Chiriquí, it has been necessary first to ascertain the measurements of this original lot. This has been possible through the kind cooperation of J. D. Macdonald of the British Museum (Natural History), who has verified the information that the two skins had been collected by Arcé, and says further that a definite type had not been selected between them. He has furnished measurements of both right and left wings, for the chord, and with the wing flattened. One specimen had the tip of the left wing much worn. The chord of the right wing in these two is 109.0 and 108.0 mm., measurements that fall within the limits of the larger group, as is shown by the following data from Costa Rican skins. The series includes those in the Museum of Comparative Zoölogy and in the Carnegie Museum, which I have examined through the assistance of J. L. Peters and W. E. Clyde Todd.

Males, 8 specimens, wing 108.5-115.4 (110.7), tail 37.7-40.7 (38.9), culmen from base 4.8-5.5 (5.1), tarsus 9.9-11.8 (10.6) mm.

Females, 8 specimens, wing 105.5-113.4 (109.9), tail 39.3-41.5 (39.8), culmen from base 4.6-6.0 (5.3), tarsus 9.6-11.6 (10.6) mm.

Specimens of the typical form examined from Costa Rica come from Pozo Azul de Pirris and El General. Intergradation between the two races is assumed to take place between eastern Chiriquí and the western part of the Province of Panamá, an area from which no specimens are at present available to me.

Hellmayr,[2] in discussing *fumosa,* considered the type to be "Arcé coll. Nr. 3328," which is the bird noted above as having the left wing much abraded at the tip. It is evidently this worn left wing that Hellmayr measured to arrive at the length of 106 mm. that he lists in the reference cited, since Mr. Macdonald gives 107 mm. for flattened left wing in this same bird. The right wing, on the contrary, Macdonald writes, measures 112.5 mm. flattened, which is in line with Hellmayr's measurements for the other specimen from the type locality.

Family TROCHILIDAE: Hummingbirds

HYLOCHARIS GRAYI HUMBOLDTII (Bourcier and Mulsant)

Trochilus humboldtii Bourcier and Mulsant, Ann. Sci. Phys. Nat. Agr. Ind., Soc. Roy. Agr. Lyon, sér. 2, vol. 4, 1852, p. 142 (Río Mira, Esmeraldas, Ecuador).

A male and two females that W. M. Perrygo and I collected near Jaqué on the coast of Darién on March 18 and 26 and April 11, 1946, are the first reported north of the Baudó region of northwestern Colombia.

Family FURNARIIDAE: Ovenbirds

XENERPESTES MINLOSI UMBRATICUS, new subspecies

Characters.—Similar to *Xenerpestes minlosi minlosi* Berlepsch [3] but decidedly darker above, without definite light streaks on the crown; hindneck, back, wings, and tail darker.

Description.—Type, U.S.N.M. No. 443152, male, Río San Juan at Punto Muchimbo, Valle, Colombia, December 24, 1950, M. A. Carriker, Jr. (orig. No. 19079). Anterior half of crown dull black, shading gradually to blackish mouse gray across the posterior section of the pileum to the hindneck, the feathers, except on the forecrown, edged slightly with deep mouse gray; back and scapulars dark olive-gray; rump and upper tail coverts light grayish olive; primaries and secondaries sooty black, edged lightly with hair brown; wing coverts

---

[2] Verh. Orn. Ges. Bayern, 1907, vol. 8, 1908, p. 161.

[3] *Xenerpestes minlosi* Berlepsch, Ibis, 1886, p. 53, pl. 4 (near Bucaramanga, Colombia).

blackish mouse gray, the middle and greater series tipped with white spots that form two well-marked wing bars; middle rectrices and outer webs of others deep olive-gray, the concealed portions of the outer ones deep mouse gray, the two outermost edged lightly at the tip, mainly on the inner web, with pale olive-gray; lores olive-buff, beginning at the nostril, becoming dull white, and passing backward above the eye as a prominent superciliary stripe; sides of head deep olive-buff anteriorly, passing into mouse gray posteriorly; under surface dull whitish, washed indistinctly with primrose yellow, with a few small, indistinct flecks of dark neutral gray on the sides of the upper breast; bend of wing and axillars marguerite yellow; under wing coverts white; inner webs of primaries edged with dull white; under tail coverts olive-buff. Maxilla dark neutral gray; tip of mandible neutral gray, base grayish olive; tarsus and toes deep neutral gray, claws whitish. (From dried skin.)

Measurements.—Males, 2 specimens, wing 57.1-57.3 (57.2), tail 41.6-45.6 (43.6), culmen from base 13.4 (one specimen only), tarsus 15.3-16.0 (15.6) mm.

Females, 2 specimens, wing 52.5-54.9 (53.7), tail 42.2-42.6 (42.4), culmen from base 12.8-13.7 (13.2), tarsus 14.8-15.1 (14.9) mm.

Type.—Male, wing 57.1, tail 41.6, (extreme tip of culmen broken), tarsus 16.0 mm.

Range.—From eastern Darién, Panamá (Garachiné, Río Sambú, Cituro), to northern Valle, northwestern Colombia (Malaguita, Punto Muchimbo). (A record from Tierra Alta on the lower Río Sinú, western Bolívar, may refer to this form.)

Remarks.—The four specimens of the new race seen have been compared with two topotypes of *minlosi* in the U. S. National Museum from Hacienda Santana, above Bucaramanga, Santander. The two *minlosi* are definitely paler above, and have the fore part of the crown clearly streaked with whitish, a character noted in the original description and shown in the plate accompanying it. It is supposed that the records from Boyacá and Cundinamarca pertain to the typical subspecies, while that from Tierra Alta in western Bolívar may be the new form.

The type specimen of *umbraticus* was shot high up in a tall tree, on the south side of the Río San Juan, near the mouth of Río Calima.

As further specimens have come to hand from widely scattered localities it has begun to seem probable that this bird is more common than has been supposed. Because of small size and lack of striking markings it is often overlooked.

PREMNOPLEX BRUNNESCENS MNIONOPHILUS, new subspecies

Characters.—Similar to *Premnoplex brunnescens distinctus* Griscom[4] but definitely grayer; back, rump, and upper tail coverts more olive, less rufescent; crown slightly grayer; under surface lighter, grayer, with throat and other markings lighter buff.

Description.—Type, U.S.N.M. No. 443674, male, south face of Cerro Campana, Provincia de Panamá, Panamá, at 3,000 feet elevation, March 19, 1951, A. Wetmore and W. M. Perrygo (orig. No. 16437). Crown chaetura black, each feather being lighter centrally, the light markings being dull colonial buff on the forehead, becoming progressively duller posteriorly, shading to olive-buff in center of crown, and to citrine drab on nape, the feathers therefore with a squamate appearance; lores chamois, mixed with bristly projecting filaments chaetura black in color; a somewhat indistinct superciliary chamois; auricular region chaetura drab, with indistinct shaft streaks of chamois; feathers on hindneck very dull colonial buff centrally, forming an indistinct collar; back dull snuff brown, with faintly indicated darker distal edgings, producing indistinct squamations; rump and upper tail coverts Prout's brown; lesser wing coverts sepia; middle and greater wing coverts Prout's brown; primaries and secondaries chaetura black, edged broadly on outer web with Prout's brown; rectrices bister with fuscous shafts; throat chamois; chin paler, nearer cream-buff, the feathers tipped very faintly with dusky neutral gray; feathers of upper breast cream-buff, with well-marked edgings of dark olive, producing prominent light spots; lower breast and abdomen deep olive, with elongate, tear-shaped central spots of cream-buff, these becoming progressively narrower and less in size until they disappear on the lower abdomen; sides and flanks sepia, the sides with a few elongate central markings of cream-buff; under tail coverts Prout's brown, with indistinct spots of buckthorn brown; under wing coverts deep olive, mixed with chamois; edge of wing, at base of outer primary, chamois barred with deep olive. Maxilla blackish; mandible pale olive-buff with a blackish line along tomium; tarsus and toes fuscous; claws light drab (from dried skin).

Measurements.—Males, 2 specimens, wing 61.2-61.6 (61.4), tail 55.9-56.2 (56.1), culmen from base 14.6-15.6 (15.1), tarsus 18.9-19.1 (19.0) mm.

Female, 2 specimens, wing 60.0-60.4 (60.2), tail 56.1-56.8 (56.4), culmen from base 16.0-16.3 (16.1), tarsus 19.1-19.6 (19.3) mm.

---

[4] *Premnoplex brunnescens distinctus* Griscom, Amer. Mus. Nov., No. 280, September 10, 1927, p. 5 (Chitrá, 4,000 feet elevation, Veraguas, Panamá).

Type.—Male, wing 61.2, tail 55.9, culmen from base 15.6, tarsus 19.1 mm.

Range.—Known only from 3,000 feet elevation on the more humid areas of Cerro Campana, Provincia de Panamá, Panamá.

Remarks.—The new form here described differs from *Premnoplex brunnescens albescens* Griscom, of the mountains of eastern Darién, in being more olive, less rufescent above, and definitely more buffy on the throat and other light markings of the lower surface. In general the new race is more or less intermediate in appearance between its two geographically nearest relatives, *distinctus* of Veraguas and *albescens* of Darién, but differs from both in being more olive, less rufescent above. All three are closely similar in size.

SCLERURUS GUATEMALENSIS ENNOSIPHYLLUS,[5] new subspecies

Characters.—Similar to *Sclerurus guatemalensis salvini* Salvadori and Festa,[6] but lighter, grayer above; paler below; outer webs of primaries more olive.

Description.—Type, U.S.N.M. No. 392775, female, from Volador (near El Tigre), 2,600 feet elevation, 25 miles west of Simití, Bolívar, Colombia, May 27, 1947, by M. A. Carriker, Jr. (orig. No. 11123). Crown, hindneck, and upper back sepia, the forehead tipped lightly with isabella color; lesser and middle wing coverts and lower back bister; lower rump and upper tail coverts chestnut-brown; outer webs of greater wing coverts, primaries and secondaries Mars brown; inner webs fuscous; rectrices sooty black; throat white, with the feathers edged with dusky neutral gray, producing a scalloped appearance; sides of head sepia, with slight shaft streakings of isabella color, which become broader in a line from below rictus back under the auricular region, producing a faint streak; sides of neck mingled sepia and Saccardo's umber; feathers of lower foreneck and upper breast sayal brown centrally, tipped with bister, with shaft lines of cinnamon-buff, producing an indistinct spotting; lower breast and sides between Saccardo's umber and sepia; abdomen and under tail coverts between bister and sepia; under wing coverts tawny-olive; inner webs of central primaries edged with avellaneous on under surface. Maxilla brownish black; tip of maxilla fuscous, base buffy brown; tarsus

---

[5] From *ἐννοσίφυλλος*, shaking or scattering leaves, in allusion to the active habit of this bird in overturning and throwing dead leaves about in search for food.

[6] *Sclerurus salvini* Salvadori and Festa, Boll. Mus. Zool. Anat. Comp. Torino, vol. 14, No. 362, November 17, 1899, p. 23 (Río Peripá, Ecuador).

blackish brown, becoming buffy brown on upper end of posterior face; feet blackish brown, claws slightly browner (from dried skin).

Measurements.—Males, 9 specimens, wing 85.3-90.1 (87.5), tail 58.2-64.2 (60.9), culmen from base 22.6-24.9 (23.8), tarsus 21.4-23.9 (22.1) mm.

Females, 5 specimens, wing 85.8-90.0 (87.9), tail 56.8-59.0 (57.6), culmen from base 22.0-23.9 (22.7), tarsus 21.4-22.6 (22.1) mm.

Type.—Female, wing 88.3, tail 57.6, culmen from base 22.6, tarsus 22.5 mm.

Range.—From the Río Sinú valley (Nazaret, Tierra Alta, Quebrada Salvajín) eastward through the foothill area to the western slopes above the lower Río Magdalena (Santa Rosa, Volador), Bolívar, Colombia.

Remarks.—Description of the present form marks a considerable extension of range for this species through north-central Colombia, as previously these birds have been reported only from the west-coast area and the upper reaches of the Río Sinú. The three geographic races now recognized are based on small differences in color that change almost insensibly over intermediate areas of considerable extent. No appreciable variation in size is evident in the three forms. The type race, which is brighter, more reddish brown above, extends from Guatemala (where few have been found to date) to Panamá, being found in typical form to the Canal Zone. Beyond this area there is a gradual change through eastern Panamá Province and Darién to the darker, more sooty *salvini,* which ranges on the Pacific slope from eastern Darién to Ecuador. The previously unrecognized form described here on basis of more grayish olive color, extends eastward in Colombia from the Sinú valley through the forested hill country of southern Bolívar to the western side of the Magdalena valley west of Simití. This race intergrades with *salvini* in the eastern part of the Río Atrato valley, specimens from Villa Artiaga, near Pavarondocito, being intermediate. The record from Quimarí on the upper Sinú, reported by de Schauensee [7] under the name *Sclerurus guatemalensis guatemalensis,* belongs without question under *ennosiphyllus,* as the typical race extends to the south and east only to western Darién.

SCLERURUS MEXICANUS OBSCURIOR Hartert

Sclerurus mexicanus obscurior Hartert, Nov. Zool., vol. 8, October 5, 1901, p. 370 (Lita, Esmeraldas, Ecuador).

Three collected April 17, 19, and 24, 1912, by E. A. Goldman at the head of Río Limón, on Cerro Pirri, Darién, agree fully with birds

---

[7] Caldasia, vol. 5, No. 24, July 10, 1950, p. 690.

from extreme western Colombia and northwestern Ecuador. This race has not been reported previously north of the Province of Valle, western Colombia.

Family FORMICARIIDAE: Ant-thrushes

MYRMORNIS STICTOPTERA (Salvin)

Rhopoterpe stictoptera Salvin, Bull. Brit. Orn. Club, vol. 1, No. 6, March 1, 1893, p. 32 (Santo Domingo, Nicaragua).

Peters[8] gives the first record of this bird for Colombia from El Umbo, Boyacá, the specimen being in the Museum of Comparative Zoölogy. M. A. Carriker, Jr., collected a pair at Socarré, Bolívar, on the Río Sinú, April 21 and 22, 1949, and another pair at Unguía, Chocó, March 10 and 16, 1950. On careful comparison with an excellent series from Nicaragua I find no differences in these birds from points far distant from the type locality.

All material that I have seen is so clearly distinct from *M. torquata* that I consider *stictoptera* and *torquata* specifically separated.

Family FRINGILLIDAE: Grosbeaks, Finches, Buntings

ZONOTRICHIA CAPENSIS ORESTERA, new subspecies

Characters.—Similar to *Zonotrichia capensis costaricensis* Allen,[9] but decidedly darker, less buffy brown above; dark markings of dorsal surface blacker; gray of crown darker; chestnut of nuchal collar deeper; paler edgings darker; rump darker gray; tail darker; sides and flanks grayer, less buffy; under surface, in general, whiter.

Description.—Type, U.S.N.M. No. 434103, male adult, southeast face of Cerro Campana, Provincia de Panamá, Panamá, 2,000 feet elevation, March 2, 1951, A. Wetmore and W. M. Perrygo (orig. No. 16122). Median crown stripe and auricular area, extending forward toward gape, mouse gray; superciliary stripe light mouse gray, changing to pale mouse gray behind the eye; a few whitish feathers behind nostril; broad lateral crown stripes, an indistinct circle around eye, and indistinct edgings on gray auriculars and rictus dull black; circlet of feathers on eyelids dull whitish with whitish bases on feathers immediately in front of eye; hindneck and sides of neck Mikado brown, forming a distinct collar; feathers of back and scapu-

---

[8] Check-list Birds of the World, vol. 7, 1951, p. 256.

[9] *Zonotrichia capensis costaricensis* Allen, Bull. Amer. Mus. Nat. Hist., vol. 3, September 29, 1891, p. 374 (San José, Costa Rica.)

lars black centrally, forming heavy longitudinal streaks, bordered broadly with snuff brown laterally and tipped with deep olive-buff; rump hair brown; upper tail coverts olive-brown; lesser wing coverts sooty black, edged lightly with mouse gray; middle coverts similar but tipped prominently on the distal part of the outer web with white, forming a distinct bar; greater wing coverts olivaceous-black, edged with snuff brown, and tipped lightly with white to form a second bar; primaries and secondaries fuscous-black, edged lightly with pale smoke gray; tertials dull black, margined with snuff brown; rectrices fuscous-black; throat pure white; sides of foreneck black, the two sides united across the front by an indistinct band where the feathers are white tipped with deep to dusky neutral gray; breast paler than pale olive-gray; abdomen white; under tail coverts pale olive-buff; sides drab, becoming slightly more buffy brown on flanks; under wing coverts light grayish olive, edged with dull white; edge of wing dark mouse gray, with a distinct spot of white at base of ninth primary; inner webs of primaries edged on lower surface with a line of pale olive-buff. Bill dull black, with a wash of fuscous at base of mandible; tarsus and toes buffy brown; claws fuscous (from dried skin).

Measurements.—Males, 8 specimens, wing 60.5-64.6 (62.9), tail 50.4-54.9 (52.6, average of 7 individuals), culmen from base 12.2-13.2 (12.8, average of 7 individuals), tarsus 21.0-22.7 (21.6) mm.

Female, 1 specimen, wing 59.5, tail 51.6, culmen from base 12.6, tarsus 21.2 mm.

Type.—Male, wing 63.2, tail 52.1, culmen from base 13.2, tarsus 21.0 mm.

Range.—Open slopes of Cerro Campana, in the western part of Provincia de Panamá, Panamá.

Remarks.—It is only recently that these birds have been noted in the mountains immediately west of the Canal Zone, and the series recorded here includes the first specimens that have been taken in this section, so far as I am aware. The type locality of *orestera* in an airline is distant only 50 kilometers from Balboa.

The birds range over open, grass-covered ridges where exposures of volcanic rock thrust out from the poor, stony soil, and woody vegetation is composed of low, scrubby growth in sheltered valleys, only scattered shrubs appearing elsewhere. The sparrows remain mainly in the grassland, perching on boulders or in the low bushes. They were found from 1,800 feet upward. Their haunt is now easily accessible, as it is possible to drive in a passenger car to the slopes where the birds are common. In fact this was one of the first birds that I saw on my visit to this mountain. While inconspicuous, these sparrows are not especially shy, so that the species is one that is easily found when its proper haunts are known.

The extent of the range is at present uncertain. Three specimens in the American Museum of Natural History from Calobre and Santa Fé in eastern Veraguas are to be placed with *orestera,* though slightly intermediate toward *costaricensis.* An old skin in the U. S. National Museum marked Cascajal, Coclé, appears nearer *costaricensis.* Presumably this was taken on the high open slopes on the Pacific side, above the head of the Río Cascajal, which is a tributary of the Río Coclé del Norte. Dr. Matthew W. Stirling, who has been on the Cascajal, informs me that the Caribbean slope is heavily forested, but that there are open, grassy slopes just over the divide toward La Pintada. All specimens from Chiriquí that I have seen are to be placed definitely with *costaricensis,* so that the area of intergradation between the two forms would appear to be in Veraguas. A sight record from Cerro Chame by Gerald Rogers[10] presumably refers to *orestera,* since this mountain lies adjacent to Cerro Campana a few miles to the southeast, the two being separated by a low divide.

---

[10] Auk, 1945, p. 641.

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 117, NUMBER 3

RELATIONSHIPS OF CERTAIN GENERA OF FUNGUS GNATS OF THE FAMILY MYCETOPHILIDAE

BY
F. R. SHAW AND M. M. SHAW
Amherst, Mass.

(Publication 4053)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
DECEMBER 27, 1951

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

RELATIONSHIPS OF CERTAIN GENERA OF FUNGUS GNATS OF THE FAMILY MYCETOPHILIDAE

By F. R. SHAW and M. M. SHAW[1]
Amherst, Mass.

The present study represents a continuation of a preliminary investigation of the possible value of thoracic sclerites in determining the relationships of certain insects. Dr. G. C. Crampton was the first to demonstrate the use of these sclerites as a means of determining the systematic position of insects. In 1925, he published a classical study of the comparative morphology of the thorax of nontipuloid Nematocera. In 1948 Shaw presented a paper in which he indicated the value of thoracic sclerites as an aid in determining the phylogeny of the Mycetophilidae. Although the number of genera he studied was admittedly small, principles were developed that have been of value in distinguishing the phylogenetic relationships of certain genera.

Edwards (1925) was the first to indicate that the structure of thoracic sclerites might be of value in determining generic characters in this group. In his monograph of the British fungus gnats he noted that in certain genera the sclerites differed in form and that such differences might be of value in separating groups of these insects.

---

[1] We wish to express our thanks to the Society of Sigma Xi for a grant-in-aid that made possible the preparation of the illustrations for this paper. Also, in the progress of this research, several others have been of invaluable assistance. To Elmer Smith much credit is due for preparing the figures and for his keen interest and observations. To Dr. John Lane, of São Paulo, Brazil, we are indebted for specimens of certain genera and for helpful suggestions. Dr. E. G. Fisher offered pertinent suggestions relating to the phylogeny of the group. Dr. Paul Freeman, of the British Museum of Natural History, kindly lent certain specimens for examination.

Owing to the comparative scarcity of specimen material of some of the fungus gnats of this family, it was not possible in all cases to prepare specimens properly for morphological study. Consequently, no figures were made for the genera *Manota, Lygistorhina, Stenophragma, Platyroptilon,* and *Allactoneura,* but sufficient observations were made from pinned specimens in most instances to determine the generic affinities.

In Shaw's 1948 paper 21 mycetophilid genera were figured and discussed. He indicated the features that appeared primitive and using these as principles was able to indicate the relationships of the forms studied from a phylogenic standpoint.

Of the genera studied, 45 are figured herein. While thoracic sclerites are primarily used, in some cases venation and chaetotaxy are also considered. Representatives of all but two subfamilies, the Lygistorhininae and the Manotinae, are figured. On the basis of the present investigation, certain genera are no longer considered as distinct. In some instances the position of certain genera within tribes is questioned, and two new tribes are proposed. Certain genera formerly united to others are recognized as distinct on the basis of thoracic sclerites.

To aid the reader in visualizing the scope of the work the following table is presented. The position of the genera is indicated as they are placed as a result of these studies. Genera indicated by an asterisk are not figured but have been studied. A question mark indicates that the affinities of the genus are still somewhat uncertain.

Subfamily	*Tribe*	*Genera represented*
Bolitophilinae		*Bolitophila* Meigen (including *Bolitophilella* Landrock)
Ditomyiinae		*Centrocnemis* Phillipi ?
		Nervijuncta Marshall
		Symmerus Walker
		Calliceratomyia Lane
Diadocidinae		*Diadocidia* Ruthe
Ceroplatinae (including Macrocerinae: genera *Macrocera* and *Fenderomyia*)		*Palaeoplatyura* Meunier
		Proceroplatus Edwards
		Ceroplatus Bosc
		Platyroptilon Westwood *
		Apemon Johannsen ?
		Platyura Meigen
		Macrocera Meigen
		Fenderomyia Shaw
Sciophilinae	Mycomyiini	*Mycomyia* Rondani
	Sciophilini	*Eudicrana* Loew
		Monoclona Mik *
		Neuratelia Rondani
		Parvicellula Marshall
		Phthinia Winnertz
		Polylepta Winnertz
		Sciophila Winnertz
		Stenophragma Skuse *
		Syntemna Winnertz

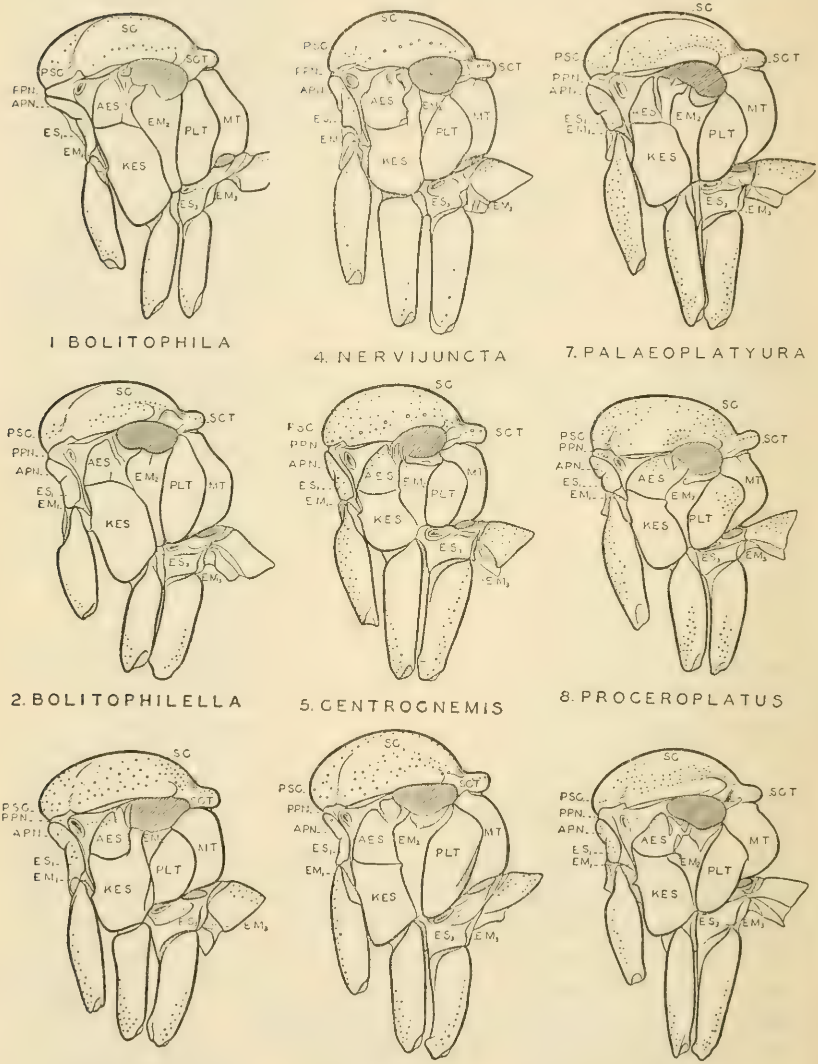
Subfamily	*Tribe*	*Genera represented*
Sciophilinae	Gnoristini	*Gnoriste* Meigen
		Boletina Staeger
		Coelosia Winnertz
		Paratinia Mik
		Dziedzickia Johannsen
	Leiini	*Leia* Meigen
		Tetragoneura Winnertz
		Ectrepesthoneura Enderlein
		Docosia Winnertz
		Anomalomyia Hutton
	Cycloneurini	*Cycloneura* Marshall
		Procycloneura Edwards
	Allactoneurini	*Allactoneura* De Meijere *
Mycetophilinae	Exechini	*Allodia* Winnertz
		Brachypeza Winnertz
		Exechia Winnertz
	Mycetophilini	*Cordyla* Meigen
		Epicypta Winnertz
		Mycetophila Meigen (including *Mycothera* Winnertz)
		Opistholoba Mik
		Phronia Winnertz
		Sceptonia Winnertz
Manotinae		*Manota* Williston *
Lygistorhininae		*Lygistorhina* Skuse *
Family Sciaridae		*Sciara* Meigen
		Pseudosciara Schiner

Subfamily BOLITOPHILINAE

The subfamily Bolitophilinae is represented by the two genera *Bolitophila* (fig. 1) and *Bolitophilella* (fig. 2), which have been distinguished on the basis of the termination of R_4 of Edwards. In *Bolitophila* this vein ends in the costa, whereas in *Bolitophilella* it ends in R_{1+2}. The value of this character is somewhat open to question as far as its use to separate genera is concerned. From the thoracic sclerites, only minor differences are apparent. The episternum of the prothorax is more elongate in *Bolitophila* and the mesepimeron is slightly broader. However, the structures are so similar that we would not recognize the two genera as distinct.

Subfamily DITOMYIINAE

The subfamily Ditomyiinae is represented by *Centrocnemis* (fig. 5), *Symmerus* (fig. 3), and *Nervijuncta* (fig. 4). On the basis of thoracic



1 BOLITOPHILA

2. BOLITOPHILELLA

3. SYMMERUS

4. NERVIJUNCTA

5. CENTROGNEMIS

6. DIADOCIDIA

7. PALAEOPLATYURA

8. PROCEROPLATUS

9. CEROPLATUS

FIGS. 1-9.—Genera of the family Mycetophilidae.

sclerites *Symmerus* and *Nervijuncta* seem closely related. Both genera possess a dorsal projection from the katepisternum of the mesothorax. In reality this structure represents a fusion of the posterior portion of the anepisternite with the katepisternite. In *Symmerus* the mesepimeron is greatly reduced, with only the dorsal and ventral portions remaining. In *Nervijuncta* this reduction has gone even further, with only the dorsal portion remaining.

We have never seen a specimen of *Calliceratomyia* Lane, but through the courtesy of John Lane we have a sketch of the thorax of a specimen of this genus. Though lacking in certain details, the drawing clearly indicates that *Calliceratomyia,* on the basis of thoracic sclerites, is closely related to *Nervijuncta* and *Symmerus.*

We are uncertain whether the genus *Centrocnemis* is correctly placed in the Ditomyiinae. Unfortunately, we were not able to obtain specimens of *Ditomyia* for study. The only characteristic that *Centrocnemis, Symmerus,* and *Nervijuncta* show in common is the well-developed metapleura. Otherwise, from the standpoint of thoracic sclerites there is not much similarity. *Centrocnemis* possesses a well-developed and broad mesepimeron resembling that of *Apemon.* The dorsal lobe of the katepisternum, as found in both *Symmerus* and *Nervijuncta,* is lacking. From the standpoint of venation, *Centrocnemis* is more closely related to *Mycetobia* (Anisopodidae) than to *Symmerus* or *Nervijuncta.* Until the opportunity to study *Ditomyia* is presented we reserve judgment as to the ultimate systematic position of *Centrocnemis.*

Subfamily DIADOCIDINAE

The subfamily Diadocidinae is represented by the genus *Diadocidia* (fig. 6). The position of *Diadocidia* is not entirely clear. From the standpoint of venation, this genus must be considered as more highly evolved than either the Bolitophilinae or the Ceroplatinae. The radius is 2-branched and the stem of media is lacking. The affinities of *Diadocidia* seem to be closer to the Bolitophilinae than to the Ceroplatinae. Both *Bolitophila* and *Diadocidia* exhibit a remnant of a meron. In both genera the anepisternal cleft is not so pronounced as it is in *Palaeoplatyura.* The structure of the prothorax is similar for *Bolitophila* and *Diadocidia.*

Subfamily CEROPLATINAE

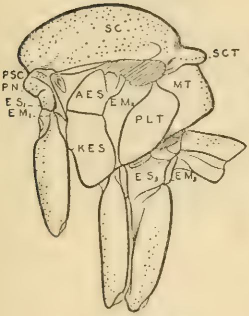
The Ceroplatinae figured represent the seven genera *Palaeoplatyura* (fig. 7), *Proceroplatus* (fig. 8), *Ceroplatus* (fig. 9), *Platyura* (fig.

10), *Apemon* (fig. 11), *Macrocera* (fig. 12), and *Fenderomyia* (fig. 13). In addition we have examined a specimen determined by Edwards as *Platyroptilon miersi* Westwood. This specimen lacked antennae; the pleurotergites were not hairy as Tonnoir (1929) states them to be in this genus; and there was no evidence of setae on the anepisternite. There may therefore be some question as to the correct identity of the insect. In any case the specimen we examined identified as *Platyroptilon* was very close to *Ceroplatus* on the basis of thoracic sclerites.

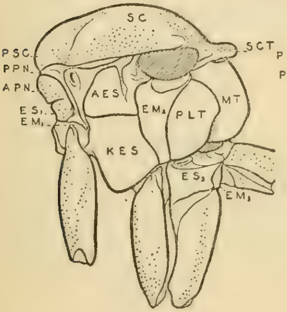
If *Apemon* be excluded, it is fairly simple to consider the other genera of the Ceroplatinae as having developed from a form similar to *Palaeoplatyura.* All exhibit the reduction of the mesepimeron and a dorsoventral compression of the thorax resulting in an apparent shifting of the sclerites posteriorly to a more nearly horizontal position. Such a shift becomes very prominent in certain genera of the Mycetophilini.

Apemon, as indicated in an earlier paper (Shaw, 1948), is somewhat of an anomaly. On the basis of thoracic sclerites its affinities seem closer to *Centrocnemis, Symmerus,* and *Nervijuncta* of the Ditomyiinae. As in *Centrocnemis,* the mesepimeron is broad. The cleft in the anepisternite is very distinct and indicates what has probably happened in both *Symmerus* and *Nervijuncta* where the katepisternite seems to have a dorsal lobe extending to the wing basis. On the basis of thoracic sclerites *Apemon* occupies an intermediate position between the Ditomyiinae and Ceroplatinae; from the standpoint of venation it seems to be intermediate between *Palaeoplatyura* and *Platyura.* As in *Palaeoplatyura* the stem of media is distinct. However, as in *Platyura* the r-m cross vein is lost, apparently through the fusion of a portion of the stem of media with Rs. *Apemon* also exhibits the dorsoventral flattening of the thorax as also found in *Proceroplatus* and *Platyura.*

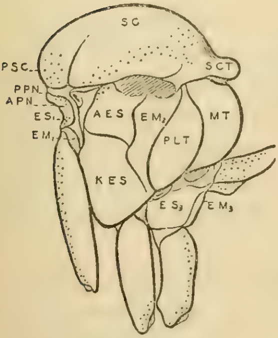
The systematic position of the Macrocerinae has been somewhat in question. Some workers, including Lane and Coher, consider this subfamily inseparable from the Ceroplatinae. We have two representatives of the Macrocerinae, *Macrocera* (fig. 12) and *Fenderomyia* (fig. 13). *Macrocera* on the basis of thoracic sclerites is intermediate between *Palaeoplatyura* and *Platyura.* However, in *Palaeoplatyura, Ceroplatus,* and *Platyura* there is a rather indistinct indication of a meron in the mesothoracic leg. This is lacking in *Macrocera, Fenderomyia,* and also in *Proceroplatus. Macrocera, Proceroplatus, Platyura,* and *Ceroplatus* all exhibit one characteristic in common—the reduction of the lower portion of the epimeron of the mesothorax. This



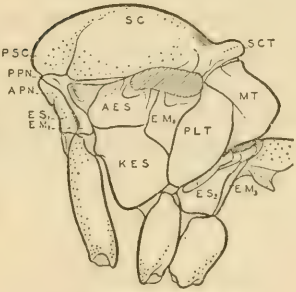
10. PLATYURA



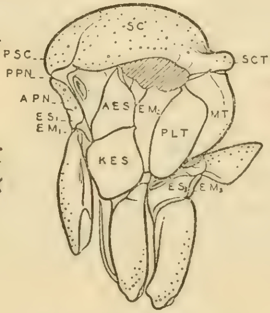
11 APEMON



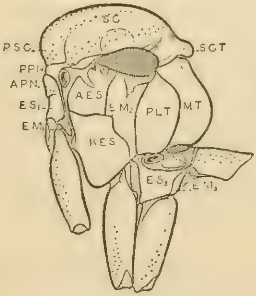
12. MACROCERA



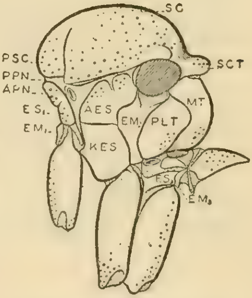
13 FENDEROMYIA



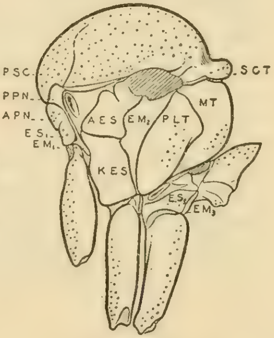
14. MYCOMYIA



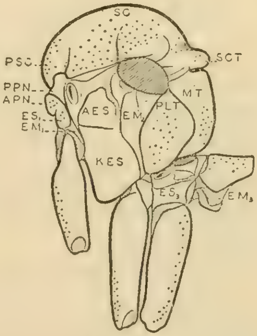
15. PARATINIA



16. PARVICELLULA



17. POLYLEPTA



18. NEURATELIA

FIGS. 10-18.—Genera of the family Mycetophilidae.

culminates in the condition shown in *Fenderomyia* where the pleurotergite and the katepisternite touch each other, obliterating practically all the lower half of the epimeron but the tip. *Ceroplatus, Proceroplatus, Platyura,* and *Fenderomyia* also possess another characteristic in common—the mediotergite instead of being rounded, as in *Palaeoplatyura* and *Macrocera,* becomes distinctly angulated. This might result from a dorsoventral flattening of the thorax and is also indicated in the position of the pleurotergies, which shift to a more horizontal position. Our present opinion would be that the Macrocerinae should be included in the Ceroplatinae.

Subfamily Sciophilinae

The Sciophilinae are represented by six tribes: The Mycomyiini, the Sciophilini, the Gnoristini, the Leiini, the Cycloneurini, and the Allactoneurini.

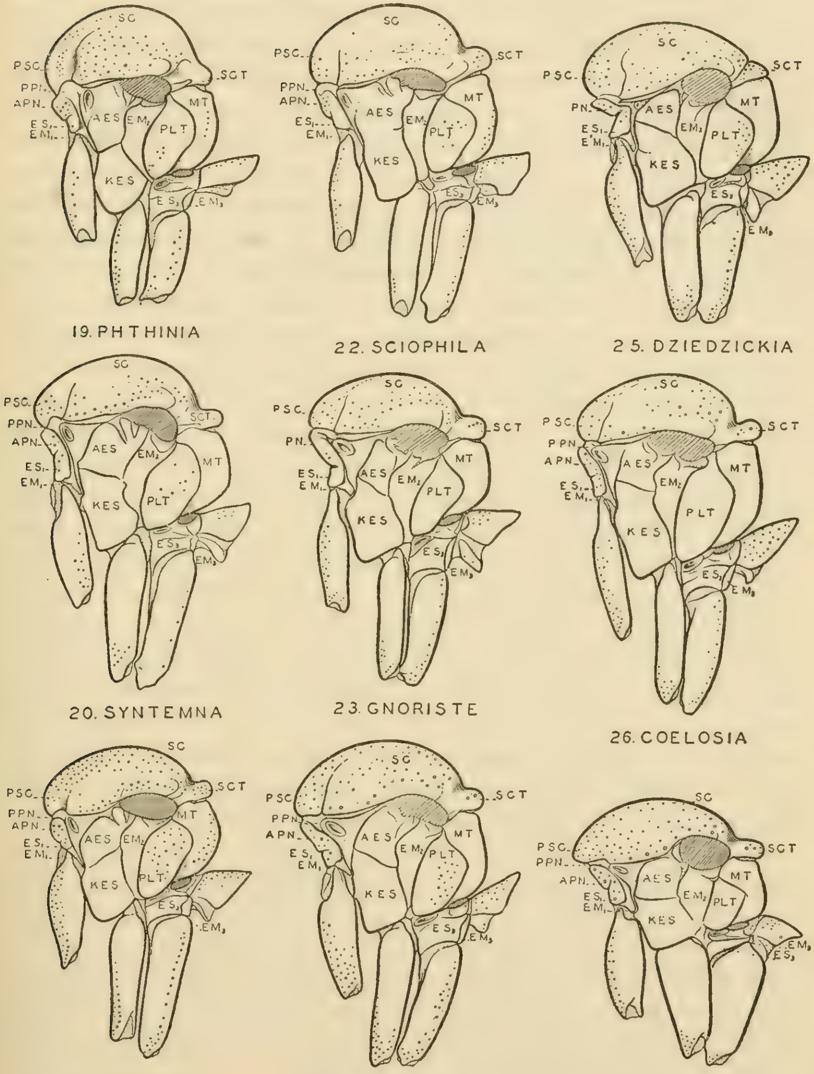
Tribe MYCOMYIINI

The Mycomyiini are represented only by the genus *Mycomyia* (fig. 14). Shaw (1948) indicated that *Mycomyia* might be an annectant form between the Sciophilinae and the Mycetophilinae. Such a belief is based on the structure of the pleura, and also, as pointed out by Fisher, the male hypopygium indicates such a relationship.

Tribe SCIOPHILINI

Edwards (1925) states that the possession of macrotrichia on the wing membrane is diagnostic of the tribe. The value of this character for generic recognition may be open to question. He adds that where the microtrichia have disappeared it may not always be easy to determine which set of hairs is present. Another characteristic of value in delimiting this group is the possession of some hairs or bristles on the postnotum (mediotergite). This characteristic is not common to all genera.

The Sciophilini figured in this study include eight genera—*Eudicrana* (fig. 21), *Neuratelia* (fig. 18), *Paratinia* (fig. 15), *Parvicellula* (fig. 16), *Phthinia* (fig. 19), *Polylepta* (fig. 17), *Sciophila* (fig. 22), and *Syntemna* (fig. 20). *Monoclona* was examined but not figured. Of the species studied, all but *Paratinia, Syntemna,* and *Monoclona* have hairs or setae on the mediotergite. All but *Paratinia* have setae on the pleurotergites. Concerning the latter genus, Edwards (1925) states: "It does not seem to be very closely related to the other genera of the Sciophilini but I include it here on account of macrotrichia on



19. PHTHINIA

22. SCIOPHILA

25. DZIEDZICKIA

20. SYNTEMNA

23. GNORISTE

26. COELOSIA

21. EUDICRANA

24. BOLETINA

27. CYCLONEURA

FIGS. 19-27.—Genera of the family Mycetophilidae.

the apical half of the wing and the elongate abdomen with large seventh segment. It may be related to *Phthinia* and in some respects appears intermediate between that genus and *Speolepta*."

On the basis of the thoracic sclerites we see no evidence to support such a belief. The structure of epimeron, the indication of fusion of the posterior part of the anepisternite with the epimeron, and the absence of setae on both mediotergites and pleurotergites indicate that the affinities of the genus are closer to those of certain of the Gnoristini than to the Sciophilini. If the possession of macrotrichia is considered as the important characteristic, then *Paratinia* must be included with the Sciophilini. If so placed it would be closer to *Parvicellula* than to other members studied. Possibly too much value has been placed on the presence or absence of macrotrichia on the wing in the past. The genus *Parvicellula,* according to Tonnoir and Edwards (1926), is peculiar to New Zealand. In venation it most closely resembles *Monoclona.* On the basis of the shape of the anepisternite, *Monoclona* resembles *Mycomyia.* In fact, *Parvicellula, Monoclona,* and *Mycomyia* seem fairly closely related on the basis of thoracic sclerites. *Parvicellula* is not too closely allied to other members of the Sciophilini on the basis of thoracic sclerites. The anepisternite and katepisternite are more nearly equal in size in *Parvicellula,* and in this respect the genus is more closely related to *Phthinia* than to the other genera of this tribe represented in this study. The shape of the mesepimeron differs in both genera. The course of the dorsal half of the mesopleural suture in *Parvicellula* may indicate that the posterior part of the anepisternite may be fused with the epimeron at times. If the pleural suture were to extend in a straight line dorsally from the juncture of the anepisternite and the katepisternite, then the epimeron would have the structure as shown in *Paratinia.* The indication is that the posterior portion of the anepisternite may be fused with either the mesokatepisternite or the mesepimeron. The genus *Polylepta,* as indicated by Shaw (1948), has thoracic sclerites resembling those of *Platyura* except that the dorsoventral flattening, as indicated in *Platyura,* is not so marked in *Polylepta.* The possession of setae on the anepisternite, pleurotergite, and mediotergite is possibly evidence that *Parvicellula* and *Polylepta* are related.

The structure of the mesepimeron indicates that *Polylepta* and *Tetragoneura* (Leiini) were related. This may be only a superficial resemblance. *Tetragoneura* does not possess setae on the anepisternite, the pleurotergite, or the mediotergite. In the wing venation *Polylepta* and *Neuratelia* are very similar except for loss of vein R_4 (Edwards) in *Neuratelia.* From the standpoint of thoracic sclerites the arching of the posterior pronotum is common to both genera. In *Neuratelia* the posterior portion of the anepisternite seems to be in the process of fusing with the epimeron.

Phthinia resembles in some ways *Polylepta.* Like *Polylepta* it has setae on the mediotergite and pleurotergites. The anepisternites in both genera have fine hairs. *Phthinia* shows evidence of specialization in venation and also in the subequal anepisternite and katepisternite of the mesothorax. Edwards (1925) has indicated that *Phthinia* may be related to *Speolepta.* However, the latter genus lacks setae on the mediotergite and on the pleuroterga. Since we do not have material to study the sclerites of *Speolepta,* we cannot state whether these structures affirm Edwards' beliefs.

The genus *Syntemna* seems to be somewhat closely related to *Neuratelia* and *Polylepta* on the basis of thoracic sclerites. The epimeron of *Polylepta* might result from the fusion of a part of the posterior lobe of the anepisternite with the mesepimeron. The venation of *Syntemna* does not appear especially close to that of either of these genera. Edwards (1925) has indicated that *Syntemna* may be more closely related to the Gnoristini, apparently considering that *Dziedzickia* and this genus were similar. The thoracic sclerites do not indicate too close a relationship. The prothorax of *Dziedzickia* is greatly modified. Apparently the posterior lobe of the anepisternite has fused with the mesepimeron in *Dziedzickia.* This would indicate that the latter genus was more specialized than *Syntemna.* This view is not supported by venation. Edwards' inclusion of certain species of *Syntemna* in *Dziedzickia* on the absence of macrotrichia on the wing might be questionable unless supported by other characteristics.

The genus *Sciophila* seems to be the most specialized of the genera studied in this tribe. While it has maintained a relatively broad mesepimeron, the suture between the anepisternite and katepisternite of the mesothorax is almost lost. This condition is found also in the genus *Anomalomyia* (Leiini). Moreover, there is a reduction in the size of the epimeron of the prothorax.

The genus *Stenophragma,* represented by *Stenophragma nigricauda* Edwards, on the basis of thoracic structures seems very closely allied to *Sciophila.*

On the basis of venation *Monoclona* is close to *Sciophila* except for the unbranched cubitus and poor development of anal veins. Edwards (1925) indicated that the macrotrichia of the wing are reflexed in *Monoclona* and not decumbent as in *Sciophila.* The thoracic sclerites do not indicate a close relationship of the two genera. The anepisternite of *Monoclona* resembles that of *Mycomyia* more closely than it does that of *Sciophila*.

The genus *Eudicrana* is closely related to *Sciophila*. The suture between the mesothoracic anepisternite and katepisternite is beginning to disappear. The prothoracic epimeron shows a reduction in its width. From the standpoint of venation, *Eudicrana* seems more primitive. Only in the absence of the median ocellus is *Eudicrana* more specialized than *Sciophila*.

Tribe GNORISTINI

The tribe Gnoristini is represented by four genera—*Boletina* (fig. 24), *Coelosia* (fig. 26), *Dziedzickia* (fig. 25), and *Gnoriste* (fig. 23). On the structure of the thoracic sclerites the group appears to be quite homogeneous. All possess an epimeron that is broad dorsally and narrowed ventrally. *Gnoriste* seems to be most primitive on the basis of the structure of the epimeron. However, *Gnoriste* shows evidence of specialization in the possession of an elongate proboscis.

We believe that in all this group the posterior part of the anepisternite of the mesothorax is in the process of being fused or has been fused with the mesepimeron. This condition is most marked in *Dziedzickia*.

Boletina and *Dziedzickia* differ from *Gnoriste* and *Coelosia* in the possession of setae on pleurotergites. In regard to *Coelosia,* Edwards (1925) removed *Phthinia thoracia* Winnertz and *P. curta* Johannsen to this genus. Only future examination of specimens of these will determine if the thoracic sclerites indicate the validity of this grouping. Another feature shared in common by the four genera studied is the position of a suture between the anepisternite and katepisternite of the mesothorax. This suture does not extend in a horizontal line, as in many genera, but dips posteriorly. Both *Gnoriste* and *Boletina* show a reduction in the size of the propleura. They also exhibit a tendency for the pronotum to be compressed and eventually to assume an almost horizontal position, as shown in *Dziedzickia*.

The venation of the genera studied varies considerably. Thus *Dziedzickia* is the only one of the genera studied that possesses the upper branch of the radial sector (R_4 of Edwards) ; in other respects the venation resembles that of *Syntemna* of the Sciophilini. *Boletina* and *Gnoriste* have a similar venation. *Coelosia* resembles the genus *Phthinia* of the Sciophilini, differing primarily in the loss of Sc_2.

Johannsen (1911) has noted that certain species of *Boletina, Coelosia,* and *Gnoriste* share the peculiarity of having one claw of each foot of the male modified.

Tribe LEIINI

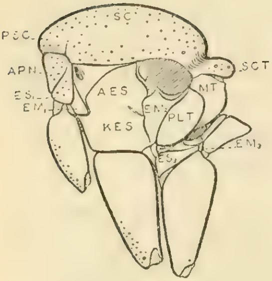
The tribe Leiini is represented by the genera *Leia* (fig. 33), *Tetragoneura* (fig. 30), *Ectrepesthoneura* (fig. 29), *Docosia* (fig. 31), *Anomalomyia* (fig. 32). The genera *Cycloneura* and *Procycloneura,* formerly placed in the Leiini, are considered to represent a distinct tribe, the Cycloneurini.

All these genera lack setae on the mediotergite. *Leia* and *Anomalomyia* possess setae on the pleurotergites. *Procycloneura* and *Anomalomyia* have lost the suture separating the mesothoracic anepisternite from the katepisternite. The condition has been noted already in *Sciophila* (Sciophilini). The significance of some of these apparent relationships may be open to question.

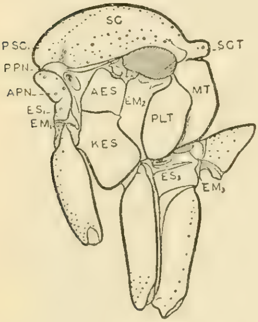
Ectrepesthoneura and *Tetragoneura* are closely related. Some slight differences in the shape of the pronotum, the mesothoracic katepisterna, and epimera. These are probably of sufficient importance to justify the maintaining of the two genera as distinct. The two genera differ in venation: *Tetragoneura* has Sc short and ending free and Cu forking near the middle of the wing; *Ectrepesthoneura* has Sc longer, ending in R, and Cu forking near the base of the wing. Edwards (1925) calls attention to the forking of the cubitus near the wing base, supporting the conclusion that this group of genera are more or less related to the Sciarinae. On the basis of thoracic sclerites, the similarity between *Tetragoneura* and *Ectrepesthoneura* is not so evident as would be indicated from the venation. *Docosia,* on the basis of thoracic sclerites, more closely resembles the Sciaridae. However, the resemblance is more or less superficial. *Sciara* possesses a midpleural pit, the division of the pronotum into an anterior and a posterior division, and a precoxal bridge. All these characteristics are lacking in *Docosia. Docosia,* on the basis of thoracic structures, is not closely related to either *Leia* or *Anomalomyia.*

Edwards (1925) pointed out that *Docosia* in life much resembles *Sciara.* He adds that *Docosia* also resembles *Tetragoneura* in appearance and habits and concludes that the genus is not distantly related to *Tetragoneura.* The shape of the epimeron, the pleurotergite, and the course of its suture separating the mesothoracic anepisternite from the katepisternite do not support the close relationship of *Tetragoneura* and *Docosia.* The absence of pleurotergal setae is common to *Docosia, Ectrepesthoneura,* and *Tetragoneura.*

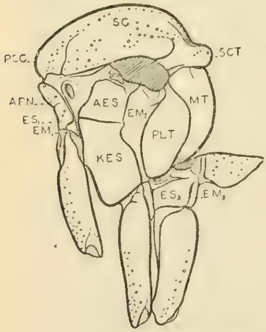
Anomalomyia, on the basis of venation, resembles rather closely *Rondaniella.* It would not be too difficult to derive the shape of the thoracic sclerites as found in *Anomalomyia* from those of *Leia.* If



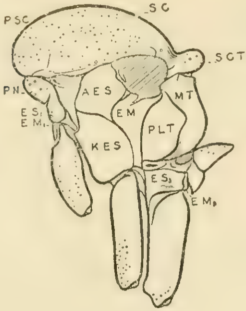
28. PROCYCLONEURA



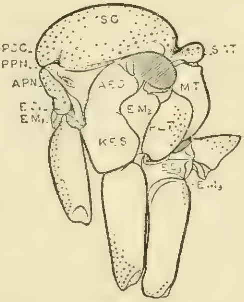
29. ECTREPESTHONEURA



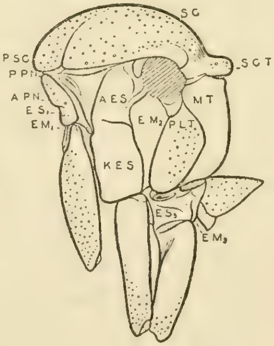
30. TETRAGONEURA



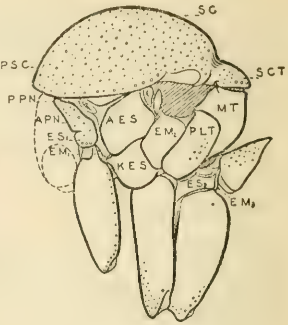
31. DOCOSIA



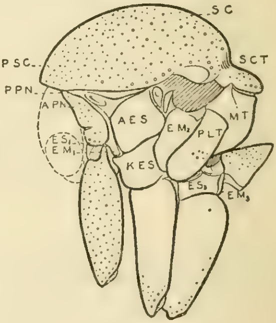
32. ANOMALOMYIA



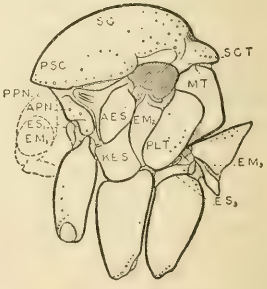
33. LEIA



34. EXECHIA



35 ALLODIA



36. BRACHYPEZA

Figs. 28-36.—Genera of the family Mycetophilidae.

the posterior lobe of the anepisternite were fused with the epimeron as somewhat indicated in *Leia*, and if the suture between the anepisternite and the katepisternite were completely lost, the two thoraces would be quite similar. There are indications of loss of the suture between the anepisternite and the katepisternite in *Leia*.

Cycloneura and *Procycloneura* might be placed in a tribe by themselves. Their inclusion in the Leiini seems questionable to us. In some respects they seem closer to the Mycetophilinae. Both have Sc short ending free. *Procycloneura* has the lateral ocelli touching the eye margin. They lack setae on the anepisternites, the pteropleurites, the pleurotergites, and the mediotergites. However, there is some variation in the distribution of setae in the representatives of the Mycetophilinae studied. The coxae appear stouter and more compact as in *Sceptonia* or *Epicypta* (Mycetophilinae). Until more material is made available for study it may be well to maintain *Cycloneura* and *Procycloneura* in the Sciophilinae. We do consider it valid to designate a new tribe—the Cycloneurini—which we establish here for these two genera and characterize as follows:

CYCLONEURINI, new tribe

Wing venation of the same general type as in *Leia*. Some species of *Cycloneura* with a fusion of Cu_2 and the anal vein, resulting in the formation of a closed cell. Thorax showing dorsoventral depression. Coxae stout and compact. Metapleura reduced in size.

In those forms possessing a suture between the anepisternite and the katepisternite, the thoracic sclerites are subequal in size. In this respect, the two genera placed in the Cycloneurini differ from the Leiini studied, which have the katepisterna larger than the anepisterna. We would expect *Paracycloneura* to fall in this tribe, but not having seen specimens we cannot definitely place it here.

Of the two genera, *Cycloneura,* on the basis of thoracic sclerites, appears the more primitive. The suture between the anepisternite and the katepisternite of the mesothorax persists but is lost in *Procycloneura*. Also the dorsoventral compression of the thorax is more marked in the latter genus.

ALLACTONEURINI, new tribe

A specimen of *Allactoneura argentosquamosa* Enderlein, determined by Edwards, was made available for examination by Dr. Freeman. Edwards (1925) erected a new subfamily, the Manotinae, to include this genus and *Manota.* An examination of thoracic sclerites indicates that *Allactoneura* is very similar to *Procycloneura.* The prothoracic region is more modified, being more dorsally produced. The pleurotergites are setose. The venation does not resemble either of the genera included thus far in the Cycloneurini. *Allactoneura* in our opinion is not closely allied to *Manota* but is more closely related to the Cycloneurini. It does not seem to agree with the Cycloneurini in venation or in chaetotaxy. Edwards (1925) called attention to the shape of the head of this genus, reminding one of the *Brachycera* and *Cyclorrhapa,* and also to the presence of scales on the thorax and abdomen. We consider it best to erect the above-named new tribe, the Allactoneurini, for this genus. It may be characterized as follows: Wing venation—Sc long, ending in costa, Sc_2 present. R 2-branched, M 2-branched. Cu 2-branched with fork at base of wing. Prothorax projecting dorsally into mesoscutum. Suture between anepisternite and katepisternite of mesothorax lost. Legs robust. Thorax and abdomen with scales. At present this tribe includes only one genus—*Allactoneura.*

Subfamily LYGISTORHININAE

This subfamily was proposed by Edwards for *Lygistorhina* Skuse, including *Probolaeus* Williston and *Palaeognoriste* Meunier. Johannsen (1911) included *Probolaeus* with the Mycetophilinae but stated, "It is possible that this genus should be placed with the Sciarinae." Although lacking proper material for a detailed study of the thorax, an examination of some slides indicates that the affinities of *Lygistorhina* are with those of the Sciophilinae, possibly being closest to the Gnoristini. However, the peculiar head structure, the elongate proboscis wholly unlike that of other mycetophilids, and the venation warrant the maintenance of a separate subfamily.

Subfamily MYCETOPHILINAE

The subfamily Mycetophilinae has been divided into two tribes on the following characteristics by Edwards (1925):

Anepisternal bristles present, hind coxa usually lacks a basal seta..Mycetophilini
Anepisternal and pteropleural bristles absent, hind coxa usually with a strong basal seta..Exechini

Tribe EXECHINI

The Exechini are represented by *Allodia* (fig. 35), *Brachypeza* (fig. 36), and *Exechia* (fig. 34) in this study.

Exechia and *Allodia* are closely allied. They are separated by the position of the fork of Cu, which is beyond that of media in *Exechia* and before the medial fork in *Allodia.* On the basis of thoracic sclerites there are no significant differences between the two. This substantiates the view of Edwards (1925).

Brachypeza, on the basis of thoracic sclerites, is not too closely allied to either *Allodia* or *Exechia.* In fact, our material has a setose anepisternite and on this basis would not be placed in the Exechini. It possesses one strong and two weaker setae on the base of the hind coxa. Thus it possesses characters of both the Exechini and the Mycetophilini.

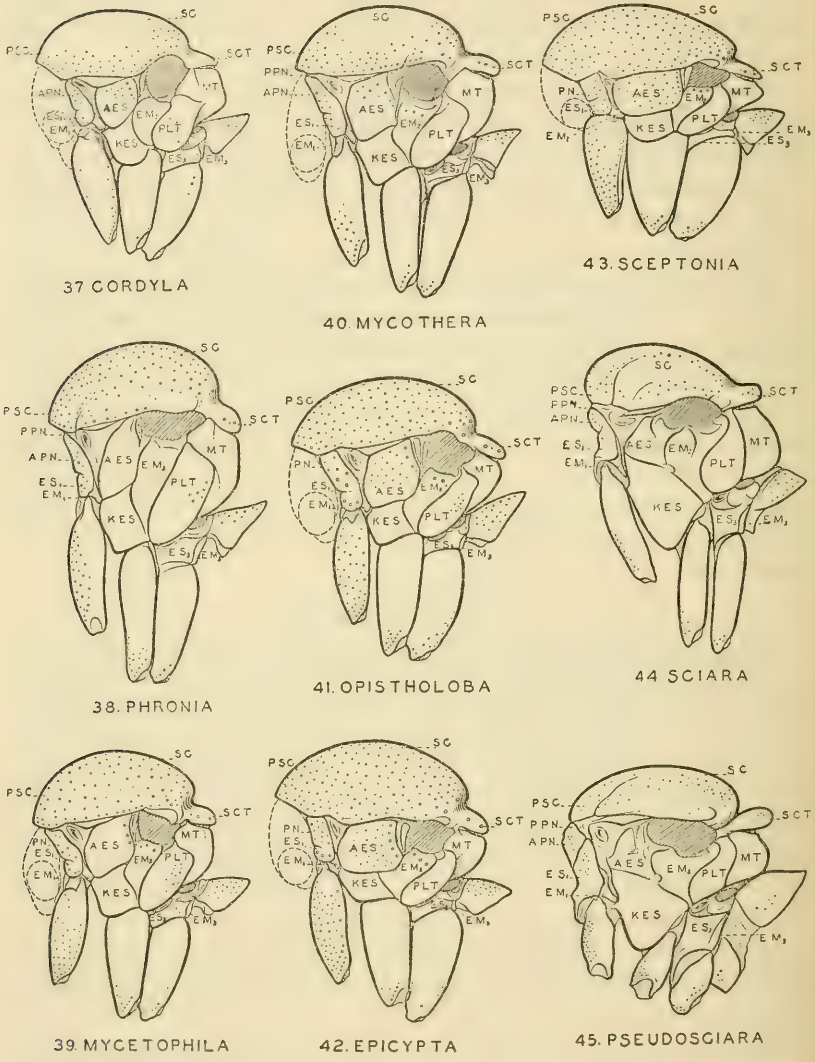
On the basis of venation *Brachypeza* appears closely related to *Rhymosia.* The anepisternite in some specimens of *Rhymosia* we have examined resembles more closely the anepisternite in *Brachypeza* than it does that of *Allodia.* This sclerite in *Brachypeza* is roughly hexagonal in shape, as in some of the species of *Rhymosia* we have examined. Possibly this may be of value in distinguishing between *Allodia* and *Rhymosia.* An investigation should be made of the two genera *Allodia* and *Rhymosia* to determine whether both are valid and also to reevaluate the systematic position of the species of the two genera.

Tribe MYCETOPHILINI

The tribe Mycetophilini is represented by *Cordyla* (fig. 37), *Epicypta* (fig. 42), *Mycetophila* (fig. 39), *Mycothera* (fig. 40), *Opistholoba* (fig. 41), *Phronia* (fig. 38), and *Sceptonia* (fig. 43). There seems to be a logical division of these genera on the absence or presence of pteropleural (mesepimeral) setae. On this basis, *Dynatosoma, Cordyla, Trichonta,* and *Phronia* form one group and the remaining genera of the tribe Mycetophilini another. This division seems to be supported by the structure of the thoracic sclerites. We have not examined *Dynatosoma* as far as the thoracic sclerites are concerned. From the standpoint of venation, this genus seems close to *Trichonta.* In general appearance the genus resembles *Mycetophila* but lacks mesepimeral bristles.

Edwards (1925, p. 587) has figured the thorax of *Trichonta.* While somewhat lacking in detail, it indicates that *Phronia* and *Trichonta* are closely allied. Both have the anepisternite more or less hexagonal in shape; the structure of the epimera is very similar.

Cordyla seems to be the most specialized of this group. It shows more marked dorsoventral compression of the thorax. Evidence of specialization is also indicated by the enlarged second palpal segment



37 CORDYLA

40. MYCOTHERA

43. SCEPTONIA

38. PHRONIA

41. OPISTHOLOBA

44 SCIARA

39. MYCETOPHILA

42. EPICYPTA

45. PSEUDOSCIARA

FIGS. 37-45.—Genera of the families Mycetophilidae and Sciaridae.

and the reduction of number of segments of the antennae. There is a difference in specialization between the males and females in regard to this aspect, since in general the females have fewer segments.

The remaining Mycetophilini are all characterized by the possession of mesepimeral setae. It would seem possible to subdivide further the genera studied, *Epicypta, Mycetophila, Mycothera, Opistholoba,* and *Sceptonia.* In all but *Mycetophila* and *Mycothera* the mesepimeron shows a tendency to occupy somewhat of a horizontal position. This group of genera also shows a marked dorsoventral compression of the thorax.

Mycetophila and *Mycothera* are very closely related. Edwards, (1925) united *Mycothera* and *Opistholoba* with *Mycetophila.* In an earlier paper, Shaw (1948) indicated his reasons for regarding *Opistholoba* as a distinct genus. Though minor differences do exist in the thoracic sclerites of *Mycetophila* and *Mycothera,* it would be difficult to define such differences in a way to justify the separation of these two genera.

The genera *Opistholoba, Epicypta,* and *Sceptonia* form a closely related group. Edwards (1925, p. 587) figured *Delopsis,* and this genus would seem to culminate the tendencies shown in this series. The modifications include—

1. A progressively increasing dorsoventral compression of the thorax.
2. The mesepimeron tends to become more nearly horizontal in position.
3. The prothorax pushes dorsally, thus forming a concave region in the lateral margin of the mesoscutum.

These genera can be separated on the basis of characteristics in the thoracic sclerites. Thus *Epicypta* has the mesepimeron widened at the apex. In degree of dorsoventral compression, it is intermediate between *Opistholoba* and *Sceptonia.* Both *Sceptonia* and *Delopsis* have the anepisternite subrectangular in shape. *Sceptonia* lacks the expanded apex of the mesepimeron; moreover the mediotergite is quite pointed. The pronotum has pushed noticeably into the mesoscutum. The genus *Delopsis* seems to be the most highly specialized of the genera studied. The mesepimeron is greatly reduced; the pronotum extends deeply into the margin of the mesoscutum.

Subfamily MANOTINAE

Edwards (1925) recognized a separate subfamily for *Allactoneura* and *Manota.* As discussed elsewhere in this paper, *Allactoneura* appears to us much more closely related to the Cycloneurini of the Sciophilinae. However, *Allactoneura* does not agree with our concepts of the Cycloneurini, and therefore we have erected a new tribe —Allactoneurini—for this genus.

A specimen of *Manota defecta* Williston was lent for examination. Since the specimen could not be boiled, it was impossible to make a detailed study. Sufficient details could be observed to substantiate the belief that a separate subfamily should be recognized. The prothoracic region is large, expanded, and somewhat shieldlike. No distinct suture could be seen between the prothoracic pleura and tergum. The katepisternum and epimeron of the mesothorax appears to be fused, thus forming a large single sclerite. The head is unlike that of other Mycetophilidae with which we are familiar. The maxillary palpi are wholly different from those of any other genus of Mycetophilidae.

Family SCIARIDAE

Two genera of the related family Sciaridae are included. There has been much discussion as to the systematic position of this group. Edwards (1925) indicated their similarity in appearance to *Tetragoneura* and *Docosia* (Leiini). He held that the Leiini and Sciarinae probably had common origin, but since some of the more primitive genera of sciarids maintain macrotrichia, he did not consider that this group evolved from *Tetragoneura* or its near relatives.

The similarities in venation between the two groups represent a case of parallel development of a characteristic by two separate groups. This phenomenon has been noted elsewhere by Crampton. It indicates the need for use of many characteristics rather than one or two in grouping genera.

Sciara (fig. 44), as indicated in an earlier paper (Shaw, 1948), is sufficiently distinct from the true Mycetophilidae on the basis of thoracic sclerites to warrant its being placed in a separate family.

Pseudosciara (fig. 45) was placed with the Mycetophilinae by Johannsen (1909), who states: "The form of the head and the course of media remind one of *Sciara,* but the long coxae and position of Cu show relationship of Mycetophilini." Edwards (1925) considered this genus to be allied to the Leiini (Mycetophilinae). In 1932 he placed the genus with the Sciarinae.

On the basis of thoracic sclerites it is evident that *Pseudosciara* is a true sciarid and that any similarities of this genus with the Mycetophilinae are more apparent than real. Both *Sciara* and *Pseudosciara* possess a distinct precoxal bridge, which is lacking in all the genera of the Mycetophilidae we have studied. The shape of the other sclerites is similar in both genera, with *Pseudosciara* appearing more specialized. Both possess a midpleural pit.

SUMMARY

The pleural sclerites of 45 genera of fungus gnats are herein illustrated. A discussion of the relationships of these and certain other genera is presented.

On the basis of the structure of the thoracic pleura, the genus *Bolitophilella* is not considered as distinct from *Bolitophila.* The genus *Calliceratomyia,* placed in the Ceroplatinae by Lane, is considered to be more closely related to *Nervijuncta* and *Symmerus* (Ditomyiinae) than to the genera of the Ceroplatinae we have studied. The systematic position of *Centrocnemis* is somewhat uncertain at present. The genus *Apemon* appears to be intermediate between the Ditomyiinae and the Ceroplatinae. It is logical to include *Macrocera* and *Fenderomyia* in the Ceroplatinae. The genus *Paratinia* seems to be more closely allied to the Gnoristini than to the Sciophilini, where it had been placed by Edwards (1925). The genera *Parvicellula, Monoclona,* and *Mycomyia* are fairly closely related and are apparently intermediate between the Sciophilinae and the Mycetophilinae. Since *Cycloneura* and *Procycloneura* do not appear closely related to the other genera of the Leiini in which they were placed on the basis of wing venation, a new tribe—the Cycloneurini—is proposed for these two genera and probably for *Paracycloneura.* The genus *Allactoneura* is removed from the Manotinae and placed in a new tribe—the Allactoneurini. The affinities of *Lygistorhina* seem to be closest to certain of the Gnoristini, but we consider that a separate subfamily should be recognized for *Lygistorhina.* The genus *Mycothera* does not appear to be distinct from *Mycetophila.* However, *Opistholoba* seems to be sufficiently distinct to warrant its maintenance as a separate genus. The genus *Manota* is so different from the other genera that a separate subfamily should be recognized for it.

Two genera (*Sciara* and *Pseudosciara*) of the related family Sciaridae are figured. *Pseudosciara* has been variously grouped by earlier investigators, some of whom have placed the genus in the Mycetophilinae. The thoracic sclerites indicate that it should be included with the other Sciaridae.

CONCLUSIONS

As suggested in an earlier paper (Shaw, 1948), the shape of the pleural sclerites is of value as a means to indicate phylogenetic relationships of the Mycetophilidae. Future investigators would do well to include these structures in describing new genera and species.

ABBREVIATIONS USED ON FIGURES

AES,	Anepisternum of mesothorax.
APN,	Anterior pronotum.
EM_1,	Prothoracic epimeron.
EM_2,	Mesothoracic epimeron.
EM_3,	Metathoracic epimeron.
ES_1,	Prothoracic episternum.
ES_2,	Metathoracic episternum.
KES,	Katepisternum of mesothorax.
MP,	Midpleural pit.
MT,	Mediotergite.
PLT,	Pleurotergite.
PPN,	Posterior pronotum—pronotal scutellum.
PSc,	Prescutum of mesonotum.
Sc,	Scutum of mesonotum.
ScT,	Scutellum of mesonotum.

REFERENCES

Crampton, G. C.

1925. A phylogenetic study of the thoracic sclerites of the non-tipuloid nematocerous Diptera. Ann. Ent. Soc. Amer., vol. 18, pp. 49-74, pls. 3-7.

1942. The external morphology of the Diptera. Diptera of Connecticut, fasc. 1, pp. 10-165, figs. 1-14.

Edwards, F. W.

1925. British fungus gnats. Trans. Ent. Soc. London, 1924, pp. 505-670, pls. 49-61.

1932. New Brazilian Mycetophilidae. Rev. Ent., vol. 2, pp. 138-149, figs. 1-6.

Johannsen, O. A.

1909. Mycetophilidae. Genera insectorum, fasc. 93, pp. 1-140, pls. 1-7.

1909. The fungus gnats of North America: Pt. I. Maine Agr. Exp. Stat. Bull. 172, pp. 209-276, 3 pls.

1910. The fungus gnats of North America: Pt. II. Maine Agr. Exp. Stat. Bull. 180, pp. 125-192, 4 pls.

1911. The fungus gnats of North America: Pt. III. Maine Agr. Exp. Stat. Bull. 196, pp. 249-328, 5 pls.

1912. The fungus gnats of North America: Pt. IV. Maine Agr. Exp. Stat. Bull. 200, pp. 57-146, 6 pls.

Landrock, K.

1940. Pilzmucken oder Fungworidae. Tierwelt Deutschlands, vol. 38, pp. 1-166, figs. 1-338.

Shaw, F. R.

1935. Notes on the Mycetophilidae with descriptions of new species. Psyche, vol. 42, pp. 84-91, figs. 1-5.

1948. A contribution to the phylogeny of the Mycetophilidae. Ann. Ent. Soc. Amer., vol. 41, pp. 189-199, pls. 1-3.

Tonnoir, A. L.

1929. Australian Mycetophilidae. Proc. Linn. Soc. New South Wales, vol. 54, pp. 584-614, figs. 1-7, pls. 22, 23.

Tonnoir, A. L., and Edwards, F. W.

1926. New Zealand fungus gnats. Trans. New Zealand Inst., vol. 57, pp. 747-878, pls. 58-80.

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 117, NUMBER 4

A REVISED CLASSIFICATION FOR THE BIRDS OF THE WORLD

BY
ALEXANDER WETMORE
Secretary, Smithsonian Institution

(Publication 4057)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
NOVEMBER 1, 1951

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

A REVISED CLASSIFICATION FOR THE BIRDS OF THE WORLD

By ALEXANDER WETMORE

Secretary, Smithsonian Institution

Since the revision of this classification published in 1940[1] detailed studies by the increasing numbers of competent investigators in avian anatomy have added greatly to our knowledge of a number of groups of birds. These additional data have brought important changes in our understanding that in a number of instances require alteration in time-honored arrangements in classification, as well as the inclusion of some additional families. A few of these were covered in an edition issued in mimeographed form on November 20, 1948. The present revision includes this material and much in addition, based on the author's review of the work of others and on his own continuing studies in this field. His consideration necessarily has included fossil as well as living birds, since only through an understanding of what is known of extinct forms can we arrive at a logical grouping of the species that naturalists have seen in the living state. The changes from the author's earlier arrangement are discussed in the following paragraphs.

Addition of a separate family, Archaeornithidae, for the fossil *Archaeornis siemensi,* reflects the evident fact that our two most ancient fossil birds, *Archaeopteryx* and *Archaeornis,* are not so closely related as their earlier union in one family proposed. The characters marking the two have been under dispute in literature, mainly between Petronievics and von Nopsca. Lambrecht[2] has analyzed the data, finding 10 points of difference that hold. Though some of these appear trivial, enough are of sufficient weight from a taxonomic standpoint to warrant family status. Neither the suggestion that what we now recognize as *Archaeornis* is merely a young individual of *Archaeopteryx lithographica,* so that the differences seen are those of immaturity, nor the more extreme view that *Archaeopteryx* and *Archae-*

---

[1] Wetmore, A., A systematic classification for the birds of the world. Smithsonian Misc. Coll., vol. 99, No. 7, Oct. 10, 1940, pp. 1-11.

[2] Handbuch der Palaeornithologie, 1933, p. 86.

ornis have given rise respectively to our flightless and our flying birds in separate lines of descent is supported by the facts.

In the Neornithes one important result has been the arrival at a more even continuity of characters that has led to the reduction of superorders recognized in the subclass from four to three, through the combination under Neognathae of the orders formerly separated as the Palaeognathae. For years I have felt that recognition of the Palaeognathae, as a separate group apart from other birds, on the basis of a supposed peculiarity in the palate, stood on very flimsy ground. The recent studies of McDowell[3] demonstrate that the structure of the palaeognathous palate, in which the palatine and pterygoid bones are articulated by a squamous suture, is variable from order to order, and that in fact the details of this union vary considerably in the different groups. For example, McDowell points out that in *Dromiceius* the palatine and pterygoid are not in contact, while in a number of families placed in the Neognathae, as in the Anatidae, to name only one, the two bones are in articulation. As there is no clear-cut separation, the former Palaeognathae must be combined with the Neognathae.

The question of the weight to be given the peculiarities of uniform pterylosis, extreme specialization of the wing as a flipper for submarine progression, and incomplete fusion in the metatarsal elements, as well as such other details as erect posture in standing and walking and the anatomical adjustments involved, found in the penguins, is one that has merited careful review. It seems reasonable after this examination to retain the Impennes as a superorder, at least until we have further evidence through fossils as to their line of evolution. It is necessary, however, to remove the fossil family Cladornithidae, since Simpson[4] has found that the two genera *Cruschedula* and *Cladornis* placed in this family have no apparent relationship to the Sphenisciformes. These two, described by Ameghino from the Deseado formation of Patagonia, now placed in the Oligocene, are based on fragmentary, considerably flattened metatarsi. The descriptions and figures that have appeared thus far are not sufficiently definite to demonstrate clearly characters of importance in classification. However, from what we now know these ancient birds cannot be considered as ancestral penguins of terrestrial habit, as has been supposed. The only suggestion that has come to me is that possibly they may belong

---

[3] The bony palate of birds. Part 1, the Palaeognathae. Auk, vol. 65, Oct. 1948, pp. 520-549, 6 figs.

[4] Simpson, George Gaylord, Fossil penguins. Bull. Amer. Mus. Nat. Hist., vol. 87, art. 1, 1946, pp. 1-99, 33 figs.

in the order Pelecaniformes, in which I have placed the family tentatively in the suborder Odontopteryges, where it is located with two others of almost equally uncertain status. This allocation is wholly tentative and is no indication of belief in close relationship in the three diverse groups there assembled.

The family Eleutherornithidae is introduced for the fossil *Eleutherornis helveticus* Schaub, from the Eocene of Switzerland, described from a fairly well preserved pelvis. Apparently this is representative of an ancestral group from which the living ostriches have come. Its greatest importance is found in its indication of relationship with carinate groups though of unquestioned ratite stock. It is thus important as definite indication that the struthious birds have come from flying ancestors, and not from some distinct cursorial line that always has been flightless, as some have contended.

The family segregation in the order Procellariiformes has been oversimplified in some recent considerations, probably through misunderstanding of the group characters produced by anatomical studies, possibly also through somewhat confusing names that have been applied to familial and generic categories. The Diomedeidae and Pelecanoididae have been accepted without apparent question, but the remaining species have been combined by some under a single family name. Lowe,[5] however, has shown that the genera included in the Hydrobatidae have a simplified condition in the quadrato-tympanic region of the skull in which the opening of the upper tympanic recess is small and is so located that it separates the squamosal and opisthotic facets. In addition, the posterior border of the sternum is truncated and entire, and basipterygoids are absent or are represented only by small spines. In the Procellariidae, on the other hand, the foramen of the upper tympanic recess is greatly enlarged and lies anterior to the two facets for the quadrate, which are joined by a bridge of bone; the posterior border of the sternum is notched; and basipterygoid processes are present. These constitute distinctive characters at the family level.

In the arrangement of suborders in the order Pelecaniformes we encounter in marked degree the standard difficulty of logical placement in linear alignment of groups that really stand in three-dimensional relationship. Lanham [6] has made a summary of the major anatomical characters of the group in which he points out the differences that set off the Phaëthontes and the Fregatae from the Pelecani. There

---

[5] Proc. Zool. Soc. London, 1925 (Jan. 14, 1926), pp. 1436-1443.

[6] Auk, vol. 64, 1947, pp. 65-70.

is no question that the first two carry primitive characters, which may be presumed to be similar to those found in an ancient ancestral stock, since in these resemblances they are more like other types of birds, notably the Procellariiformes. From this style the other families of the Pelecani have become widely divergent. Although the tropic-birds and the frigate-birds both have retained a part of what may be regarded as a basic pattern, they are so widely divergent in other respects that it seems more reasonable to relate them individually as branches from the common stock rather than to combine the two on one line, separate from the Pelecani. The Phaëthontes possibly may have separated earlier than the Frigatae. Among interesting differences other than those of internal anatomy, it may be noted that the tropic-birds have the young covered with down at birth and that the adults possess series of air cells under the skin on the forepart of the body like those found in pelicans and boobies. The frigate-birds have the young naked at hatching, and the emphysematous condition is mainly lacking. In view of this discussion I prefer to continue to align these groups on either side of the Pelecani.

Though there is no question that the cormorants and snake-birds are closely allied, they differ in such degree that they should be retained in separate family status. The snake-birds are marked by a peculiar conformation of the cervical vertebrae through which the beak becomes a triggered spear in feeding. The bridge of Dönitz on the ninth vertebra is an important part of this arrangement. The stomach also is unusual in possessing a curious pyloric lobe, lined with a mat of hairlike processes. And there is only one carotid artery.

The Odontopteryges, as has been noted above, are of highly doubtful status and require further study.

The family Cochleariidae, which some wish to unite with the Ardeidae, is marked externally by the strangely expanded bill, which is not only broad, but has the gonys remarkably shortened. Internally the pattern set by the broadened premaxillae is reflected in correspondingly widened palatines, which in addition have a curious flaring expansion of the lateral margin. The lachrymals are greatly reduced in size, and there are other minor peculiarities. Ridgway[7] lists four powder-down tracts for *Cochlearius,* a larger number than the two or three pairs that he found in the Ardeidae. This, however, needs further checking, since there is some uncertainty as to the correctness of these figures. There is no question that the boat-bills are closely related to the herons, but the greatly modified forepart of the skull

---

[7] Studies of the American Herodiones. Bull. U. S. Geol. Geogr. Surv. Terr., vol. 4, No. 1, 1878, p. 220.

seems sufficient to warrant separation in a distinct family. Herons, with riflelike precision, habitually spear or seize their prey, while the boat-bill has the advantage of a broadened scoop. Possibly this is more efficient in shallow waters, particularly in nocturnal feeding.

In view of the fact that the structural characters of the Balaenicipitidae have been summarized clearly by Stresemann,[8] it seems strange that the status of this family has been a matter of question. The single species shows affinity both with storks and with herons, in addition to outstanding peculiarities of its own.

The flamingos, which show affinity with both Ciconiiformes and Anseriformes, have been placed by Stresemann and others in a separate order, but they seem best allocated as a suborder of the first-named group.

The superfamily Neocathartoidea, and family Neocathartidae, for the curious vulture *Neocathartes grallator* (Wetmore),[9] discovered recently in the Upper Eocene fossil beds of Wyoming, introduce a new element in our known avifauna in the form of a small-winged, strong-legged vulture that evidently was terrestrial with limited powers of flight. It had about the same relation to the other American vultures that the secretarybird has to the hawks and falcons. Its inclusion also requires a separate superfamily, the Cathartoidea, for the previously known cathartine families.

The Numididae, which have been placed by some as a subfamily of the Phasianidae, differ in completely lacking the tuberosity or plate on the inner side of the second metacarpal that is so prominent in pheasants and grouse. The Tetraonidae, in contrast with the Phasianidae, have the pelvis relatively much broader and different in proportion, and the tarsus relatively shorter in relation to the length of the tibiotarsus. With these differences in mind it seems reasonable to retain the three groups in family status, at least until more detailed knowledge of their anatomy as a whole warrants change.

In the Turnices the two genera of bustard-quails, *Turnix* and *Ortyxelus,* have no hind toe, the wing is eutaxic, only the left carotid is present, and the eggs are rounded oval. The plain-wanderer of Australia, *Pedionomus,* has a small hind toe, the wing is diastataxic, right and left carotids are found, and the large eggs are pyriform. It seems desirable to continue these as separate families, rather than

---

[8] Aves, in Kükenthal and Krumbach, Handbuch der Zoologie, vol. 7, pt. 2, sect. 8, 1934, p. 809.

[9] For the substitution of *Neocathartes* for *Eocathartes* Wetmore, 1944, preoccupied by *Eocathartes* Lambrecht, 1935, see Auk, vol. 67, 1950, p. 235.

as subfamilies of one group, an arrangement that Stresemann[10] has accepted.

In the suborder Phororhaci the family Psilopteridae is to be added for the South American fossils *Psilopterus* and *Smiliornis,* from the studies of Patterson.[11] Another group of doubtful position that may be placed tentatively in this suborder, at least until it is better known, is the family Cunampaiidae, for the fossil *Cunampaia simplex,* named by Rusconi[12] from the Oligocene of western Argentina.

In the Charadriiformes the main disagreements of the present day are found in the superfamily Charadrioidea and the suborder Lari, in which the groups have been regarded by some as of family value and by others have been allocated the rank of subfamilies. The various structural studies that have been made have not been complete from a taxonomic point of view except for part of the species, and the conclusions derived from the data available have been in the main more philosophical than concrete. The picture therefore still remains confused.

In view of the diverse specializations that are apparent, and the obvious long evolutionary history, it appears better to me to continue to acknowledge the main segregations as families, at least until the subjects involved have been more thoroughly investigated. A family, Rhegminornithidae, is added for the fossil *Rhegminornis calobates* Wetmore, described from the Lower Miocene of Florida. This was as large as a medium-sized curlew, of peculiar form as regards the foot, the only part of the skeleton known, which shows certain characters that seems to point toward the jaçanas, though the bird is to be placed in the Charadrioidea.

In the Lari the terns and the gulls are regarded as one family, though there are some reasons that make further examination of this treatment desirable. The Rynchopidae differ decidedly in absence of the ambiens and the biceps slip, and in the completely different form of the bill. The iris opens and closes vertically in slitlike form, a condition that I have not seen in any other bird.[13]

The Stercorariidae possess a 2-notched sternum, large caeca, a cere, and a complex rhamphotheca. In the Laridae ambiens and biceps slip are present, the sternum is 4-notched, there is no cere, and the rhamphotheca is simple in form.

---

[10] Loc. cit., p. 760.

[11] Field Mus. Nat. Hist., geol. ser., vol. 8, No. 8, Oct. 31, 1941, pp. 52-53.

[12] Bol. Pal. Buenos Aires, No. 21, May 2, 1946 (p. 1).

[13] Wetmore, A., A note on the eye of the black skimmer (*Rynchops nigra*). Proc. Biol. Soc. Washington, vol. 32, Dec. 31, 1919, p. 195.

Old World ornithologists in the main have regarded the owls as belonging to a single family, but while all are deceivingly similar in general aspect, the decided differences found in the barn-owl group merit family recognition. Ridgway [14] years ago summarized the considerable structural characters separating the Tytonidae and the Strigidae. It is necessary here only to point out the more outstanding structural differences of the Tytonidae in the lack of the manubrium, and the different form of the posterior margin of the sternum, which is entire or has two shallow notches, the union of the furculum with the carina sterni, the straight outline of the palatines, and the ventral pteryla where the outer branch joins posteriorly to the main tract. The Strigidae possess a manubrium, the sternum is 4-notched, the furculum is separate, the palatines are greatly expanded posteriorly, and the posterior end of the ventral pteryla does not join the main tract at the posterior end.

Lucas [15] long ago demonstrated the differences between the true swifts and the crested swifts, though his work seems latterly to have been largely overlooked in view of the recent inclusion of the two in one group, as by Stresemann and by Mayr and Amadon. The skull in the Hemiprocnidae is quite distinct in the general form of the cranium and in the development of the nasals, vomer, and palatines, while the hypotarsus has a tendinal foramen (like that found in hummingbirds), and the plantar tendons have the flexor longus hallucis connected with the branch of the flexor perforans digitorum, which extends to the fourth digit. Coupled with this there may be noted the curious nest, which, fastened to the side of a branch, is barely large enough to contain one egg, and the further fact that these birds perch regularly on branches and twigs in trees.

As *Apus* Scopoli, published in 1777, is recognized now in place of *Micropus* Meyer and Wolf, 1810, for the type genus of the swifts, the terms in the classification change to order Apodiformes, suborder Apodi, and family Apodidae, which replace the former terms Micropodiformes, Micropodi, and Micropodidae, respectively.

The proposal of Mayr and Amadon [16] to include the rollers in one family, the Coraciidae, with three subfamilies, goes back to the arrangement of Dresser in his monograph of the group.[17] Sclater,[18]

---

[14] U. S. Nat. Mus. Bull. 50, pt. 6, 1914, p. 598.

[15] Auk, vol. 6, 1889, pp. 8-13; vol. 12, 1895, pp. 155-157.

[16] A classification of recent birds. Amer. Mus. Nov., No. 1496, Apr. 2, 1951, pp. 9, 35.

[17] A monograph of the Coraciidae, or family of the rollers. London, 1893, pp. i-xx, 1-111, 27 plates.

[18] Proc. Zool. Soc. London, 1865, pp. 682-688, 8 figs.

however, many years ago, pointed out the pelvic powder-down tracts, the small manubrium and other peculiarities of *Leptosoma,* and set it apart in a distinct family. The anatomy of the syrinx and feet was further elaborated by Forbes.[19] The family Leptosomatidae therefore should be recognized.

The ground rollers, *Brachypteracias, Atelornis,* and *Uratelornis,* usually have been included as a subfamily of the Leptosomatidae, but Stresemann [20] places them in a separate family, the Brachypteraciidae. There seems to be reason for this in their general appearance, though their anatomy is not well known. *Brachypteracias,* in its skeleton, differs from *Coracias* and *Eurystomus* in the much greater depth of the outer notch on the posterior border of the sternum, in the much broader and stronger pelvis, the heavier femur, and the greater curvature of the shaft and reduction of the crista superior of the humerus. I have not seen the skull. The habit of life is markedly different. Although anatomical material of the other genera is not presently available, it seems reasonable to accept Stresemann's proposal. These peculiar birds certainly are not closely allied to *Leptosoma.*

Lack of information on the anatomy of the wood-hoopoes must be the reason for the recent nonrecognition of the Phoeniculidae as a family separate from the Upupidae, since the two are quite distinct and have been so recognized for many years. The external differences are readily apparent. In the skeleton in *Phoeniculus* (of which I have seen several examples) the posterior part of the nasal area is ossified, there being only a small, narrow, elongated nasal opening; the ectethmoid is much reduced; the anterior end of the pterygoids is broadly expanded; the sphenoidal rostrum is swollen at the anterior end, where the expanded ends of the pterygoids join it; the quadrates are decidedly larger; the keel of the sternum is greatly reduced, being only half as high as in *Upupa;* the furculum is broader; the pelvis is narrowed, and considerably elongated posterior to the acetabulum, with the ischio-pubic fenestra greatly enlarged; and the tarsus is heavier and broader, with two definite fenestra below the head. There are other minor details. In all of the above the characters of *Upupa* are directly opposite. The two groups appear to me to be sharply set off as distinct families.

The Passeriformes, with more living species than all the other

---

[19] Proc. Zool. Soc. London, 1880, pp. 465-475, 5 figs.

[20] Loc. cit., p. 829.

orders combined, and far fewer fossil forms discovered to date, present many difficult problems in their logical arrangement. The major groups are clear, whether we rank them as suborders or superfamilies being a matter of opinion. But the limits of numerous families contained in these larger categories are uncertain. The internal anatomy is known fully for so few kinds that details of difference are poorly understood. The superficial resemblances, on the other hand, are so obvious in many cases that there is much confusion. Under the circumstances it continues to seem appropriate to me to accept the family grouping that has been current for many years, except in those cases where detailed studies clearly indicate change. There is much supposition in these matters, that has led to various proposals for combination, some part of which undoubtedly will prove correct. It is equally probable that a part, possibly a considerably larger part, may prove to be unfounded when details are more clearly known. If change is accepted under these circumstances it may prove unwarranted, necessitating further change, perhaps a return to the original supposition. Since this can only prove confusing I prefer the conservative course. In the remarks that follow I will discuss only a few matters on which I have more or less concrete ideas.

In the superfamily Furnarioidea, Von Ihering[21] unites the Furnariidae and the Dendrocolaptidae, since he is unable to separate two groups on the basis of the form of the posterior border of the nasal opening. The variation that he shows seems quite true, but there are numbers of other points of supposed difference concerned in the osteology and other structural details, and therefore his suggestion is far from established. Pycraft,[22] though seemingly uncertain in the beginning, finally retained the two families. It may prove that some genera are wrongfully allocated at present between the two groups, and that their shifting, when we have sufficient information, will clear our understanding.

In the Tyrannoidea, the family Oxyruncidae is known through external characters that seem to warrant separation. If the sharpbills have other affinities it is doubtful that these are within the Tyrannidae, where some have placed them.

In the family Cracticidae, recognized by Australian ornithologists, the skull according to Pycraft[23] (mainly from examination of *Gymnorhina*) has the zygomatic process of the squamosal bifurcate, the postorbital process large, the orbitosphenoid ossified, the interorbital

---

[21] Auk, vol. 32, 1915, pp. 145-153, pls. 11-12.

[22] Proc. Zool. Soc. London, 1906, pp. 133-159, figs. 49-52.

[23] Proc. Zool. Soc. London, 1907, pp. 355-365.

septum with a single opening, the prefrontals unusually large, and the form of the palate peculiar. In his phylogenetic tree Pycraft places the group on a common stem with the Artamidae, and not far from the Paradiseidae. His account is mainly descriptive and difficult to summarize in concrete form.

The family Grallinidae is likewise recognized officially by Australian ornithologists for *Grallina cyanoleuca,* the magpie-lark. The principal study of the osteology is that of Shufeldt,[24] but the account is mainly descriptive and without definite conclusion. Amadon [25] recently has placed *Corcorax* and *Struthidea* here tentatively, though this seems subject to further proof.

Stonor [26] has outlined excellent reasons for recognition of the Ptilonorhynchidae, finding that they differ from Paradiseidae, with which they have been united, in having an apterium in the center of the dorsal feather tract, the tip of the vomer convex, larger, more developed maxillo-palatines, the margin of the palatines angular, smaller ectethmoid, much larger lachrymal, and slender, greatly elongated orbital ramus of the quadrate. The genera *Loria* and *Loboparadisea,* usually included here, he transfers to the Paradiseidae. His conclusion is that "the Ptilonorhynchidae constitute a singularly complete and isolated family of the acromyodian passerine birds and show no special relationship to any other, being sharply marked off by the structure of the skull, the colour-pattern, and the bower-building habit."

Oberholser [27] has set up a distinct family Irenidae for the fairy bluebirds (*Irena*), and Delacour [28] a family Aegithinidae for the leafbirds, which would cover *Irena, Aegithina,* and *Chloropsis.* Inasmuch as the internal anatomy of these seems as yet unknown, I have not included such a family, pending further information.

The proper allocation of the genus *Chamaea* for the wren-tits, at present accepted by the A. O. U. Committee on Classification and Nomenclature as a separate family, the Chamaeidae, is one of considerable uncertainty. Delacour [29] has suggested that they be located in the

---

[24] Emu, vol. 23, July 1923, pp. 16-19, pl. 6.

[25] Emu, vol. 50, Oct. 1950, pp. 123-127.

[26] Proc. Zool. Soc. London, vol. 107, ser. B, pt. 3, Sept. 1937, pp. 475-490, figs. 1-9. It should be noted that the names on figures 6 and 8 have been transposed, figure 6 being *Semioptera wallacei,* and figure 8 *Amblyornis subalaris,* and not the reverse as printed on pp. 481 and 483.

[27] Journ. Washington Acad. Sci., vol. 7, Oct. 19, 1917, pp. 537-541.

[28] Zoologica, vol. 31, 1946, p. 3.

[29] L'Oiseaux, vol. 16, 1946, pp. 18, 25, 35.

family Timaliidae in a special subfamily in which he includes also such diverse genera as *Chrysomma* (*Moupinia*), *Panurus, Conostoma,* and *Paradoxornis* (combining under this name *Suthora, Psittiparus, Neosuthora,* and *Cholornis*). This is an obviously heterogeneous assemblance, in which *Chamaea* has slight resemblances to the first only. From *Moupinia poecilotis* (placed in *Chrysomma* by Delacour) the wren-tit differs definitely in weaker, less arched bill and in differently proportioned feet. It has no close resemblance to any of the others that are mentioned. Although the relationships of *Chamaea* are obviously uncertain, it is retained as a family pending other information.

The recent suggestions for the union of the Bombycillidae, Ptilogonatidae, and the Dulidae in one family are not substantiated by examination of the skeleton. *Dulus,* the palm-chat, is widely different from the other two, a structural distinction that is further emphasized by its curious communal nesting habits. The first two seem more closely related but are separated clearly by characters found in the ectethmoid region of the skull, and in the manubrium, to mention only two points that are easily apparent. Delacour and Amadon [30] consider *Hypocolius* closely allied to *Ptilogonys.*

While Zimmer [31] believes that the family Vireolaniidae should be included in the Vireonidae, separate family rank in my opinion is definitely justified. In addition to characters assigned by Pycraft[32] for the shrike-vireos I have found recently that in the pterylosis the dorsal tract on the lower back is forked, the arms being broad at the ends, and separated from the narrowed line that continues onto the caudal area. This is completely different from the usual rhomboid found in the vireos, and may indicate that the family eventually should be removed from the vicinity of the Vireonidae.

The family characters of the pepper-shrikes, likewise outlined by Pycraft in the reference given above, are easily apparent on examination of the skeleton.

The family Callaeidae has been separated by Stonor [33] on the weakened keel of the sternum, the great development of the lower limb, coupled with reduced powers of flight, and the presence of a mouth wattle, for three peculiar genera, *Callaeus, Heterolocha,* and *Philesturnus* of New Zealand.

---

[30] Ibis, 1949, pp. 427-429, pl. 19.

[31] Amer. Mus. Nov., No. 1160, Jan. 30, 1942, p. 10.

[32] Proc. Zool. Soc. London, 1907, pp. 352-379.

[33] Ibis, 1942, pp. 1-18, figs. 1-10, tables 1-3.

The former family Melithreptidae becomes the family Meliphagidae, since the name of the type genus is now accepted as *Meliphaga* Lewin, 1808.

In a similar way the family Compsothlypidae for the wood warblers becomes the family Parulidae, since the former *Compsothlypis* Cabanis, 1851, is replaced by the older *Parula* Bonaparte, described in 1838.

The order of arrangement in the Passeriformes is in part necessarily arbitrary, through the easily perceptible and often remarked fact that we are under necessity of listing groups in linear order in a two-dimensional alignment when actually they stand in three-dimensional relationship to one another. (There is, further, another element that may be regarded almost as a fourth dimension, in some of the extinct groups known only as fossils that have no close relatives alive today.) The sequence that I have adopted is the one that best represents my present understanding, based on personal studies that now have extended over a period of nearly 50 years. I will repeat what I have said elsewhere, that I have placed the Fringillidae at the end of the list, because of my feeling that this group is the modern expression of a main core or stem that through the earlier Tertiary periods has given rise to more specialized assemblages that we now recognize as distinct families. Further specialization is apparent in some parts of the existing fringilline assemblage that, if undisturbed, may lead to further differentiation, should these variants be able to persist for the necessary millenniums in our rapidly changing world. Adjacent to the Fringillidae I place the other groups that obviously are closely allied to them. Attempts to arrange the avian families with the Corvidae and their allies in the terminal position, as accepted in various earlier classifications, and as followed now by Mayr and Amadon, because of supposed more advanced development of the brain appear to me quite uncertain, particularly in view of our decidedly limited information in this field. Should this idea be coupled with belief in superior mental reactions in the corvine assemblage, I would consider this more an anthropomorphic interpretation than one supported by scientific fact.

The formation of the group names has been one of recent interesting discussion. The suffixes -idae and -inae for families and subfamilies are accepted rather universally so that they do not require examination. In view of the limited number of species covered in ornithology I see no point in the introduction of tribes as another category between the subfamily and the genus. This may be useful to entomologists with their tens of thousands of species, but seems unnecessary and cumbersome with birds. In some of the more comprehensive avian genera there are groups of species more closely allied to one another than to their fellows, but the taxonomist may discuss these at need as groups without imposing another burden on a classification that now is highly divided. For the group names above the family level, I believe it preferable to use suffixes that allow immediate identification of the rank, coupled with a stem that, like the family name, is based on a current generic term. Where ordinal and subordinal names are both formed as Latin plurals there is possibility of confusion.

The detailed classification that follows shows as its main improvements our better understanding of some of the peculiar birds found in Australia and New Zealand, and some additional historical data of importance in our slowly growing knowledge of extinct forms in the fossil record. Stresemann, and more recently Amadon and Mayr, have made many valuable suggestions as to the relationships of numerous peculiar genera that in part are still of uncertain position. It remains intriguing to observe the vast amount of information still to be secured before our basis for final classification may be considered complete.

October 1, 1951.

Class Aves, Birds.
  Subclass Archaeornithes, Ancestral Birds.
    Order Archaeopterygiformes, *Archaeopteryx, Archaeornis.*
      Family Archaeopterygidae, *Archaeopteryx* (fossil),
        Archaeornithidae, *Archaeornis* (fossil).
  Subclass Neornithes, True Birds.
   Superorder Odontognathae, New World Toothed Birds.
    Order Hesperornithiformes, Hesperornithes.
      Family Hesperornithidae, *Hesperornis, Hargeria* (fossil).
        Enaliornithidae,[34] *Enaliornis* (fossil).
        Baptornithidae, *Baptornis* (fossil).
    Order Ichthyornithiformes, Ichthyornithes.
      Family Ichthyornithidae, *Ichthyornis* (fossil).
        Apatornithidae, *Apatornis* (fossil).

---

[34] Position provisional. Lambrecht, Handbuch der Palaeornithologie, 1933, pp. 255-261, unites the Baptornithidae with this group, which he considers closely related to the loons and grebes.

Superorder Impennes, Penguins.
  Order Sphenisciformes, Penguins.
    Family Spheniscidae, Penguins.
Superorder Neognathae, Typical Birds.
  Order Caenagnathiformes, Caenagnathus.
    Family Caenagnathidae, *Caenagnathus*[35] (fossil).
  Order Struthioniformes, Ostriches.
    Family Eleutherornithidae, *Eleutherornis* (fossil).
      Struthionidae, Ostriches.
  Order Rheiformes, Rheas.
    Family Rheidae, Rheas.
  Order Casuariiformes, Cassowaries, Emus.
    Family Casuariidae, Cassowaries.
      Dromiceidae, Emus.
      Dromornithidae, *Dromornis* (fossil).
  Order Aepyornithiformes, Elephantbirds.
    Family Aepyornithidae, *Aepyornis* (fossil and extinct).
  Order Dinornithiformes, Moas.
    Family Dinornithidae, Moas (fossil and extinct).
      Anomalopterygidae, *Anomalopteryx, Emeus,* and Allies (fossil and extinct).
  Order Apterygiformes, Kiwis.
    Family Apterygidae, Kiwis.
  Order Tinamiformes, Tinamous.
    Family Tinamidae, Tinamous.
  Order Gaviiformes, Loons.
    Family Gaviidae, Loons.
  Order Colymbiformes, Grebes.
    Family Colymbidae, Grebes.
  Order Procellariiformes, Albatrosses, Shearwaters, Petrels, and Allies.
    Family Diomedeidae, Albatrosses.
      Procellariidae, Shearwaters, Fulmars.
      Hydrobatidae, Storm Petrels.
      Pelecanoididae, Diving Petrels.
  Order Pelecaniformes, Tropic-birds, Pelicans, Frigate-birds, and Allies.
   Suborder Phaëthontes, Tropic-birds.
    Family Phaëthontidae, Tropic-birds.

---

[35] This interesting genus, listed tentatively in the above superorder, possibly is not avian.

- Suborder Pelecani, Pelicans, Boobies, Cormorants, Snake-birds.
  - Superfamily Pelecanoidea, Pelicans and Allies.
    - Family Pelecanidae, Pelicans.
      - Cyphornithidae, *Cyphornis, Palaeochenöides* (fossil).
  - Superfamily Suloidea, Boobies, Cormorants, and Allies.
    - Family Pelagornithidae, *Pelagornis* (fossil).
      - Sulidae, Boobies, Gannets.
      - Elopterygidae, *Elopteryx, Eostega, Actiornis* (fossil).
      - Phalacrocoracidae, Cormorants.
      - Anhingidae, Snake-birds
- Suborder Fregatae, Frigate-birds.
  - Family Fregatidae, Frigate-birds.
- Suborder Odontopteryges, Odontopteryx, Pseudodontornis, Cladornithes (fossil).
  - Family Odontopterygidae, *Odontopteryx* (fossil).
    - Pseudodontornithidae,[36] *Pseudodontornis* (fossil).
    - Cladornithidae, *Cladornis, Cruschedula* (fossil).

Order Ciconiiformes, Herons, Storks, and Allies.

- Suborder Ardeae, Herons, Bitterns.
  - Family Ardeidae, Herons, Bitterns.
    - Cochleariidae, Boat-billed Herons.
- Suborder Balaenicipites, Whale-headed Storks.
  - Family Balaenicipitidae, Whale-headed Storks.
- Suborder Ciconiae, Storks, Ibises, Spoonbills.
  - Superfamily Scopoidea, Hammerheads.
    - Family Scopidae, Hammerheads.
  - Superfamily Ciconioidea, Storks.
    - Family Ciconiidae, Storks, Jabirus.
  - Superfamily Threskiornithoidea, Ibises.
    - Family Threskiornithidae, Ibises, Spoonbills.
- Suborder Phoenicopteri, Flamingos.
  - Family Agnopteridae, *Agnopterus* (fossil).
    - Scaniornithidae, *Scaniornis, Parascaniornis* (fossil).
    - Phoenicopteridae, Flamingos.

---

[36] Position not certain; see Lambrecht, Handbuch der Palaeornithologie, 1933, pp. 305-308.

Order Anseriformes, Screamers, Ducks, Geese, Swans.
Suborder Anhimae, Screamers.
Family Anhimidae, Screamers.
Suborder Anseres, Ducks, Geese, Swans.
Family Paranyrocidae, *Paranyroca* (fossil).
Anatidae, Ducks, Geese, Swans.
Order Falconiformes, Vultures, Hawks, Falcons.
Suborder Cathartae, New World Vultures.
Superfamily Neocathartoidea, Neocathartes.
Family Neocathartidae, *Neocathartes* (fossil).
Superfamily Cathartoidea, New World Vultures.
Family Cathartidae, New World Vultures.
Teratornithidae, *Teratornis, Cathartornis* (fossil).
Suborder Falcones, Secretarybirds, Hawks, Falcons.
Superfamily Sagittarioidea, Secretarybirds.
Family Sagittariidae, Secretarybirds.
Superfamily Falconoidea, Hawks, Falcons, and Allies.
Family Accipitridae, Hawks, Old World Vultures, Harriers.
Pandionidae, Ospreys.
Falconidae, Falcons, Caracaras.
Order Galliformes, Megapodes, Curassows, Pheasants, Hoatzins.
Suborder Galli, Megapodes, Curassows, Grouse, Pheasants.
Superfamily Cracoidea, Megapodes, Curassows.
Family Megapodiidae, Megapodes.
Gallinuloididae, *Gallinuloides* (fossil).
Cracidae, Curassows, Guans, Chachalacas.
Superfamily Phasianoidea, Grouse, Pheasants, Turkeys.
Family Tetraonidae, Grouse.
Phasianidae, Quails, Pheasants, Peacocks.
Numididae, Guineafowl.
Meleagrididae, Turkeys.
Suborder Opisthocomi, Hoatzins.
Family Opisthocomidae, Hoatzins.
Order Gruiformes, Cranes, Rails, and Allies.
Suborder Mesoenatides, Roatelos, Monias.
Family Mesoenatidae, Roatelos, Monias.
Suborder Turnices, Bustard-quails, Hemipodes.
Family Turnicidae, Bustard-quails.
Pedionomidae, Plain-wanderers.

Suborder Grues, Cranes, Limpkins, Trumpeters, Rails.
  Superfamily Gruoidea, Cranes, Limpkins, Trumpeters.
    Family Geranoididae, *Geranoides* (fossil).
      Eogruidae, *Eogrus* (fossil).
      Gruidae, Cranes.
      Aramidae, Limpkins.
      Psophiidae, Trumpeters.
  Superfamily Ralloidea, Rails.
    Family Orthocnemidae,[37] *Orthocnemus, Elaphrocnemus* (fossil).
      Rallidae, Rails, Coots, Gallinules.
Suborder Heliornithes, Sun-grebes.
    Family Heliornithidae, Sun-grebes.
Suborder Rhynocheti, Kagus.
    Family Rhynochetidae, Kagus.
Suborder Eurypygae, Sun-bitterns.
    Family Eurypygidae, Sun-bitterns.
Suborder Phororhaci, *Phororhacos* and Allies.
    Family Phororhacidae, *Phororhacos* and Allies (fossil).
      Psilopteridae, *Psilopterus* and Allies (fossil).
      Brontornithidae, *Brontornis, Liornis,* and Allies (fossil).
      Opisthodactylidae, *Opisthodactylus* (fossil).
      Cunampaiidae, *Cunampaia* (fossil).
Suborder Cariamae, Cariamas and Allies.
    Family Bathornithidae, *Bathornis* (fossil).
      Hermosiornithidae, *Hermosiornis, Procariama* (fossil).
      Cariamidae, Cariamas.
Suborder Otides, Bustards.
    Family Otididae, Bustards.
Order Diatrymiformes, *Diatryma, Omorhamphus,* and Allies.
    Family Diatrymidae, *Diatryma* (fossil).
      Gastornithidae, *Gastornis, Remiornis* (fossil).
Order Charadriiformes, Shorebirds, Gulls, Auks.
  Suborder Charadrii, Shorebirds.
    Superfamily Jacanoidea, Jaçanas.
      Family Jacanidae, Jaçanas.

---

[37] Position provisional. See Lambrecht, Handbuch der Palaeornithologie, 1933, pp. 490-493.

Superfamily Charadrioidea, Plovers, Sandpipers, and Allies.
Family Rhegminornithidae, *Rhegminornis* (fossil).
Rostratulidae, Painted Snipe.
Haematopodidae, Oystercatchers.
Charadriidae, Plovers, Turnstones, Surfbirds.
Scolopacidae, Snipe, Woodcock, Sandpipers.
Recurvirostridae, Avocets, Stilts.
Presbyornithidae, *Presbyornis* (fossil).
Phalaropodidae, Phalaropes.
Superfamily Dromadoidea, Crab-plovers.
Family Dromadidae, Crab-plovers.
Superfamily Burhinoidea, Thick-knees.
Family Burhinidae, Thick-knees.
Superfamily Glareoloidea, Pratincoles, Coursers.
Family Glareolidae, Pratincoles, Coursers.
Superfamily Thinocoroidea, Seed-snipe.
Family Thinocoridae, Seed-snipe.
Superfamily Chionidoidea, Sheath-bills.
Family Chionididae, Sheath-bills.
Suborder Lari, Gulls, Terns, Skimmers.
Family Stercorariidae, Skuas, Jaegers.
Laridae, Gulls, Terns.
Rynchopidae, Skimmers.
Suborder Alcae, Auks.
Family Alcidae, Auks, Auklets, Murres.
Order Columbiformes, Sand-grouse, Pigeons, Doves.
Suborder Pterocletes, Sand-grouse.
Family Pteroclidae, Sand-grouse.
Suborder Columbae, Pigeons and Doves.
Family Raphidae, Dodos, Solitaires.
Columbidae, Pigeons, Doves.
Order Psittaciformes, Lories, Parrots, Macaws.
Family Psittacidae, Lories, Parrots, Macaws.
Order Cuculiformes, Plantain-eaters, Cuckoos.
Suborder Musophagi, Plantain-eaters.
Family Musophagidae, Plantain-eaters.
Suborder Cuculi, Cuckoos, Roadrunners, Anis.
Family Cuculidae, Cuckoos, Roadrunners, Anis.

Order Strigiformes, Owls.
    Family Protostrigidae, *Protostrix* (fossil).
        Tytonidae, Barn Owls.
        Strigidae, Owls.
Order Caprimulgiformes, Oilbirds, Goatsuckers.
  Suborder Steatornithes, Oilbirds.
    Family Steatornithidae, Oilbirds.
  Suborder Caprimulgi, Frogmouths, Goatsuckers.
    Family Podargidae, Frogmouths.
        Nyctibiidae, Potoos.
        Aegothelidae, Owlet-frogmouths.
        Caprimulgidae, Goatsuckers.
Order Apodiformes, Swifts, Hummingbirds.
  Suborder Apodi, Swifts.
    Family Aegialornithidae,[38] *Aegialornis* (fossil).
        Apodidae, Swifts.
        Hemiprocnidae, Crested Swifts.
  Suborder Trochili, Hummingbirds.
    Family Trochilidae, Hummingbirds.
Order Coliiformes, Colies.
    Family Coliidae, Colies.
Order Trogoniformes, Trogons.
    Family Trogonidae, Trogons.
Order Coraciiformes, Kingfishers, Bee-eaters, Rollers, Hornbills.
  Suborder Alcedines, Kingfishers, Todies, Motmots.
   Superfamily Alcedinoidea, Kingfishers.
    Family Alcedinidae, Kingfishers.
   Superfamily Todoidea, Todies.
    Family Todidae, Todies.
   Superfamily Momotoidea, Motmots.
    Family Momotidae, Motmots.
  Suborder Meropes, Bee-eaters.
    Family Meropidae, Bee-eaters.
  Suborder Coracii, Rollers, Hoopoes.
    Family Coraciidae, Rollers.
        Brachypteraciidae, Ground-rollers.
        Leptosomatidae, Cuckoo-rollers.
        Upupidae, Hoopoes.
        Phoeniculidae, Wood-hoopoes.

---

[38] Placed here provisionally. See Lambrecht, Handbuch der Palaeornithologie, 1933, pp. 623-624.

Suborder Bucerotes, Hornbills.
    Family Bucerotidae, Hornbills.
Order Piciformes, Jacamars, Barbets, Toucans, Woodpeckers.
  Suborder Galbulae, Jacamars, Barbets, Toucans.
    Superfamily Galbuloidea, Jacamars, Puffbirds.
      Family Galbulidae, Jacamars.
        Bucconidae, Puffbirds.
    Superfamily Capitonoidea, Barbets, Honey-guides.
      Family Capitonidae, Barbets.
        Indicatoridae, Honey-guides.
    Superfamily Ramphastoidea, Toucans.
      Family Ramphastidae, Toucans.
  Suborder Pici, Woodpeckers.
      Family Picidae, Woodpeckers, Piculets.
Order Passeriformes, Perching Birds.
  Suborder Eurylaimi, Broadbills.
      Family Eurylaimidae, Broadbills.
  Suborder Tyranni, Ovenbirds, Tyrant Flycatchers, and Allies.
    Superfamily Furnarioidea, Ovenbirds, Woodhewers, and Allies.
      Family Dendrocolaptidae, Woodhewers.
        Furnariidae, Ovenbirds.
        Formicariidae, Ant-thrushes.
        Conopophagidae, Ant-pipits.
        Rhinocryptidae, Tapaculos.
    Superfamily Tyrannoidea, Tyrant Flycatchers, Pittas, and Allies.
      Family Cotingidae, Cotingas.
        Pipridae, Manakins.
        Tyrannidae, Tyrant Flycatchers.
        Oxyruncidae, Sharpbills.
        Phytotomidae, Plant-cutters.
        Pittidae, Pittas.
        Acanthisittidae, New Zealand Wrens.
        Philepittidae, Asities, False Sunbirds.
  Suborder Menurae, Lyrebirds.
      Family Menuridae, Lyrebirds.
        Atrichornithidae, Scrub-birds.
  Suborder Passeres, Songbirds.
      Family Alaudidae, Larks.
        Palaeospizidae, *Palaeospiza* (fossil).

Hirundinidae, Swallows.
Campephagidae, Cuckoo-shrikes.
Dicruridae, Drongos.
Oriolidae, Old World Orioles.
Corvidae, Crows, Magpies, Jays.
Cracticidae, Bell Magpies, Australian Butcher-birds.
Grallinidae, Magpie-larks.
Ptilonorhynchidae, Bowerbirds.
Paradiseidae, Birds of Paradise.
Paradoxornithidae, Parrotbills, Suthoras.
Paridae, Titmice.
Sittidae, Nuthatches.
Hyposittidae, Coral-billed Nuthatches.
Certhiidae, Creepers.
Chamaeidae, Wren-tits.
Timaliidae, Babbling Thrushes.
Pycnonotidae, Bulbuls.
Cinclidae, Dippers.
Troglodytidae, Wrens.
Mimidae, Thrashers, Mockingbirds.
Turdidae, Thrushes.
Zeledoniidae,[39] Wren-thrushes.
Sylviidae, Old World Warblers.
Regulidae, Kinglets.
Muscicapidae, Old World Flycatchers.
Prunellidae, Accentors, Hedge-sparrows.
Motacillidae, Wagtails, Pipits.
Bombycillidae, Waxwings.
Ptilogonatidae, Silky Flycatchers.
Dulidae, Palm-chats.
Artamidae, Wood-swallows.
Vangidae, Vanga Shrikes.
Laniidae, Shrikes.
Prionopidae, Wood-shrikes.
Cyclarhidae, Pepper-shrikes.
Vireolaniidae, Shrike-vireos.
Callaeidae, Wattled Crows, Huias, Saddlebacks.
Sturnidae, Starlings.

---

[39] For notes on *Zeledonia* see Ridgway, U. S. Nat. Mus. Bull. 50, pt. 4, 1907, p. 885.

Meliphagidae	Honey-eaters.
Nectariniidae	Sunbirds.
Dicaeidae	Flower-peckers.
Zosteropidae	White-eyes.
Vireonidae	Vireos.
Coerebidae	Honey-creepers.
Drepanididae	Hawaiian Honey-creepers.
Parulidae	Wood Warblers.
Ploceidae	Weaver-finches.
Icteridae	Blackbirds, Troupials.
Tersinidae	Swallow-tanagers.
Thraupidae	Tanagers.
Catamblyrhynchidae	Plush-capped Finches.
Fringillidae	Grosbeaks, Finches, Buntings.

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 117, NUMBER 5

ANNOTATED LIST OF BIRDS OF BARRO COLORADO ISLAND, PANAMA CANAL ZONE

BY
EUGENE EISENMANN

(Publication 4058)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
FEBRUARY 7, 1952

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 117, NUMBER 5

ANNOTATED LIST OF BIRDS OF BARRO COLORADO ISLAND, PANAMA CANAL ZONE

BY
EUGENE EISENMANN

(Publication 4058)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
FEBRUARY 7, 1952

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

ANNOTATED LIST OF BIRDS OF BARRO COLORADO ISLAND, PANAMA CANAL ZONE

By EUGENE EISENMANN

Few localities in tropical America have been visited by so many naturalists as the biological station on Barro Colorado Island. Yet after nearly 30 years since the island was reserved for scientific purposes, even the inventory of its resident bird life is probably incomplete. A number of species collected in nearby parts of the Canal Zone still remain unrecorded, and almost every year students report one or two birds previously unknown from the island. This will surprise no one having field experience with the type of lofty tropical forest covering the island, where some woodland species are represented by few individuals, and others, though more numerous, are likely to be overlooked unless one is familiar with their notes.

In regard to the behavior and ecological relations—or, indeed, such fundamentals as breeding habits and season—of even most of the common species little is known and less has been published. Our ignorance applies to such species generally, not merely to their status on Barro Colorado Island. Thus the facilities of this very accessible area[1] afford students extraordinary opportunities for adding to our knowledge of tropical birds.

LOCATION AND ADMINISTRATION

Barro Colorado is the largest island in Gatún Lake, Panama Canal Zone, lying opposite the station of Frijoles on the Panama Railroad. Though situated on the Atlantic slope of the Continental Divide and less than 15 miles from the Caribbean Sea, it is only 20 miles from the Pacific. It was formed by the damming of the Chagres River for the Canal construction which converted the lowlands into Gatún Lake and the hilltops into islands. The ship channel through the Lake, in view of the laboratory, affords a fascinating contrast between the crisp modernity of ocean-going steamers and the wild, green islands and shores, against an ever-changing background of distant mountains, blue sky, and billowing clouds.

---

[1] Frijoles station, where one gets the launch for the island, is only a short train ride from the cities of Colón and Panamá. At present, daily airplanes from Miami reach Panamá in 4½ hours.

Barro Colorado rises to a height of about 452 feet above the lake surface and 537 feet above sea level. Irregular in outline, with over 25 miles of shore line formed by many deeply indented bays and inlets, the island has a maximum diameter of about 3 miles and an area of some 3,609 acres, or 5.6 square miles. But its surface habitable for animal life is much greater than if it were level ground, for the whole is broken by numerous drainage ravines whose slopes are covered with luxuriant vegetation. Despite the well-kept trails, crossing the island on foot takes far more time and effort than the air-line diameter might suggest.

Barro Colorado Island, under its official title of Canal Zone Biological Area, is at present administered by the Smithsonian Institution. The island was set aside as a biological station on April 17, 1923, through the efforts of Thomas Barbour and of James Zetek, who from the start has served as resident manager. It was operated by the Institute for Research in Tropical America until 1940. Then, on July 2, 1940, Congress gave the area a permanent status, but World War II suspended normal activities. It was placed under the Smithsonian Institution by Presidential order on July 16, 1946. Since then visitors and students have again been welcomed and provided the means of becoming acquainted with the biological wealth of a humid tropical forest under comfortable and healthful conditions.

The station provides laboratory and library facilities, as well as the basic needs of food and lodging, in an environment of unusual beauty and interest. Well-marked trails crisscross the forest, and at various points on the periphery small houses are strategically located, so that the night may be spent in the more remote portions of the island.

Those wishing to visit Barro Colorado Island should communicate with the Secretary of the Smithsonian Institution, Washington 25, D. C., or with the Resident Manager, Canal Zone Biological Area, Drawer C, Balboa, C. Z.

ECOLOGICAL CONDITIONS

Barro Colorado Island is in the humid division of the Lower Tropical Zone, but there is a distinct dry season. The average annual rainfall (1925-1949) is about 107 inches, almost all of it between May and December; November is the wettest month. The four dry-season months, January, February, March, and April, all together supply on the average only about 7 inches (Zetek, 1950). The rainy season usually begins late in April and ends late in December. Even in this season precipitation comes chiefly at night and in the afternoon. During the dry season, while rainfall may be less than 1 inch in some months, the high relative humidity (about 75 percent) suffices to keep the forest green, though in February and March some of the higher trees drop their leaves and produce masses of brilliant flowers. Daily temperatures range between 70° and 90° (average below 80°); variation is between night and day rather than between seasons (Zetek, 1948). During the dry season strong northeast trade winds blow; during the rainy season there is generally a pleasant breeze from the lake.

Except for a few acres of clearing, the island is entirely wooded. About half is mature forest; the remainder is in various stages of succession (Kenoyer, 1929).

For its size and relatively uniform environment Barro Colorado Island has a strikingly rich and varied flora and fauna. Standley (1933) lists 1,259 species of plants. Of vertebrates, other than birds, 56 species of mammals, 62 reptiles, 33 amphibians, and 22 fishes are reported (Zetek, 1951). The regularly resident larger mammals include monkeys (4 species), puma, ocelot, tayra, coati, kinkajou, deer (2 species), peccary (2 species), tapir, sloths (2 species), anteaters (2 species), and agouti (Enders, 1935).

In all, 306 species of birds are here listed as satisfactorily identified from the island; 52 are migrants from North America and 1 is probably a migrant from South America. The remainder are "resident" in the sense that they breed within the Republic of Panamá, though some of them, including certain water birds that one sees daily, definitely do not nest on Barro Colorado Island, and others merely appear occasionally from the mainland. Although direct breeding evidence (in the form of nests or fledglings) is presently available for fewer than 100 species, it is probable, on the basis of their year-round presence and known habits, that about 200 species breed more or less regularly on the island.[2] The population is by no means static. This can readily be noted around the clearing: from day to day one observes different species, and birds breeding there one year may be wholly absent the next at the very same period. Diurnal movements

---

[2] The number of species one may expect to see on a short visit is smaller, as conditions in the forest make many birds very elusive. For example, during a 2-week period in June and July (when there are no migrants), covering the laboratory clearing and perhaps a third of the trails, I ordinarily note between 120 and 125 species; over a hundred in or about the clearing. In fact, without leaving the clearing, on almost any day I can count (including birds heard) 55 to 65 species; but it takes a good deal of effort to raise a day's list beyond 75 at this season.

to and from the island, by such birds as the parrots, are very obvious. To what extent there are also seasonal movements by the "resident" birds is not known, but that they occur in some species seems likely.

Though essentially a humid neotropical forest environment, from the bird student's viewpoint the island habitats may conveniently be considered under four headings.

1. *The clearing.*—As here used this includes a narrow strip extending from the dock or entrance cove up the hillside to and around the laboratory buildings, and connecting with another narrow strip (sometimes called the plantation) running some 300 yards along the lake. This is largely a grassy area, interspersed with small trees (chiefly cultivated citrus) and banana plants. Crowding closely around the clearing a lofty forest rises sharply. About the clearing may be observed the greatest variety of birds. In fact, from there most of the species recorded on the island have at one time or another been seen or heard. A number of species requiring relatively open country, otherwise absent from the island, have become established or occasionally appear. The densely grown borders are favored by thicket inhabitants. The extensive "edge effect" exerts its well-known attractiveness. Best of all, the hillside location enables one to view the lake, the sky, the grassy slope, and the upper levels of the nearby forest. Many birds of the forest canopy are rarely noted except when flying across the clearing or moving in the adjacent treetops. Here, unlike the forest, bird activity is apparent throughout the day. Much smaller cleared areas are maintained at the summit of the island (where there is an observation tower) and at a few scattered points along the lake shore, but these are relatively insignificant, though they have attracted some birds absent from the forest.

2. *The mature or primary forest* covers about half the island, particularly the western portion. Though some exists near the laboratory, it is most impressive in the more level southwestern quarter. This forest is characterized by three arboreal strata, the upper canopy being between 75 and 100 feet, with scattered overtopping trees rising 125 feet or more (Allee, 1926b). There is relatively little undergrowth. Where best developed, the mature forest, with its dim filtered light and columnar structure, produces a cathedral solemnity. The constant hum of the cicadas soon fades into an unnoticed background, and the effect on a windless day is of silence—a silence interrupted at long intervals by the screeches of parrots or toucans, the roaring or chattering of monkeys, or the rapid passage of a mixed band of birds, perhaps accompanying a train of army ants. The mature forest seems to be preferred by most of the larger birds and mammals. The flowering and fruiting trees attract many smaller species, but it is

usually impossible to see, and often even to hear, such birds in the canopy. Except early in the morning, and to a less extent late in the afternoon, few birds are noticeable in the forest.

3. *The secondary forest* occupies the remainder of the island. It varies from areas that 25 years ago were clearings to forest well advanced toward maturity. The trees are lower and the canopy less closed than in the mature forest, so more light reaches the floor. As a result the undergrowth is thicker—in some places impenetrable without cutting. Epiphytes grow nearer the ground; ropelike, woody lianas and smaller vines are abundant. The secondary forest has a much wilder appearance than the mature forest, and more closely approximates the popular conception of a tropical jungle. Some birds are found only in the lighter woodland, others favor the denser tangles. But the correlation of neotropical birdlife to the forest succession remains largely an untilled field.

4. *The water borders.*—While these habitats vary, depending on exposure, maturity of the forest, and other factors, they have in common the favorable combination of standing water, abundant light, and large trees. The light encourages the growth of a green wall of vegetation down to the water's edge, providing haunts for thicket dwellers. In addition to birds for which the proximity of water is a requirement, this environment attracts a number of other species, particularly flycatchers, usually considered clearing birds. The most beautiful water borders are the margins of the esteros, narrow inlets (actually drowned stream valleys), deeply indenting the island, and best explored by cayuco, the native dug-out canoe. Along the quiet esteros aquatic plants grow luxuriantly, and the "edge effect" is apparent in the variety of birds. Extensive marshy vegetation is found only on the southwest margin of the island, where, protected from the waves raised by the trade winds and the wake of steamers, little grassy islets have formed around projecting tree stumps, thus affording homes for gallinules, rails, and jaçanas.

Gatún Lake itself, despite its richly forested shores, seems strangely unattractive to waterfowl. While masked ducks breed in its narrower reaches, none has ever been reported from the vicinity of Barro Colorado. Pied-billed grebes and anhingas occur, but the only swimming bird commonly seen is the ubiquitous cormorant.

ORNITHOLOGICAL WORK RELATING TO BARRO COLORADO ISLAND

In the first few years of the station's existence, careful collecting, chiefly by Dr. Frank M. Chapman and Dr. Josselyn Van Tyne, determined the basic avifauna. For many years now collecting of birds has been prohibited, except in very special cases. Most additions to the bird list since 1928 have been based on sight observations.

In 1929 Dr. Chapman, in his first delightful book on Barro Colorado, "My Tropical Air Castle"—which every prospective visitor should read—listed some 200 species of birds personally recorded by him in the course of four dry seasons (late December to early April). In his equally enjoyable sequel, "Life in an Air Castle" (1938), published after 12 such seasons on the island, he appended a list of 251 species, including records by other observers. Dr. Chapman also wrote elaborate studies on the breeding habits of the manakin, *Manacus vitellinus* (1935), and of the oropéndola, *Zarhynchus wagleri* (1928).

It would serve no purpose to list all the bird students who have briefly visited Barro Colorado Island. Many of them are mentioned below among those who have contributed to the preparation of this list. The station has served to introduce students from all over the world to neotropical wildlife. Aside from Dr. Chapman, those ornithologists who have spent most time there are Dr. Alfred O. Gross, Dr. Alexander F. Skutch, and Dr. Josselyn Van Tyne. Dr. Gross has written several articles describing the nesting of various Barro Colorado birds (1927, 1929, 1930, 1950). Dr. Van Tyne published a monograph on the toucan, *Ramphastos brevicarinatus* (1929), and shorter accounts of breeding by other species (1926, 1929, 1950). Dr. Skutch, the most assiduous student of Middle American bird behavior, has published many papers containing life-history material obtained on Barro Colorado Island (1931-1951). Much of the Barro Colorado breeding data here given is derived from his observations.

Partly on the basis of studies on Barro Colorado, Mrs. Bertha B. Sturgis wrote the "Field Book of Birds of the Panama Canal Zone" (1928), which gives descriptions, with many illustrations, of most species known to occur in the Canal Zone. It is, I believe, the only pocket-sized descriptive bird book in English covering any part of the continental neotropics.

My own interest in Panamá bird life dates back to my childhood. I first visited Barro Colorado in 1937. Since then I have sojourned there for periods between June and September in 1938, 1945, 1948, 1949, 1950, and 1951. Though I have had dry-season experience in Panamá, all my stays on the island have been during the rainy season; thus my personal observations are somewhat complementary to the dry-season studies of Dr. Chapman.

In an effort to make the list as complete as present information permits, an appeal for Barro Colorado Island data was made through the columns of the Auk, Condor, Wilson Bulletin, and Linnaean News-Letter, as well as by direct correspondence. The following supplied me with helpful information: Dr. A. A. Allen, Robert S. Arbib, Jr., Dr. F. Bourliere, Geoffrey Carleton, Dr. Nicholas E. Collias, G. W. Cottrell, Jr., Dr. David E. Davis, Miss Hazel Ellis, Mrs. Gladys Gordon Fry (including observations of her companions, Mrs. A. Edey, Mrs. M. Edey, Mrs. L. J. Francke, and Mrs. French), Thomas Gilliard, Dr. A. O. Gross, Dr. David Harrower, Mrs. Dorothy M. Hobson (including data of her companion Miss C. A. Moore), Thomas Imhof, Dr. Lawrence Kilham, Robert Laughlin, Dr. Frederick W. Loetscher, Jr., Philip Longenecker, Drs. Lorus J. and Margery Milne, Dr. Charles W. Quaintance, Dr. Robert T. Scholes, Dr. Alexander F. Skutch, Dr. Ken W. Stott, Jr., Dr. Josselyn Van Tyne, Jay A. Weber, and Dr. Alexander Wetmore.

Both published and unpublished data, including that contained in the species index on Barro Colorado Island, have been critically examined, bearing in mind the fact that several of the observers had had no prior experience with neotropical birds. Some doubtful reports have been omitted, in almost all cases with the approval of my correspondent.[3] I have examined specimens in the collections of the American Museum of Natural History and on Barro Colorado Island, and Dr. Van Tyne and Dr. Gross kindly checked for me the species represented in their respective collections.

No one who has enjoyed the facilities of Barro Colorado can fail to acknowledge his gratitude to James Zetek, the resourceful and hospitable guardian of the island, but for whom there would be no biological station. In connection with the preparation of this paper I wish particularly to note the help of Dr. Gross, who originally urged me to this task, of Dr. Van Tyne, who generously provided me with much valuable data and criticism, and of Dr. Wetmore, who as Secretary of the Smithsonian Institution has had the island under his sympathetic supervision; all three read the manuscript and gave me excellent suggestions.

THE ANNOTATED LIST

In this list species are marked with an asterisk when actual specimens taken on Barro Colorado Island are known. In view of the policy against collecting on the island, the absence of such specimens has little

---

[3] In a few instances the footnotes refer to certain reports by competent observers of species whose reported presence, while unlikely or subject to possible misidentification, seems worth mentioning.

significance; actually of the 306 species here listed all (except *Phaeoprogne tapera*) have been collected within nearby parts of Panamá, and almost all within the Canal Zone.

Technical names.—The nomenclature followed is basically that of Griscom's Panamá checklist (1935), with modifications suggested by more recent studies of Hellmayr, Friedmann, Peters, Wetmore, and Zimmer.

English names.—These are intended to be comprehensive names applicable to the species as a whole—not merely to the Canal Zone subspecies—and thus sometimes differ from names that have been used for the local race.[4]

Unfortunately no published list of English species names exists for Middle American birds, as the older authorities generally provided only subspecies names, which usually did not indicate conspecific relationship.[5] Until some committee acts, the individual writer or student is forced to make his own selection.

For migrants from the area of the A. O. U. Check-list of North American Birds the species names here used are those so far adopted by the A. O. U. Committee.

For tropical species the literature was examined to find a name appropriate to each species (not misleading as to any of its races or confusing with the name of other species), and, if possible, with some associative or recognition value. Hence names suggestive of some character of the appearance, behavior, habitat, or general distribution of the species were favored, and patronymics and lesser geographic designations were avoided (see Eisenmann and Poor, 1946). Preference was given to appropriate names used for the species or one of its subspecies in Ridgway's Birds of North and Middle America or in Hellmayr's Catalogue of Birds of the Americas; and when a choice existed among the names of several subspecies, that of the nominate

---

[4] To facilitate reference, where a name selected is materially different from that used in the Sturgis Field Book (1928), that name is indicated in parentheses.

[5] This practice (often criticized) not only obscured relationships but uselessly multiplied the number of disparate names to be memorized. It has been particularly burdensome in the neotropics, where most species are divided into many local and intergrading subspecies, so that there is frequently uncertainty as to the subspecific status of the local population. The amateur, for whom English names are primarily intended, often has no name available unless he pretends to make a subspecific discrimination that cannot possibly be made in the field. The use of appropriate comprehensive names avoids these difficulties, facilitates recognition throughout the range, and can aid in identification.

subspecies was favored. Resort was also had to the writings of others.[6] Effort was made to avoid novelty, although some names were modified to prevent confusion or misleading effect.

Status.—Status and habitat on Barro Colorado Island are indicated where known, but our information is still very tentative and incomplete. In the case of migrants, the spotty Barro Colorado data have been supplemented with migration dates from Panamá, derived from published records, from labels on specimens in the American Museum, and from sight records of my own or of a few other observers.

Notes.—The descriptions of calls and song are not intended as a complete account of the notes of any species. They are given primarily as an aid to identification, in the full realization that verbal interpretations tend to be extremely personal. In a few instances I include interpretations by other writers.

Breeding.—All breeding dates from Barro Colorado reported to me have been summarized. Since this information is meager, I have added supplemental data (also very incomplete) of nesting dates elsewhere in the Canal Zone and nearby parts of Panamá. On the information presently available it can be said that, while there are birds nesting on Barro Colorado at all times of the year, the greatest number seem to breed between March and June. The breeding periods of Central American birds are still inadequately known, but helpful accounts have been prepared by Harrower (1936a) and Skutch (1950a).

Descriptions.—Certain species recorded from Barro Colorado Island are not described in the Sturgis Field Book (1928). For the convenience of visitors I have supplied a brief diagnosis of such birds, other than migrants from North America.

Order TINAMIFORMES: Tinamous

Family TINAMIDAE: Tinamous

**Tinamus major castaneiceps:* Great Tinamou (Chestnut-headed).

Common in the forest; heard daily from the clearing at dusk and dawn, occasionally at other times. *Notes:* A sad, flutelike whistle of two long-drawn, tremulous notes, the second beginning slightly higher but sliding down; sometimes the first note is repeated once or twice before the second is given; sometimes the 2-noted phrase is twice uttered. *Breeding:* February 26, 1934, 8 young just able to fly

---

[6] Particularly Sutton's Mexican Birds (1951), the recent Distributional Check-list of the Birds of Mexico (Friedmann et al., 1950), and publications of Beebe, Gould, and Skutch.

(Davis); February 28, 1938, 2 eggs (Gilliard); April 28, 1926, 6 eggs (Van Tyne); June 21, 1951, 4 eggs (Milne, Eisenmann); June 26, 1927, 4 eggs (Van Tyne); June 30, 1948, 2 downy young (Eisenmann).

**Crypturellus soui panamensis:* Little Tinamou (Pileated).

Status uncertain; formerly not uncommon near the laboratory; not seen in recent years, though reported calling, by Wetmore, on April 24, 1947, April 5, 1948. Prefers second growth and forest edge. *Notes:* A series of tremulous, ascending whistles, increasing in volume and rapidity, then usually dying away suddenly with a few falling notes. Most often heard early in the morning or late in the afternoon. *Breeding:* March 16, 1926, 2 eggs (Van Tyne); July 13, 1927, 2 eggs, hatched July 29, 1927 (Gross and Van Tyne); August 4, 1925, 2 eggs (Gross).

Order COLYMBIFORMES: Grebes

Family COLYMBIDAE: Grebes

**Podilymbus podiceps antarcticus:* Pied-billed Grebe.

Male in breeding condition collected August 5, 1927 (Van Tyne); others seen March 8, April 14, and June 3, 1927 (Van Tyne).[7]

Order PELECANIFORMES: Totipalmate Swimmers

Family PELECANIDAE: Pelicans

**Pelecanus occidentalis carolinensis:* Brown Pelican.

Small groups fly daily over the lake on their way across the isthmus. They nest on islands in the Gulf of Panamá.[8]

Family PHALACROCORACIDAE: Cormorants

**Phalacrocorax olivaceus olivaceus:* Olivaceous Cormorant (Brazilian).

Very common on the lake, especially on projecting tree trunks.

---

[7] The least grebe (*Colymbus dominicus*) occurs, and probably breeds, on Gatún Lake, but has never been reported from Barro Colorado Island.

[8] Four blue-faced boobies (*Sula dactylatra*) are reported by Mrs. G. G. Fry flying together over the Lake on February 14, 1940, "within easy identification distance." As no storm had occurred, this is very surprising, for the species, though often noted off Colón Harbor, is distinctly pelagic.

Family ANHINGIDAE: Anhingas

**Anhinga anhinga leucogaster:* Anhinga.

Not common; occasionally seen in the laboratory cove and the narrow esteros.

Family FREGATIDAE: Frigatebirds

Fregata magnificens rothschildi: Magnificent Frigatebird.

Small groups fly daily over the lake on their way across the isthmus. They nest on islands in the Gulf of Panamá.

Order CICONIIFORMES: Herons, Storks, Ibises, and Allies

Family ARDEIDAE: Herons

Ardea herodias: Great Blue Heron.

Individuals occur at all seasons, including May, June, July, and August (Van Tyne, Eisenmann, Loetscher, Longenecker, Stott). Wetmore believes that some of these are migrant individuals of the northern great blue heron and that some may be of another subspecies.

Casmerodius albus egretta: Common Egret (American).

Casual on the island. Seen March 11, 1946, February 22, 1948, April 5, 1948, February 28, 1951 (Wetmore).

**Hydranassa tricolor ruficollis:* Tricolored Heron (Louisiana).

Individuals infrequently noted (Chapman). Female collected October 30, 1927 (Gross).

**Florida caerulea:* Little Blue Heron.

Individuals seen throughout the year along the lake shore; the heron most frequently noted in the laboratory cove; most birds are immature.

Leucophoyx thula thula: Snowy Egret.

February 27, 1940 (Mrs. A. Edey and Mrs. M. Edey). The rarity here of this common Canal Zone species is probably caused by the absence of mud flats.

**Butorides virescens:* Green Heron.

Birds of the genus *Butorides* are the most numerous of the family on the island. Almost all students have reported seeing green herons. Wetmore writes: "Two forms of this species undoubtedly occur, one resident and one migrant, but field records are confused owing to the fact that the two differ only in size. The northern *virescens* winters in the Canal Zone (specimens identified from near Gatún and Tabernilla) ; the smaller race *maculatus,* presumably resident, is also found (specimens seen from near Gatún). Birds, supposedly *maculatus,* have been reported breeding on the Island by Chapman and others: March 24, 3 eggs (Gilliard) ; April 28, 1935, 2 eggs (Skutch). Additional breeding specimens are needed to determine the true composition of the resident population."

**Butorides striatus patens:* Striated Heron.

Common along the wooded lake margins.[9] Van Tyne (1950) attributes to this form all breeding birds of this genus collected by him on the island. *Breeding:* April 11, 1927, male taken in full breeding condition; July 28, 1925, nest, 2 eggs; August 11, 1925, 2 half-grown young (Van Tyne).

Agamia agami: Agami or Chestnut-bellied Heron.

Estero west of Salud Point, May 10, 1935 (Skutch). A fairly large (length, 32 inches) slender heron. Adult is bottle green above with lavender crown and back plumes, and largely maroon and chestnut below. Immature is dark brown above with slaty crown, tail, and wing tips, and has creamy-buff underparts with dusky streaks on the sides.

Nycticorax nycticorax hoactli: Black-crowned Night Heron.

Occasional (Chapman). Breeds in Canal Zone, March 21 (Hallinan).

Tigrisoma mexicana: Bare-throated Tiger-heron (Cabanis's).

"Observed rarely. No specimens" (Chapman).[10]

---

[9] Some individuals approach *B. virescens* in being quite brownish-necked. As to this Wetmore says: "Adults are never deep chestnut on the neck like *B. virescens,* but show various shadings of lighter brown toward the purely gray-necked *B. s. striatus,* which is found in eastern Panamá. Immature birds may be separated in the field with difficulty from *B. v. maculatus.*"

[10] The common tiger-heron (*T. l. lineatum*), which has a feathered throat and the adults of which have the head and neck chestnut, may be expected to occur.

Ixobrychus exilis: Least Bittern.

Infrequently seen in marshy islets on southwestern shore (Chapman). The northern *exilis* may occur in winter; the South American *erythromelas* may breed; both have been collected in the Canal Zone.

Family CICONIIDAE: Storks

Mycteria americana: Wood Ibis.

One seen flying over the island on February 12, 1940 (Mrs. Fry, Mrs. Francke, and Mrs. Teague).[11]

Order FALCONIFORMES: Birds of Prey

Family CATHARTIDAE: Vultures

**Sarcoramphus papa:* King Vulture.

Not common, but seen from time to time, often flying over the clearing. Rarely more than one individual, but four soaring together February 8, 1950 (Wetmore), and September 18, 1951 (Bourliere).

**Coragyps atratus:* Black Vulture.

One or two individuals generally can be seen daily.

**Cathartes aura aura:* Turkey Vulture.

Four to eight individuals generally can be seen daily. Large flocks of migrating birds, apparently one of the northern forms, have been noted: February 25-April 5 (Chapman, Cottrell).

Family ACCIPITRIDAE: Hawks

**Elanoïdes forficatus yetapa:* Swallow-tailed Kite.

Not uncommon; from time to time small groups are seen flying over the clearing. A flock of 20 noted June 30, 1949 (Eisenmann).

**Leptodon cayanensis:* Gray-headed Kite.

Adult female collected, perched on a forest trail, August 18, 1927 (Van Tyne). Fairly large (length, 18-24 inches), bill very hooked.

---

[11] Eight all-dark unidentified ibises, apparently of the family Threskiornithidae, were seen flying over by Mrs. Fry February 9, 1940. While the green ibis (*Mesembrinibis cayennensis*), a bottle-green bird with greenish bill and legs, is the only all-dark ibis so far taken in the Canal Zone, two or three other such species may possibly occur.

Adults: Above blackish with a contrasting slaty-gray head; underparts white, sometimes tinged with pearl gray, tail with two or three whitish bands. *Immatures:* Similar, but head mainly white with black crown, a creamy white collar, and white underparts. There are also melanistic phases with blackish head and streaking below.

**Chondrohierax uncinatus uncinatus:* Hook-billed Kite (Red-collared Hawk).

Occasionally noted near the edge of the clearing. Collected May 18, 1926 (Van Tyne); seen July 10, 11, 1950 (Eisenmann).

**Harpagus bidentatus fasciatus:* Double-toothed Kite.

Occasionally seen at the edge of the clearing and in the forest. Rather small (length, 14 inches). *Adults:* Above (including sides of head) slaty; below largely chestnut, breast and abdomen usually barred with white, the bars often edged with gray. *Immatures:* Above brown; below yellowish white, throat and chest sparsely streaked with dusky, belly and flanks barred with brown. *Notes:* A high shrill *pee-yip,* also *pseeyp, pseeyp. Breeding:* Nest high in *Bombacopsis* tree at clearing edge, June 29, 1951; egg taken by toucan July 4 (Laughlin, Eisenmann).

**Ictinia plumbea:* Plumbeous Kite.

Uncommon. Collected April 9 (male, breeding condition), April 22 (female), 1926 (Van Tyne). Seen April 25, 1926 (pair), three flying over the forest August 17, 1927 (Van Tyne); February 25, 1950 (Kilham); March 19, 1950 (Cottrell).

**Buteo platypterus platypterus:* Broad-winged Hawk.

Winter visitant. A flight of over 250 hawks, some definitely this species,[12] noted March 21, 1933 (Carleton). Late date April 6, 1950 (Wetmore).

Buteo magnirostris petulans: Roadside or Insect Hawk (Large-billed).

Occasional around the clearing; the common open-country hawk over much of Panamá. Collected at Frijoles (Gilliard).

**Leucopternis albicollis costaricensis:* White Hawk (Ghiesbrecht's).

One or two birds generally frequent the forest edge near the laboratory, and often perch in the open, permitting close approach.

---

[12] Swainson's hawk (*B. swainsoni*) migrates in large flocks over the Canal Zone, but has not yet been reported from the island.

Leucopternis semiplumbea: Semiplumbeous Hawk.

"Not common" (Chapman). Rather small (length, 15 inches). *Adults:* Above lead gray; below white, usually with a few fine throat streaks; wings black, tail black with one white band. *Immatures:* Similar, but more streaked below and tail with two white bands.

Hypomorphnus urubitinga ridgwayi: Greater Black Hawk, or Urubitinga.

One seen March 8, 1949 (Wetmore). Resembles the next species but is larger and heavier (length, 26 inches) with decidedly longer legs. *Adults:* Differ also in having pure white upper tail coverts, thighs distinctly barred with white, and slaty preocular facial skin contrasting with yellow cere. *Immatures:* Also like those of next species, but head more buffy with less blackish streaking and throat generally unstreaked buffy.

Buteogallus anthracinus: Common Black Hawk or Crab Hawk.

Adult seen April 6, 1948 (Wetmore). Commonest in the coastal areas of Panamá.

**Morphnus guianensis:* Common Crested Eagle.

Collected March 30, 1936 (R. J. Niedrach and A. C. Rogers). Very large (length, 32-37 inches), with pointed crest. *Adults:* Above slaty with lighter tipping to crest; below chiefly white, more or less barred on breast and belly with rufous or brown, chest gray to brown. *Immatures:* Above ashy white with brown marbling, head (except dusky tips to crest) and entire underparts white; tail dusky with irregular lighter bands. Melanistic examples also occur.

**Morphnus taeniatus:* Banded Crested Eagle.

One seen in the forest February 8, 1950 (Wetmore). This rare bird may be a color phase of the preceding species (Lehmann, 1943; Hellmayr and Conover, 1949). It differs in having a blackish chest, with the breast and belly broadly barred black and white.

Harpia harpyja: Harpy Eagle.

Seen 1924 (Barbour), January 8, 1947 (Quaintance), June 22, 1950 (Stott).

Spizastur melanoleucus: Black-and-white Eagle-hawk.

"Rare" (Chapman). Large (length, 21-25 inches), crested, tarsus feathered to the toes. *Adults:* Head, neck, and underparts white, crest and nape with a few black markings; rest of upper parts blackish, wings and tail barred with paler. *Immatures:* Similar, but dark areas more brownish and wing coverts narrowly tipped with whitish.

**Spizaëtus ornatus vicarius:* Ornate or Crested Eagle-hawk.

Collected August 17, 1927 (Van Tyne); seen soaring over an opening on Pearson trail February 8, 1950 (Wetmore). Large (length, 24-49 inches), conspicuously crested. *Adults:* Above blackish; ear coverts and sides of neck and chest tawny rufous; a broad black mustache mark below eye; rest of underparts white, belly barred with black. *Immatures:* Above browner, entire head and neck buffy white, rest of underparts white, with a few black spots and black barring on sides.

Spizaëtus tyrannus serus: Black or Tyrant Eagle-hawk.

Seen perched in forest at edge of clearing June 28, 1949 (Eisenmann, Gross). Large (length, 26-30 inches), conspicuously crested. *Adults:* Black, with some white on crown; white barring on thighs, under wings coverts, under tail coverts, and tail. *Immatures:* Above dark brown, nape and crest white with black tips, wings barred and spotted with black and white; below largely blackish, with white on center of throat and chest and on flanks, chest streaked with brown.

Circus cyaneus hudsonius: Marsh Hawk.

Regular winter visitant (Chapman).

Geranospiza nigra nigra: Blackish Crane-hawk or Frog-hawk.

Several sight records around the clearing: February 13, 1940 (Mrs. A. Edey, Mrs. M. Edey, Mrs. H. Scherman), January 8, 1945 (Allen), July 19, 1945, July 2, 1949 (Eisenmann).

Family PANDIONIDAE: Ospreys

Pandion haliaëtus carolinensis: Osprey.

Regular winter visitant. Though not a breeder, individuals are seen in Panamá throughout the year.

Family FALCONIDAE: Falcons

**Micrastur ruficollis interstes:* Barred Forest-falcon (Cassin's Barred Hawk).

Adult female collected May 1, 1926, in forest on Barbour-Lathrop trail (Van Tyne). "Not uncommon" (Chapman). A forest species.

**Micrastur semitorquatus naso:* Collared or Pied Forest-falcon (Black-and-white Hawk).

Collected February 2, 1926 (Chapman and Potter). Occasionally seen in the forest below the canopy. March 11, 1946 (Wetmore). *Notes:* A series of deliberate laughing notes, *hah, hah, hah,* or a lower *cuh, cuh, cuh. Breeding:* July 20, 1949, two fully grown young sitting in a tree (Loetscher).

**Daptrius americanus guatemalensis:* Red-throated Caracara.

Fairly common in the forest, wandering about in small bands, which will approach an intruder with noisy protests. *Notes:* A loud, raucous *ca-ca-ca, cá-o,* sometimes *cá-ak, ca-cá-o.*

Falco peregrinus anatum: Peregrine Falcon (Duck Hawk).

Uncommon migrant and winter visitant: February 12, 1937 (Gilliard); November 8, 1944 (Allen).

**Falco albigularis albigularis:* Bat Falcon.

A pair or two probably reside on the island, for one or two birds can often be seen flying over the clearing or along the lake shore. *Notes: kee-kee-kee-kee. Breeding:* In Panamá near the Canal Zone a pair seen feeding a full-grown juvenal, June 26, 1949 (Eisenmann).

Order GALLIFORMES: Gallinaceous Birds

Family CRACIDAE: Curassows and Guans

**Crax rubra rubra:* Great Curassow (Great Panama).

Recorded only by Van Tyne: collected male (of two seen) on April 18, 1927; male seen June 25, 1925, and on three occasions in the spring of 1926. All were found "in the big forest, one not far behind the Laboratory, the others up towards the center of the island."

**Penelope purpurascens aequatorialis:* Crested Guan.

Common in the forest, occasional in the clearing. Usually found in small bands in the trees, calling loudly. *Notes:* A somewhat variable metallic yelping, *quenk, quenk, quenk,* or *keelp, keelp, keelp.* In January before sunrise drumming is reported by Chapman.

**Ortalis garrula cinereiceps:* Chestnut-winged Chachalaca (Gray-headed).

Fairly common in the lighter growth, especially near the lake shore; occasional around the clearing. *Notes:* A loud, repeated *chack, chack, chack.*

Family PERDICIDAE: Partridges and Quails

Odontophorus gujanensis marmoratus: Marbled Wood-quail.

Formerly occurred in undergrowth at edge of the clearing; not reported in recent years. *Notes:* A repeated, very rapid, ringing, musical call syllabized as *corcorovado, corcorovado, corcorovado* (Chapman) or *burst the bubble, burst the bubble, burst the bubble* (Skutch).

Order GRUIFORMES: Cranes, Rails, and Allies

Family RALLIDAE: Rails

**Aramides cajanea cajanea:* Gray-necked Wood-rail (Cayenne).

Not common; frequents damp woodland. *Notes:* Pairs duet, usually at night "resembling an aged couple singing in shaky, quavering voices" (Chapman), a "loud series of short gurgling laughs" (Aldrich), or *killi, killi, killi* followed by *cow, cow, cow* (Young).

**Laterallus albigularis albigularis:* White-throated Crake.

"Common in grassy shores and islands" of the southwestern part (Chapman). *Notes:* "A short but loud, groaning snore" (Chapman).

**Porphyrula martinica:* Purple Gallinule.

Pairs well distributed where small marshy areas occur along the bays and estero margins. *Notes:* A variety of clucking, cackling, and guttural sounds, as well as a snapping of the bill (Gross and Van Tyne, 1929). *Breeding:* March 14, 1929, 2 young about a week old (Chapman); May 15, 1935, nest, 5 eggs near Salud Point (Skutch); July 13, 1925, nest, 4 eggs near laboratory cove, hatched August 2-3 (Gross and Van Tyne); November 5, 1927, young in natal down near Frijoles, and many juvenals about 3 months old seen or collected October and early November 1927 (Gross and Van Tyne).

Family HELIORNITHIDAE: Sun-grebes

**Heliornis fulica:* Sun-grebe (American Finfoot).

Local and uncommon; all reports are from the coves and esteros of Gigante Bay on the south side of the island. Collected August 18, 1927 (Van Tyne) and November 6, 1927 (Gross). Seen March 15, 1933 (Carleton); January 3, 1937, cove near Drayton house (Skutch); March 9, 1949, cove at end of Shannon trail (Wetmore); July 8, 1950, cove near Drayton house (Eisenmann, Dr. and Mrs. F. Ryan).

Family EURYPYGIDAE: Sun-bitterns

**Eurypyga helias major:* Sun-bittern.

Rare; collected March 15, 1926, in a creek bed deep in the forest on Shannon trail (Van Tyne); "seen on the lake and along small forest streams tributary to it" (Sturgis).

Order CHARADRIIFORMES: Shorebirds, Gulls, Auks

Family JACANIDAE: Jaçanas

**Jacana jacana hypomelaena:* Wattled Jaçana (Black).

Fairly common in aquatic vegetation, especially on the southwest margin of the island. *Breeding:* March 24, 1937, four young about a day old (Gilliard).

Family SCOLOPACIDAE: Snipes and Sandpipers

**Actitis macularia:* Spotted Sandpiper.

Regular migrant and winter visitant. Late date: May 12, 1926 (collected Van Tyne). There are Canal Zone records for every month except June, and in Panamá from July 25 to May 23.

Family LARIDAE: Gulls and Terns

Larus atricilla: Laughing Gull.

Common migrant and winter visitant on the lake; occasional at other times. Collected on May 17, 1926, at Frijoles (Van Tyne). Several seen June 22, 27 and July 3, 1951 (Eisenmann). Many immature birds can regularly be found in Panamá waters throughout the year.

Larus pipixcan: Franklin's Gull.

One seen July 3, 1951, with the preceding species, on the lake between Barro Colorado Island and Frijoles. Primarily a migrant in Panamá, but immatures sometimes linger over the summer, as noted repeatedly in June-July 1951.

Sterna hirundo: Common Tern.

Seen July 1, 1950, and June 25 and July 3, 1951 (Eisenmann). Individuals, apparently immature, can regularly be found in Panamá waters even in June and July. Jewel collected a male from a flock and a lone immature female on Gatún Lake on December 3, 1911, and June 9, 1912, respectively (Stone, 1918).

**Thalasseus maximus maximus:* Royal Tern.

Regular migrant and winter visitant over the lake. Collected May 28, 1927, seen July 19 and 23, 1927, August 16, 1927 (Van Tyne), and June 25, 1951 (Eisenmann). Many immature birds regularly occur in Panamá waters throughout the year.

Thalasseus sandvicensis acuflavidus: Sandwich Tern (Cabot's).

November 7, 1944, seen over lake (Allen).

**Chlidonias niger surinamensis:* Black Tern.

Regular migrant, occasional in summer: collected November 12, 1927 (Gross). Seen November 29, 1945 (R. C. Murphy), June 28, 1949, six birds (Eisenmann, Gross), July 10, 13, 1949 (Loetscher). Considerable numbers in nonbreeding plumage remain in Panamá Bay during the summer.

Order COLUMBIFORMES: Pigeonlike Birds

Family COLUMBIDAE: Pigeons

**Columba speciosa:* Scaled Pigeon.

"Not uncommon" (Chapman). Collected by Van Tyne. An arboreal species of lighter forest and edge.

**Columba cayennensis pallidicrissa:* Pale-vented Pigeon.

Fairly common arboreal species of the lighter woodland, especially along the lake shore. *Notes:* A mournful *kúk-tu-coóoo.*

**Columba nigrirostris:* Short-billed Pigeon.

Fairly common arboreal forest species. *Notes:* A "melodious 'Je t'adore'" (Chapman); to my ear, *ho, cu-cu-coóoo.*

Columbigallina minuta elaeodes: Plain-breasted Ground-dove.

March 24, 1950, one seen in the clearing (Cottrell). An open-country bird.

Columbigallina talpacoti rufipennis: Ruddy Ground-dove.

Occasionally occurs in the clearing (Weber, Skutch). Common in the more open parts of the Canal Zone and Panamá.

**Claravis pretiosa pretiosa:* Blue Ground-dove.

A pair may usually be found at the edge of the clearing, and occasionally elsewhere in the lighter woods. Primarily a thicket bird, both terrestrial and arboreal. *Breeding:* Nests with eggs found in the Canal Zone in August (Arbib), and female about to lay in April (Stone, 1918).

Leptotila verreauxi verreauxi: White-tipped Dove (Verreaux's).

A pair or two can be found in or around the clearing, and occasionally in other fairly open areas. Favors thickets and small trees in open country, but feeds chiefly on the ground. *Notes:* A soft, inquiring *hoó-oo* or *hoo-hoo, hoo-oo. Breeding:* March 1947 (Quaintance); June 30, 1950, incubating (Eisenmann); July 1949 (Gross); August 5, 1942, two eggs (Mrs. Hobson); nests with eggs September 18, 1925, October 8, 1927 (Gross).

**Leptotila cassinii cassinii:* Gray-chested Dove (Cassin's).

Well distributed throughout the forest, occasionally seen at the edge of the clearing. Frequents the ground and lower growth. The gray head contrasting with the brown nape and back help to distinguish this species from the preceding. *Breeding:* February-April 1935 (Skutch); April 12, 1937 (Gilliard); July 30, 1934 (Arbib). In the Canal Zone also May and September (Stone, 1918).

Geotrygon montana: Ruddy Quail-dove.

Not uncommon on the ground in the forest. *Notes:* "A soft deep *coo*" (Skutch); to my ear a low humming *mmmm,* repeated after a half-second pause.

Order PSITTACIFORMES: Parrots

Family PSITTACIDAE: Parrots

**Brotogeris jugularis jugularis:* Orange-chinned or Tovi Parakeet.

Common; gathering in substantial flocks in the clearing after the breeding season, particularly late in the afternoon. More than 100 birds gathered in one tree every evening in September 1938, then flew off to the mainland to roost for the night. *Notes:* A high screeching chatter. *Breeding:* January-May (Van Tyne).

**Pionus menstruus:* Blue-headed Parrot.

Common in the forest; seen daily in the clearing, usually flying over, but sometimes perching. Distinguished in flight from the *Amazona* parrots by higher-pitched calls and deeper, freer wing strokes; the short wing strokes of the *Amazona* group suggest the flight of ducks. *Notes:* A harsh, high *keéweenk, keéweenk, keéweenk. Breeding:* April 12, 1937, young in nest (Gilliard); April 6, 1950, in stub in the water (Wetmore).

Amazona autumnalis salvini: Red-lored Parrot (Salvin's).

Common in the forest; seen daily flying over the clearing, particularly morning and afternoon. *Notes:* Harsh screeches syllabized as *chikák, chikák, oorák, oorák, ooérk* (Chapman).

Amazona ochrocephala panamensis: Yellow-headed Parrot (Panama).

Rare or casual; a bird of the lighter Pacific woodlands. Reported by Sturgis; also July 16, 1945, 2 perched at the edge of the clearing (Eisenmann); March 17, 1950, 3 or 4 on Barbour trail (Cottrell).

**Amazona farinosa inornata:* Mealy Parrot (Plain-colored).

Common in the forest; pairs seen daily flying over the clearing. *Notes:* Louder, but less raucous than those of the preceding, rendered as *stop it, stop it, quick quick quick* and *yelp, yelp, yelp, cha-cha-cha* (Chapman).

Order CUCULIFORMES: Cuckoolike Birds

Family CUCULIDAE: Cuckoos

Coccyzus americanus: Yellow-billed Cuckoo.

Migrant seen April 30, 1951 (Collias). Recorded in Panamá September 30–November 19.

**Piaya cayana thermophila:* Squirrel Cuckoo.

Individuals are well distributed where there is forest edge or high thickets. *Notes:* A dry *chick-kaw;* a loud *trrt-trrt-trrt-trrt;* a ringing, almost whistled *whep,* repeated five to eight times; a strongly accented *kyékerah* or *wípperah;* also *piscátaqua piscátaqua* (Chapman); also a sharp *peek* and a lower *chirr* (Mrs. Hobson). *Breeding:* Nest in mango tree beside the kitchen, May 1935 (Skutch).

Crotophaga major: Greater Ani.

Local; small groups are spottily distributed in shrubbery along the lake edge of various esteros. In July 1950 I noted three groups on the south shore in different esteros of Gigante Bay and three on the north shore at coves between Fuertes Estero and Salud Point. *Notes:* Most characteristic is a bubbling *prrrr* or *brrrr,* resembling the sound produced by expelling air forcibly from between tightly closed lips; also a lighter *whirrrr;* and a very different, almost mammal-like growl *grrrwa* or *grrrr.*

**Crotophaga ani:* Smooth-billed Ani.

A small group, which has on occasion included as many as 11 birds, can usually be found in the lower part of the clearing or on Slothia Island; rarely elsewhere along the shore; 2 seen northwest of Armour trail-end, June 25, 1951. *Notes:* Most characteristic is a whining *oooo-eeeek* or *oooo-eeeelk. Breeding:* January and February (Chapman, Gilliard); February-May 1935, repeated nestings, all destroyed (Skutch); June 1929 (Skutch).

Tapera naevia excellens: Striped Cuckoo.

Occasional in the clearing; a bird of open-country thickets. *Notes:* Melancholy, long-drawn whistles. One phrase is of two notes, the second note a half tone higher; another phrase is of five or six notes, the next to the last highest and longest. *Breeding:* Said to be parasitic.

**Dromococcyx phasianellus rufigularis:* Pheasant Cuckoo.

Rare; collected March 13, 1926 (Van Tyne); seen (Chapman). A bird of thick undergrowth.

**Neomorphus geoffroyi salvini:* Rufous-vented Ground-cuckoo (Salvin's).

Collected by Chapman and Potter January 7, 1926; seen at the beginning of Barbour-Lathrop trail, March 22, 1935 (Skutch). A terrestrial bird of forest undergrowth.

Order STRIGIFORMES: Owls

Family STRIGIDAE: Owls[13]

Otus choliba luctisonus: Choliba Screech Owl.

Occurs about the clearing; a bird of open woods, clearings, and gardens. "Not common" (Chapman); April 23, 1947 (Wetmore); February 1950 (Kilham). *Notes:* A short series of quick purring or bubbling notes ending in a higher catlike whine.[14]

Lophostrix cristata stricklandi: Crested Owl (Strickland's).

Two sight reports: Armour trail, January 18, 1929 (Robert S. Woods); near laboratory, July 10, 1948 (Longenecker).

**Pulsatrix perspicillata chapmani:* Spectacled Owl.

Seen from time to time near the laboratory. *Notes:* A. A. Allen attributes to this species a series of low hoots, of almost machine-gun rapidity, of which he made a sound recording. Chapman (1929) thought that a very different, deep, deliberate *woof-woof-woof,* often heard before dawn, might be uttered by this species. Neither Allen nor Chapman saw the bird when it was calling.

**Ciccaba virgata virgata:* Mottled Wood-Owl (Cassin's Barred Owl).

"One specimen; status unknown" (Chapman). A forest owl.

Order CAPRIMULGIFORMES: Goatsuckers and Allies

Family CAPRIMULGIDAE: Goatsuckers

**Chordeiles acutipennis micromeris:* Lesser Nighthawk (Texas).

Immature female collected October 30, 1927 (Gross), one of a number of migrants, large flocks having been noted from late September on (Gross, 1930a). This specimen, now in the American Museum of Natural History (wing, 173 mm., tail, 95.3 mm.), is identified by Wetmore as *micromeris,* the Central American race. Other races, including *texensis* of southwestern United States, must also occur in migration. On September 14, 1938, I saw a flock of nighthawks, but as the birds were not calling and were flying high, and

---

[13] The status of the island owls is very uncertain owing to lack of knowledge of their voices.

[14] The vermiculated screech owl (*Otus guatemalae vermiculatus*), which differs in lacking both the distinct dark facial rim and the herringbone pattern below, may also occur, for it has been collected at Frijoles.

the common nighthawk (*C. minor*) also migrates over the Canal Zone, the species could not be determined.

**Nyctidromus albicollis intercedens:* Pauraque.

Often heard and occasionally seen around the clearing. *Notes:* A hoarse whistled *cor-weéee-oo* or *por-weéeeeer;* also a *bup-bup-bup* or *hip-hip-hip* on a single tone. *Breeding:* March 1935 in laboratory clearing, April 30, 1935, on Slothia Island (Skutch).

**Caprimulgus carolinensis:* Chuck-will's-widow.

Migrant; one found dead November 1931 on steps leading to laboratory (in Barro Colorado Island collection).

Family NYCTIBIIDAE: Potoos

Nyctibius grandis: Great Potoo.

"Rare" (Chapman). A little-known nocturnal woodland species. *Notes:* Reported as *oorrr* and *oorrroo* in Surinam (Haverschmidt, 1948).

Nyctibius griseus panamensis: Common Potoo (Panama).

"Not uncommon" (Chapman). A nocturnal woodland species. *Notes:* A melancholy series of loud, rich, long-drawn wailing notes (usually six), going down scale (Chapman).

Order APODIFORMES: Swifts and Hummingbirds

Family APODIDAE:[15] Swifts

Panyptila cayennensis: Swallow-tailed Swift.

Occasional over the clearing: September 12-16, 1938, 2 to 5 birds daily (Eisenmann); April 6, 1949 (Wetmore); July 23, 1950 (Eisenmann); June 23, 1951 (Scholes, Eisenmann). *Breeding:* Found nesting in the Canal Zone in July on Ancón Hospital piazza and Pedro Miguel locks (Greenway, 1934). A velvety-black, fork-tailed swift, with white throat, nape, and sides of rump.

---

[15] Swifts of the genus *Chaetura* are often seen over the clearing, but no specimens have been taken. Chapman (1938) apparently assumed them to be *C. chapmani.* As five species of *Chaetura* have been collected in or near the Canal Zone (Rogers, 1939) and their separation in the field is very difficult, sight identifications seem unreliable—at least until more is known regarding their local status.

Family TROCHILIDAE: Hummingbirds

Glaucis hirsuta affinis: Rufous-breasted Hermit (Lesser Hairy).

Not uncommon, especially in wild plantain (*Heliconia*) thickets and around banana plants. *Breeding:* In the Canal Zone nests found in April and May (Stone, 1918).

Threnetes ruckeri ventosus: Band-tailed Barbed-throat (Rucker's Hermit).

Occasionally noted around *Heliconia* and banana plants.

Phaethornis guy coruscus: Green Hermit (Bangs's).

Not uncommon, in damp woods and *Heliconia* thickets.

**Phaethornis superciliosus*[16] *cassinii:* Long-tailed Hermit (Nicaraguan).

Fairly common; in damp woods and *Heliconia* thickets. *Breeding:* Nests at tip of palm leaf; August 5, 1925, 2 eggs (Gross), June 24, 1951, 2 eggs, 1 hatched June 26 (Milne, Eisenmann). In the Canal Zone, nest with eggs in May (Stone, 1918).

**Phaethornis longuemareus saturatus:* Little Hermit (Dusky).

Occasional in the clearing, not uncommon in the forest; always but a few feet above the ground.

Florisuga mellivora mellivora: White-necked Jacobin (Jacobin Hummingbird).

Common about the flowering shrubs of the clearing. *Breeding:* January 10, 1937, nest with eggs (Gilliard).

Anthracothorax nigricollis nigricollis: Black-throated Mango.

Not uncommon around the clearing. *Breeding:* December, January, February, and March (Chapman, Skutch, Allen).

Lophornis delattrei lessoni: Rufous-crested Coquette (De Lattre's).

Females seen near the laboratory June 30, 1948, and June 28–July 5, 1949 (Eisenmann).

---

[16] Zimmer (1950) considers *P. malaris,* not *P. superciliosus,* to be the nominate race of the wide-ranging species which includes the Middle American forms.

Chlorostilbon canivetii assimilis: Fork-tailed Emerald (Allied).

"Not common" (Chapman). A bird partial to gardens, clearings, and the more open country of the Pacific slope. *Breeding:* In the Canal Zone, nests found in January and November (Sturgis).

**Thalurania furcata venusta:* Common Wood-nymph (Colombian).

Common around the clearing and in the forest. *Breeding:* March 2, March 25, 1935, nests in the forest (Skutch).

**Damophila julie panamensis:* Violet-bellied Hummingbird (Panama).

One of the most common hummingbirds around the flowering shrubs of the clearing, at least during June-September. Chapman regarded it as "not common" during the dry season.

Lepidopyga coeruleogularis coeruleogularis: Sapphire-throated Hummingbird (Duchassain's).

Occasional around the laboratory. A common species in more open country.

Hylocharis eliciae: Blue-throated Goldentail (Elicia's).

Males seen at the laboratory July 5, 1948, July 2, 1949, June-July 1950 (Eisenmann).

**Amazilia amabilis costaricensis:* Blue-chested Hummingbird (Lovely).

Male collected March 12, 1926 (Van Tyne).

Amazilia edward edward: White-bellied Hummingbird (Wilson's).

Males seen at the laboratory July, 2, 6, 1948, and July 4, 6, 1950 (Eisenmann). Generally a bird of more open country.

**Amazilia tzacatl tzacatl:* Rufous-tailed Hummingbird (Rieffer's).

The most common hummingbird around the clearing. *Breeding:* December 1930 (Skutch); July 10, 1950, collecting nesting material (Eisenmann). In the Canal Zone, nests found in April and May (Stone, 1918).

**Chalybura buffonii micans:* White-vented Plumeleteer (Buffon's).

Occasional around the laboratory.

**Heliothryx barroti:* Purple-capped Fairy (Barrot's).

Common in flowering trees around the clearing. *Breeding:* April 1924, nest attached to side of vertical hanging liana (Sturgis).

Heliomaster longirostris longirostris: Long-billed Starthroat.

Male seen January 27, 1951, near the laboratory (Collias). Primarily an open-country species.

Order TROGONIFORMES: Trogons

Family TROGONIDAE: Trogons

**Trogon massena hoffmanni:* Slaty-tailed Trogon (Massena).

Common in the forest, often seen in the clearing. *Notes:* A loud *cah, cah, cah,* interminably repeated at the rate of about two a second. *Breeding:* In old termite nests March-June (Chapman, Gilliard); July 13, 1927, nest with young (Gross).

Trogon melanurus macroura: Black-tailed Trogon (Large-tailed).

Very few records. "Rather rare" (Chapman); woods near laboratory March, April, 1935 (Skutch).

**Trogon rufus tenellus:* Black-throated Trogon (Graceful).

Common in the forest; often seen at the edge of the clearing. *Notes: cow,* repeated three or four times, with a pause between notes, which come at the rate of about one a second; also a sharp, repeated *chirr. Breeding:* In low decaying stumps; April 1935, 2 nests (Skutch); April 20, 1951, 2 eggs (Collias); June 18, 1951, 2 eggs (Milne), 1 young had hatched June 21 (Milne, Eisenmann).

Trogon violaceus concinnus: Violaceous Trogon (Gartered).

Common in the lighter forest; often seen at the edge of the clearing. *Notes:* A rather soft *cow,* repeated at a steady pace of about two a second, 10 to 15 times. *Breeding:* February 25, 1950, 2 eggs in cavity near top of 6-foot stump (Kilham); April 1936, building in termite nest (Chapman); June-July 1950, building in termite nest (Eisenmann).

**Trogon viridis chionurus:* White-tailed Trogon.

Common in the lighter forest; often seen in the clearing. *Notes:* A rather soft *coo,* repeated at first slowly but accelerating into a roll, which sometimes ends with a few slower notes; occasionally a bird will vary the usual call with a simple *kuh, kuh, kuh, kuh. Breeding:* March 11, 1947, in termite nest (Wetmore); April, building in termite nest (Chapman); June 27, 1950, feeding young in termite nest (Stott, Eisenmann).

Order CORACIIFORMES: Kingfishers, Motmots, and Allies

Family ALCEDINIDAE: Kingfishers

**Megaceryle torquata torquata:* Ringed Kingfisher.

Common along the lake shore.

Megaceryle alcyon alcyon: Belted Kingfisher.

Common winter visitant.

**Chloroceryle americana isthmica:* Green Kingfisher.

Most common kingfisher. *Notes:* A clicking *trit-trit-trit.*

Chloroceryle inda: Green-and-rufous Kingfisher.

Seen April 17, 1942, between Frijoles and Barro Colorado Island (Imhof).

**Chloroceryle amazona mexicana:* Amazon Kingfisher.

Fairly common along the lake shore.

Chloroceryle aenea aenea: Pygmy Kingfisher (Least Green).

Occasionally seen in the narrower bays and inlets: near dock July 21, 1945 (Eisenmann); estero near Drayton house August 22, 1948 (Longenecker); at mouth of stream east of Armour trail-end, April 6, 1951 (Collias).

Family MOMOTIDAE: Motmots

**Electron platyrhynchum minor:* Broad-billed Motmot.

Fairly common in the forest; often heard from the laboratory in the early morning. *Notes:* A single loud and resonant, but somewhat nasal *cwa* or *cah,* repeated with pauses of 2 to 3 seconds; occasionally run together as *cah-cah-cah.*

**Baryphthengus ruficapillus semirufus:* Rufous Motmot.

Common in the forest; heard several times daily from the laboratory, particularly in the early morning. *Notes:* The basic phrase is a mellow, rhythmic *hoó-too-too* or *hó-hoo-hoo,* with the accent on the first syllable, often repeated, and echoed by other individuals. A common call sounds like *hoórro.* The hooting may be varied in pitch or time, and is frequently accelerated into a roll.

Momotus momota conexus: Blue-crowned Motmot (Small-billed).

"Occasional; irregular" (Chapman). A bird of more open woodland, collected at Frijoles (Gilliard).

Family BUCCONIDAE: Puffbirds

**Notharcus macrorhynchus hyperrhynchus:* White-necked Puffbird (Dyson's).

Not uncommon in the lighter forest.

**Notharcus pectoralis:* Black-breasted Puffbird.

Not uncommon in the forest. *Breeding:* April 1935, in termite nest (Skutch).

Notharcus tectus subtectus: Pied Puffbird.

Not uncommon in the forest near the laboratory.

**Malacoptila panamensis panamensis:* White-whiskered Puffbird (Panama Malacoptila).

Fairly common in the lighter forest, perching low. *Breeding:* In the Canal Zone stub-tailed fledgling seen August 19, 1933 (Arbib).

Monasa morphoeus fidelis: White-fronted Nunbird (Goldman's).

At least two seen April 6, 1950, on Wheeler trail (Wetmore).

Nonnula frontalis frontalis: Gray-cheeked Nunlet (Panama).

Seen in the forest September 7, 1935, off Drayton trail (D. W. Lamm); seen in the forest, June 23, 1950, on Wheeler trail between Barbour-Lathrop and Snyder-Molino trails (Stott).

Order PICIFORMES: Woodpeckers, Barbets, Toucans, and Allies

Family CAPITONIDAE: Barbets

Capito maculicoronatus maculicoronatus: Spotted-crowned Barbet.

Reported seen once in the forest (Sturgis).

Family RAMPHASTIDAE: Toucans

**Pteroglossus torquatus torquatus:* Collared Araçari.

Common in the forest; seen almost daily around the clearing. *Notes:* A high sneezy *ksíyik, ksíyik* (Skutch writes it *pitit, pitit*); occasionally a soft nasal groan *ang-uh;* a staccato *penk* (Skutch). *Breeding:* In natural hollow of a high horizontal branch, which was first used as a sleeping hole by a group of six; incubation began late March 1935; eggs hatched about April 11; 3 young emerged May 24, 26, 27 (Skutch).

**Ramphastos sulfuratus brevicarinatus:* Keel-billed Toucan (Short-keeled).

Very common in the forest; seen daily around the clearing. *Notes:* A dry, grunting or grinding *werrk, werrk, werrk.* The song is described by Van Tyne as beginning with a hoarse low *crr, crr, crr,* changing to *cra, cra, cra,* and finally settling to a shrill repeated *cree, cree, cree. Breeding:* In natural cavities of large trees, eggs laid in March and April (Van Tyne).

**Ramphastos swainsonii:* Chestnut-mandibled Toucan (Swainson's).

Common in the forest; seen almost daily around the clearing. *Notes:* A loud, somewhat gull-like, yelping *kee-you, tedíck-tedíck-tedíck;* sometimes *kee-you, tedíck.*

Family PICIDAE: Woodpeckers

Celeus loricatus mentalis: Cinnamon Woodpecker (Fraser's).

Occasionally seen in the forest (Chapman, Skutch, Stott).

**Centurus rubricapillus rubricapillus:* Red-crowned Woodpecker (Wagler's).

Occasional in the clearing. A very common bird in more open country. *Notes: churr, churr;* also *wícka, wícka.*

**Centurus pucherani pucherani:* Black-cheeked Woodpecker (Pucheran's).

Very common around the clearing. *Notes: cherrr;* also a higher *chírrirree, chírrirree. Breeding:* December-June (Chapman, Eisenmann).

**Dryocopus lineatus nuperus:* Lineated Woodpecker (Panama Pileated).

Common in the forest; often seen at the edge of the clearing. *Notes:* A loud flickerlike *wícka-wícka-wícka.*

**Phloeoceastes melanoleucos malherbii:* Crimson-crested Woodpecker (Malherbe's).

Fairly common in the forest; often seen at the edge of the clearing. *Notes:* A loud metallic *cheerrr. Breeding:* December-February; young left nest about February 20, 1925 (Chapman).

Order PASSERIFORMES: Perching Birds

Family DENDROCOLAPTIDAE: Woodcreepers[17]

Dendrocolaptes certhia nigriorstris: Barred Woodcreeper.

Uncommon; seen December 24, 1934, in forest on Wheeler trail (Davis); November 21, 1939 (Skutch); March 11, 1951 (two birds) between Miller trail 2-4 (Collias); July 1, 1951, at northwest edge of clearing (Eisenmann).

**Xiphorhynchus guttatus nanus:* Buff-throated Woodcreeper (Lawrence's).

Common in the lighter woodland and forest edge. *Notes:* A series of loud whistles, rising slightly in pitch and then dropping and slowing down (Sturgis); a slurred *cheer,* a *choe* (Skutch). *Breeding:* April 14, 1936, in partly covered box (Chapman); May 1935 in hole in papaya tree (Skutch).

**Xiphorhynchus lachrymosus lachrymosus:* Black-striped Woodcreeper.

Not uncommon forest species; occasionally seen at the edge of the clearing.

Campylorhamphus trochilirostris brevipennis: Red-billed Sicklebill (Venezuelan).

Seen August 17, 1935, on Snyder-Molino trail (D. W. Lamm).

---

[17] This name, used by Chapman and Sutton, is adopted in place of the misleading "woodhewer" of Sturgis and other authors.

Chapman (1938) lists *Dendroplex picus "panamensis"* (= *extimus?*) as "Not common." As this species has not been reported by any other observer, and in Panamá seems to be restricted to a narrow coastal strip along the Pacific, some error is probable.

**Glyphorynchus spirurus sublestus:* Wedgebill.

Not uncommon in the forest. *Notes: chif, chif. Breeding:* July 12, 1949, nest in natural cavity, two fully-fledged young (Gross, Loetscher).

**Dendrocincla fuliginosa ridgwayi:* Brown Woodcreeper (Dendrocincla).

Common in the forest. *Notes:* A loud squeaky *sweeach* or *scheeah.*

Family FURNARIIDAE: Ovenbirds and Allies

**Automolus ochrolaemus pallidigularis:* Buff-throated Automolus (Pale-throated).

A forest species of shrubbery and lower growth. *Breeding:* March 23, 1926, nest with two young in a clay bank (Van Tyne).

**Xenops minutus ridgwayi:* Plain Xenops (Mexican).

Fairly common in the forest, generally feeds like titmouse among outer branches of smaller trees and higher shrubs. *Notes: tseet-tseet;* a high *cheep-cheep-cheep-cheep-cheep.*

**Sclerurus guatemalensis guatemalensis:* Scaly-throated Leafscraper (Guatemalan Sclerurus).

Uncommon terrestrial forest species. *Breeding:* March 30, 1935, with one nestling in burrow on stream bank near laboratory (Skutch).[18]

Family FORMICARIIDAE: Antbirds

**Cymbilaimus lineatus fasciatus:* Fasciated Antshrike.

A pair or two can generally be found at the north edge of the clearing in the shrubbery or low trees. A bird of thickets in humid areas. *Notes:* An easily imitated series of whistles, all on one note, uttered at the rate of about two a second, and continuously repeated for 8 to 10 seconds, *cii, cii, cii, cii, cii* or *cwee, cwee, cwee,* etc. The alarm note is a nasal *wañurk.*

---

[18] The tawny-throated leafscraper (Mexican sclerurus)—*Sclerurus mexicanus andinus*—is included in Chapman's 1929 (but not in his 1938) list. In his later list, *S. guatemalensis* (omitted from the first list) is the only member of the genus mentioned; hence the original listing was probably an error.

Thamnophilus doliatus nigricristatus: White-barred Antshrike (Black-crested).

Occasional in the thickets around the clearing. Common in more open country. Collected at Frijoles (Van Tyne). *Notes:* A rapid whistled hooting, ending in a higher, more emphatic note *hu-hu-hu-hu-hu-hu-hu-hu-hu-hu-weng,* rather similar to the analogous call of the next species; a very harsh guttural *garrr* or *ahrrr;* a catlike whine. *Breeding:* In the Canal Zone, fresh eggs July 17, August 12 (Harrower, Arbib).

**Thamnophilus punctatus atrinucha:* Slaty Antshrike.

Most common antbird; a forest species. *Notes:* A rapid whistled hooting, sometimes at a steady pace, but often accelerating into a roll, ending in a nasal note, *hu-hu-hu-hu-hu-hu-hu-hu-hu-hu-wenk;* a nasal *wenk* or *wank,* given alone; a note starting as a nasal and ending in a growl, *ang-grrrrr,* or *wang-grrrrr;* a nasal, whining *ñaah;* a harsh *gr-gr-gr-gr-gr-gr.* *Breeding:* Occupied nests December 22, 1930, January 7, 1937, February 14, 1935, March 17, 1935 (Skutch); March 26, 1950 (Cottrell); May 7, 1935 (Skutch); July 4, 1949, July 6, 1950 (Eisenmann); July 5, 1947, July 30, 1947 (Mrs. Hobson); July 13, 1949 (Gross); July 20, 1948 (Longenecker). All the July nests contained eggs.

**Dysithamnus puncticeps puncticeps:* Spotted-crowned Antvireo.

Not uncommon. A forest bird of low trees and shrubbery. *Breeding:* Nests with two eggs, July 9, July 11, 1925, July 1949 (Gross); food carried to nest near Shannon trail 1, April 22, 1951 (Collias).

Myrmotherula brachyura ignota: Pygmy Antwren.

Seen July 28, 1934 (Arbib).

Myrmotherula surinamensis pacifica: Streaked Antwren (Surinam).

Not common. A bird of the lower forest trees. *Breeding:* In the Canal Zone, nest with eggs found July 13 (Stone, 1918).

**Myrmotherula fulviventris fulviventris:* Fulvous-bellied Antwren (Lawrence's).

Very common in the more open part of the forest, frequenting low trees and undergrowth. *Notes:* A squeaky *queck, queck;* a somewhat sweeter *tseep, tseep;* a rapid, continued series of chirps, *syip-*

syip-syip-syip; a series of high whistles going upscale, *pii-peh-pey-pih-piy-pee-pyee. Breeding:* Nests with eggs, January 14, 1931, March 29, 1935 (Skutch); October 20, 1944 (Allen).

**Myrmotherula axillaris albigula:* White-flanked Antwren (Black).

Very common in the forest, frequenting the lower branches of smaller trees and the higher shrubbery, often in company with other birds. *Notes:* A high piping on a descending scale, *pee-a, peh-a, pii-a;* sometimes only *peé-a, pii-a;* also *pee-pep-pip;* also *pip-pip* or *tit-tit;* also *psst, psst;* also a dry *trrrr* or *trtrtrtr;* a sharp *whoit;* also a sweet *cheeup, cheeup. Breeding:* April 3, 1935, full clutch; April 16, 1935, very young nestling; May 7, 1935, eggs (Skutch).

**Microrhopias quixensis virgata:* Dotted-winged Antwren (Panama).

Common in the more open parts of the forest, frequenting the lower branches of smaller trees and the higher shrubbery. *Notes: wit-wit* or *tit-tit;* also a higher *cheet, cheet;* a very dry *thrrrr;* a very high chick-like *cheep, cheep, cheep,* varied by a *keeya* resembling a note of *Myiozetetes. Breeding:* Nest building, February 22, 1935 (Skutch).

**Cercomacra tyrannina rufiventris:* Dusky Antbird (Tyrannine).

Common in thickets and undergrowth of forest openings and edge. *Notes:* A song of five to eight whistled notes, going upscale but not smoothly, with pauses after the first two notes, the remainder given very rapidly and rising in pitch, *pii, pii, pí-pi-pi,* or *pii, peh, pípipi-peepee.* A call, *teé-oo, teé-oo. Breeding:* Nest, April 29, 1935 (Skutch).

Myrmeciza longipes panamensis: White-bellied Antbird.

Not uncommon, in second-growth woodland, usually on the ground. *Notes:* A "loud rail-like whinny" (Chapman).

**Myrmeciza exsul exsul:* Chestnut-backed Antbird (Sclater's).

Common in the forest and forest edge; frequents thickets, keeping low, but is not terrestrial. *Notes:* A loud, emphatic, easily imitated whistle, *deh, deé-a,* or *deh, deh, deé-a,* which Chapman paraphrases as "Come here" and "Come right here." Also a clucking *quíck-ick,* and a nasal, catlike *nyaah. Breeding:* Nests with eggs, July 13, 1927, July 25 and August 5, 1925 (Gross).

**Formicarius analis panamensis:* Black-faced Antthrush (Panama).

Common terrestrial forest species; much more often seen than heard. *Notes:* A phrase of three (occasionally four) deliberate plaintive whistles, the first longer and about a half tone higher than the succeeding notes, which are on the same pitch. The bird will decoy to an imitation of this call. The alarm note is "a sharp, clear, somewhat explosive *tleet,* sometimes repeated in a continuous sequence" (Skutch). *Breeding:* Nest with one egg in tree stump, May 19, 1929 (Cleaves).

**Gymnopithys leucaspis bicolor:* Bicolored Antbird.

Fairly common in the forest, on or near the ground; often with army ants. *Notes:* A low, rather whining *chirrrrr. Breeding:* Nest with eggs, April 15, 1927 (Van Tyne, 1944).

**Hylophylax naevioides naevioides:* Spotted Antbird.

Common in forest undergrowth, generally off the ground, usually with army ants. *Notes:* Most characteristic is a rather soft, deliberate, oft-repeated *teé-de, teé-de, teé-de, teé-de, teé-de,* gradually slowing in time and slightly descending in pitch. Also a sharp, whistled *supeé, pee, pee, pipipipi,* the last group of notes very fast; also a low *chirrr* or *tsirrr.* Skutch mentions as additional alarm notes a high sharp *psip* and a short soft *peep. Breeding:* Nests with eggs, April 18, May 7, May 16, 1935 (Skutch), July 16, 1925, July 1949 (Gross); June 24, 1951, hatched July 2 (Milne, Laughlin, Eisenmann).

**Phaenostictus mcleannani mcleannani:* Ocellated Antthrush (McLeannan's).

Not uncommon in the forest; a terrestrial species most often seen with army ants. *Notes:* A soft, very fast series of 5 to 8 whistles, slightly upscale, *puhpüpehpeypihpee;* a sharp *wheerrr* or *cheerrr. Breeding:* July 10, 1950, adults feeding stub-tailed fledgling (Eisenmann).

Grallaria perspicillata perspicillata: Streak-chested Antpitta (Lawrence's).

Fairly common terrestrial forest species; more heard than seen; frequently heard from the laboratory. *Notes:* A series of clear, melancholy whistles, at first rising a little in pitch, then falling off in three descending couplets, *deh, dee, dee, dee, dee, dee, deé-eh, déh-oh, dóh-a.* The notes preceding the couplets vary in number, but the couplets are almost always three. There is usually a few minutes' pause before repetition of the song; by imitation of it the bird can be decoyed into view.

Family COTINGIDAE: Cotingas

Cotinga nattererii: Blue Cotinga (Natterer's).

A tree-top forest species; probably not uncommon, but infrequently seen; occasionally noted in the tall trees at the edge of the clearing. *Breeding:* February-March, 1927, 1928 (Chapman).

**Attila spadiceus sclateri:* Polymorphic Attila (Sclater's).

An arboreal bird of the lighter woodland, often perching fairly low. *Notes:* A "measured, emphatic *beat-it, beat-it, beat-it, no-ó-w,*" also a sharp twitter in flight (Chapman).

**Laniocera rufescens rufescens:* Speckled Mourner.

"Rare" (Chapman). Adult female collected March 3, 1926 (Van Tyne). A little-known forest species. Resembles the next species in size (length, 7.8 inches) and color, being rufous above and tawny below; but differs in having the wing coverts dusky, speckled with a rufous; a tuft of yellow feathers on the sides of the breast (usually concealed), and very indistinct barring on the chest.

**Rhytipterna holerythra holerythra:* Rufous Mourner (Rufous Lipaugus).

"Not common" (Chapman). Collected April 25, 1926 (Van Tyne). An arboreal forest species.

**Lipaugus unirufus castaneotinctus:* Rufous Piha (Panama Lathria).

Rather common arboreal forest species. *Notes:* A very loud, emphatic, whistled *chu-weé-oo,* repeated from time to time. Chapman describes it as a "staccato, explosive *see-you I-see-you,* a long sweeping silvery whistle."

Pachyramphus cinnamomeus cinnamomeus: Cinnamon Becard.

An infrequently noted arboreal forest species.

Pachyramphus polychopterus cinereiventris: Black-backed Becard (Gray-bellied).

"Infrequent" (Chapman). An arboreal bird of open woodland clearings. *Breeding:* In the Canal Zone, nest with eggs found June 18 (Stone, 1918).

Tityra semifasciata costaricensis: Masked Tityra (Costa Rican).

Common arboreal species, especially at the edge of forest clearings. *Notes:* A dry *quert, quert. Breeding:* May 28, 1935, nest with eggs in natural tree cavity (Skutch); June 29, 1948, feeding young in woodpecker hole (Eisenmann); June 28, 1951, feeding young (Ellis).

**Erator inquisitor fraserii:* Black-crowned Erator or Tityra (Fraser's).

Not uncommon arboreal forest species; occasional at the edge of the clearing. *Notes:* Like those of the preceding species, but "drier and less 'grunty'" (Skutch).

**Querula purpurata:* Purple-throated Fruit-crow.

Very common, noisy, arboreal, forest species, wandering about in small bands; frequently heard from the laboratory. *Notes:* A variety of loud, often liquid or tremulous cawing calls, *kweé-a-wuh, kweé-a-wuh; kwoo, kwoo; kwék-kwék-oo; cherkáw, cherkáw; kwek-kwek. Breeding:* Pair noted building nest at northwestern edge of clearing June 28, 1951; incubation apparently begun July 14 (Ellis, Eisenmann).

Family PIPRIDAE: Manakins

**Pipra mentalis minor:* Red-capped or Yellow-thighed Manakin.

Common in the lower levels of the lighter forest. *Notes: sick, seeeeeeeeee,* the second note very high, thin, and rising in pitch; also a *tsick* or *seck,* or *psit,* which Skutch writes is sometimes repeated. The male likewise produces a snap and whirring, doubtless with its wings. *Breeding:* Nests with eggs, 3 in March (earliest March 10), 2 in April, 1 May 7 (Skutch); July 8, 1947; young left July 29 (Mrs. Hobson); July 7, 1950 (Mrs. F. Ryan, Eisenmann).

**Manacus vitellinus vitellinus:* Golden-collared Manakin (Gould's).

Common in the lighter second-growth woodland, particularly near the lake shore, keeping low. *Notes:* Vocal notes are a whistled *peé-you,* and a softer *chee-poó* or *chee-woóoo.* Other sounds, probably made by the wings, are a loud snap, reminiscent of stones struck together; a reedy whir; a ripping sound like the tearing of cloth; and a less loud snip (Chapman 1935; Arbib). *Breeding:* Nests with eggs February 27-August 1 (Skutch, Van Tyne); July 22, 1925, July 25, 1925 (Gross). In the Canal Zone, off the island, nests with eggs have been found in March, April, May, June, and August (Stone, 1918, Harrower, Arbib).

Chiroxiphia lanceolata: Lance-tailed Manakin (Sharp-tailed).

Female seen March 11, 1946, at Fred Miller trail 15 (Wetmore). A bird of scrub and second-growth thickets, common on the Pacific slope of Panamá. *Notes:* The basic note is a mellow, but rather hollow, *doh,* with a bell-like quality, which is repeated alone, or rapidly reiterated *do-do-do-do-do,* or accelerated into a musical roll *drrrrrrr,* or varied into *dówee, dówee-oh,* and *deé-o.* Another more elaborate phrase goes *whit, coo-coó, do-do-do-do-do-whit,* and still another, with a somewhat oriole quality, *do-do-dee-do-deh.* There is also a very different nasal *whang. Breeding:* In the Canal Zone and vicinity, nests with eggs have been found on August 11 and September 13 (Hallinan).

Schiffornis turdinus panamensis: Thrushlike Manakin.

"Rare" (Chapman). A forest bird of the undergrowth. Rather large (length, 6.5 inches) for a manakin. Above plain brown; below cinnamon on throat and chest, pale olive on breast and flanks, fading to yellowish on abdomen. Immature birds are more uniformly cinnamon below, paler on throat, and grayish on abdomen.

Family TYRANNIDAE: Tyrant Flycatchers

**Tyrannus tyrannus:* Eastern Kingbird.

Common migrant; sometimes noted in numbers; March 22, 1927, 30 seen (Chapman); collected April 21, 27, 1926, seen April 12, April 17, 1927 (Van Tyne). May 6, 1935, at least 100 (Skutch); September 14-16, 1938, 6 to 8 together (Eisenmann). Recorded in Panamá March-May and August-October.

**Tyrannus melancholicus chloronotus:* Tropical Kingbird (Lichtenstein's).

Common in the clearing and along the lake shore. *Notes:* A rapid twittering *píririri,* sometimes *píriri,* also *feet-feet-feet. Breeding:* Nests February-June (Chapman, Skutch).

Tyrannus dominicensis dominicensis: Gray Kingbird.

Seen February 1940 (Davis). Migrant and winter visitant in Panamá November-April.

**Legatus leucophaius leucophaius:* Piratic Flycatcher (Striped).

Pairs occur around clearings and lake shore, and elsewhere in breeding colonies of victim species. *Notes:* A monotonously repeated *wee-yee? píririree;* often the *wee-yee?* is given alone. *Breeding:* Seizes newly built closed nests of other species that are harried until they desert. Appropriating and apparently using nests in oropéndola colony February-April (Chapman, Sturgis); appropriating *Myiozetetes* nests in late March (Chapman).

**Myiodynastes maculatus difficilis:* Streaked Flycatcher (Noble).

One or two pairs frequent the laboratory clearing and others occur along the lake shore. *Notes:* A loud heavy *chup* or *check;* also *eéchup;* also *chupeé* or *chupeét;* also, by the male, *chup, weéarooweép,* the latter phrase given after a slight pause and of such different, rather musical though squeaky quality that it seems as if made by another bird. *Breeding:* Builds nests in tree holes, roof corners, boxes, and other natural or artificial crannies and hollows. Late December 1925, woodpecker hole (Chapman); March 17, 1950, incubating (Cottrell); April 6, 1950, angle of roof, April 24, 1947, angle of roof (Wetmore); April 1935, bird box, May 1935, woodpecker hole (Skutch); June 29, 1948, feeding young in woodpecker hole, June 27, 1950, incubating in angle of roof, young fed July 7 (Eisenmann); July 1, 1947, feeding young in angle of roof (Mrs. Hobson); July 7-10, 1949, eggs laid, young hatched July 25, in angle of roof (Gross).

**Megarhynchus pitangua mexicanus:* Boat-billed Flycatcher.

A pair can generally be found in the laboratory clearing and others are well distributed along the lake shore. *Notes:* A harsh, rattling *keerrrrrik-keé* several times repeated; also *krrrrreek. Breeding:* June 27, 1925, nest with large young (Van Tyne); July 15, 1947, feeding young outside nest (Mrs. Hobson); June 28–July 3, 1951, incubating (Eisenmann). In the Canal Zone young have been found in the nest June 2 (Stone, 1918).

**Myiozetetes cayanensis harterti:* Rusty-margined Flycatcher (Cayenne).

A pair or two can often be found in the laboratory clearing; others are frequent along the lake shore and are also occasionally seen in the treetops in the forest. *Notes:* A rather high *fee-ee;* also *feéee-you. Breeding:* January-May (Chapman, Skutch). In Panama City found incubating in early July (Eisenmann).

**Myiozetetes similis columbianus:* Vermilion-crowned or Social Flycatcher (Colombian).

A couple of pairs can usually be found in the clearing and birds are common along the lake. *Notes:* The common call is a loud, harsh *keé-you* or *kreé-you,* also a longer *keé-you, kee-kee-kee-kee-kee. Breeding:* February-June (Chapman, Skutch, Van Tyne), with egg-laying chiefly March-May.

Myiozetetes granadensis granadensis: Gray-capped Flycatcher.

Occasional along the lake shore. *Notes:* A heavy *chip;* a loud, harsh *kree-you. Breeding:* In the Canal Zone, nests with eggs have been found in April and May (Hallinan).

**Pitangus lictor panamensis:* Lesser Kiskadee (Lictor Flycatcher).

Not uncommon in the coves of Gigante Bay and around the mouth of Fuertes Estero. *Notes:* Buzzy and squeaky, *dzai;* also *dzwey,* and *dzee;* also an excited *dzai-dey-dzéy-dah* repeated over and over; also *dzey-ee-dey. Breeding:* In the Canal Zone, female with egg July 9 (Stone, 1918).

**Myiarchus crinitus:* Great-crested Flycatcher.

Migrant and winter visitant. Collected March 19, 1927, and May 3, 1926 (Van Tyne). Recorded in Panamá from October 6-May 3.

**Myiarchus ferox panamensis:* Short-crested Flycatcher (Panama).

Fairly common in the clearing and in the lighter woodland, usually sitting rather low. *Notes:* A rather soft, whistled *whee;* also a whistled *whee-hee-hee-hee-hee-hee-hee-hee-hee.*

**Myiarchus tuberculifer brunneiceps:* Dusky-capped Flycatcher (Black-crested).

Fairly common at the edge of the clearing and in the lighter woodland. *Notes:* A loud, throaty, whistled *wheeeew,* with a bit of *r* in it; also a whistled *wheeeep,* suggesting the great crested flycatcher.

**Contopus virens:* Eastern Wood Pewee.

Migrant. Collected April 23, 1926, April 29, 1927, and May 14, 1927 (Van Tyne). Seen and heard calling February 9, 10, 1940, at edge of clearing (Mrs. Fry and party). In Panamá this species has been taken April 17-May 14 and September 8-November 8. Birds of this genus were noted by the writer in September 1938. As both *C. virens* and the western *C. richardsonii* migrate through the Canal Zone, sight identifications of silent birds are unreliable. The difficulty is further increased by the possible occurrence of the tropical pewee (*Contopus cinereus brachytarsus*), which is a common Canal Zone resident.

Empidonax flaviventris: Yellow-bellied Flycatcher.

Seen October 17, 1944 (Allen). A winter visitant, recorded in Panamá September 8-April 14.

**Empidonax virescens:* Acadian Flycatcher.

Collected February 19, 1927 (Chapman). A winter visitant, recorded in Panamá October 16-April 7.

Empidonax traillii: Traill's Flycatcher.

"Winter visitant; no specimens" (Chapman). Both the eastern and western forms of this species appear to winter in (and at least regularly migrate through) Panamá; records for *traillii:* August 21–May 13; for *brewsteri:* September 17-May 9.[19]

**Terenotriccus erythrurus fulvigularis:* Ruddy-tailed Flycatcher (Fulvous-throated).

Not uncommon in the forest. *Notes:* A thin *tseé-oo-tee. Breeding:* March 1935, two nests with eggs; May 18, 1935, nest with nestlings (Skutch).

**Myiobius sulphureipygius aureatus:* Sulphur-rumped Flycatcher (Myiobius).

Not uncommon along woodland streams. *Breeding:* Nests hung over stream at the rear of the clearing, March and April 1935 (Skutch).

**Myiobius atricaudus atricaudus:* Black-tailed Flycatcher (Myiobius).

Fairly common along streams and the lake shore. *Breeding:* Nests hung low over water; nests with eggs June 28, July 8, July 9, July 10, August 9, 1925 (Gross).

**Onychorhynchus mexicanus fraterculus:* Northern Royal Flycatcher (Colombian).

Uncommon woodland bird, favoring the vicinity of water. *Breeding:* Nesting over stream February-March, 1935 (Skutch).

**Platyrinchus coronatus superciliaris:* Golden-crowned Spadebill (Lawrence's).

Occasionally noted in the forest, sitting in low trees or shrubs.

---

[19] The least flycatcher (*E. minimus*) has been taken at least once in the Canal Zone.

**Cnipodectes subbrunneus panamensis:* Brownish Flycatcher.

Occasionally noted in the forest. *Breeding:* April 5, 1935, seen building nest (Skutch).

Tolmomyias sulphurescens flavo-olivaceus: Sulphury Flycatcher (Yellow-olive).

Seen May 22, 1933 (Carleton). A bird of light woodland and forest edge. *Breeding:* In the Canal Zone, nest with young found May 28 (Stone, 1918).

Tolmomyias assimilis flavotectus: Yellow-margined Flycatcher.

Uncommon in the forest. *Breeding:* April 6, 1948, building nest (Wetmore).

**Rhynchocyclus olivaceus bardus:* Olivaceous Flatbill (Equinoctial Flycatcher).

Not uncommon in second-growth woodland and forest edge. *Breeding:* April 13, 1937, young about four days old in nest (Gilliard). Four sleeping nests found in February and March, 1935 (Skutch).

Todirostrum cinereum finitimum: Common Tody-flycatcher (Northern).

Occasional in the clearing; a bird of open areas with scattered trees and thickets. *Notes:* A short *srrrr;* a sharp *chip. Breeding:* April 1937 (Chapman); 2 eggs, May 2, 1935 (Skutch); nest with 2 eggs, hatched July 10 (Eisenmann).

Todirostrum sylvia schistaceiceps: Slate-headed Tody-flycatcher.

"Not common" (Chapman). A bird of low shrubbery in clearings and open country.

**Oncostoma olivaceum:* Southern Bentbill (Lawrence's Bent-billed Flycatcher).

Not uncommon in thickets in the lighter forest. *Breeding:* Nests, April 1937 (Chapman); two eggs, May 2, 1935 (Skutch). In the Canal Zone, nest with eggs, August 7 (Harrower).

Capsiempis flaveola semiflava: Yellow Flycatcher.

Pair seen in the clearing November 1935 (Skutch). A shrub bird of open country.

**Elaenia flavogaster pallididorsalis:* Yellow-bellied Elaenia (Northern).

Male collected April 21, 1927, on Slothia Island in the laboratory cove (Van Tyne). A very common bird of open country and clearings. *Notes:* A loud, harsh *krreéup, weekrreéup;* sometimes only *krreéup* or *krreep;* also *wrrree. Breeding:* In the Canal Zone, occupied nests found March 31 (Hallinan); July 21 (Harrower); but mostly in April-June (Harrower; Stone, 1918; Eisenmann).

Elaenia chiriquensis chiriquensis: Lesser Elaenia (Lawrence's).

Occasional in the clearing; an open-country bird. *Notes:* A *wheeee* or *feeee,* sometimes slightly trilled *freeee;* also *feé-oo;* also a buzzy *peb-zii. Breeding:* In the Canal Zone and nearby Panamá, June 18, juvenals being fed by adults; June 24, nest with young a few days old (Eisenmann); July 17, nest with incubation apparently going on (Arbib); July 30, nest with young (Imhof).

Sublegatus arenarum atrirostris: Scrub Flycatcher (Smooth).

"Not uncommon" (Chapman). A bird of scrubby country; common on the Pacific slope of Panamá. *Breeding:* In the Canal Zone in April (Imhof).

Camptostoma obsoletum flaviventre: Southern Beardless Flycatcher (Yellow-bellied Camptostoma).

Occasionally noted in the clearing; a bird of open-country thickets and second growth. *Breeding:* March 7, 1949, feeding full-grown young near laboratory (Wetmore).

Tyranniscus vilissimus parvus: Paltry Tyrannulet (Lesser Paltry Flycatcher).

Common around the edge of the clearing and observed at various places on the lake shore and in the forest. *Notes: pee-ee-yíp* or *chee-yíp,* frequently uttered. Not listed by Chapman and not collected, but noted in recent years by all experienced observers.

Tyrannulus elatus panamensis: Yellow-crowned Tyrannulet.

Common in the small trees of the clearing, and noted at various places on the lake shore and at Fuertes House. *Notes:* A clear, frequently given whistle, *deé-ee, deéa. Breeding:* July 3, 1950, adults feeding a stub-tailed juvenal (Eisenmann). Not listed by Chapman and not collected, but noted in recent years by most visitors.

Microtriccus brunneicapillus brunneicapillus: Brown-capped Tyrannulet.

Fairly common in the clearing. *Notes:* A high, piping whistle usually of five notes, descending in pitch, *pee-pih-pey-peh-pii,* and uttered so fast that the whole phrase lasts only about a second; also a single high, clear *peep.* Not listed by Chapman and not collected. I have regularly noted it around the laboratory on my many visits in June, July, and August.

**Pipromorpha oleaginea parca:* Ochre-bellied Flycatcher (Bang's Pipromorpha).

Rather common woodland species, particularly in low trees of hillsides and ravines. *Breeding:* March 2, 1926, 2 nests with eggs hanging against large tree on Wheeler trail, eggs of one nest hatched March 25, 1926; July 12, 1925, 2 nests hanging against cut-bank of Lutz Stream, eggs of one nest hatched July 15, 1925 (Van Tyne); November 23, 1939, nest (Skutch). In the Canal Zone, nest with 3 eggs, May 14 (Stone, 1918).

Family HIRUNDINIDAE: Swallows

**Iridoprocne albilinea:* Mangrove Swallow.

Common, flying low over the lake. *Breeding:* Probably nests in holes in partly submerged tree trunks of the drowned forest.

Riparia riparia riparia: Bank Swallow.

Migrant; four seen April 17, 1942, with migrating barn swallows (Imhof). Reported in the Canal Zone February 22–April 17, August 26–November 30.

Stelgidopteryx ruficollis uropygialis: Rough-winged Swallow (Panama).

Fairly common, flying over the lake, sometimes over the clearing. The northern race *serripennis* has been taken in winter in the Canal Zone.

**Hirundo rustica erythrogaster:* Barn Swallow.

Common migrant; March 23 (Chapman)–May 17 (Van Tyne); occasional in winter, December 30, 1934 (Davis). Migration in the Canal Zone is chiefly from March to May and August to October.

**Progne chalybea chalybea:* Gray-breasted Martin.

Very common, flying over the lake and the clearing and often perching on trees along the shore. *Breeding:* April 6, 1950 (Wetmore); May 20, 1935 (Skutch); July 2, 1951, nestling at nest near Slothia Island (Laughlin); all three nests in tin-can channel markers.

Phaeoprogne tapera: Brown-chested Martin.

July 4, 1949, three recognized flying over the laboratory were later studied at close range, perched on a tree near the lake with the preceding species (Eisenmann), and were shown to Dr. A. O. Gross. At least 12 were noted perched on wires at Frijoles in July 3, 1951 (Eisenmann). Though never previously reported from Panamá, this South American species was regularly seen by me about the city of Panamá and in the Canal Zone during late June and July, 1949 and 1951, often perched on wires in numbers up to about 100. The race of southern South America (*fusca*) is known to be migratory. This species, though very much larger (length, 6.5 inches), closely resembles the bank swallow in color and pattern. The birds seen had noticeable speckling below the brown breastband, thus suggesting the southern *fusca.*

Family CORVIDAE: Jays, Crows, and Allies

**Cyanocorax affinis zeledoni:* Black-chested Jay (Talamanca).

Small groups are occasionally noted in the forest. *Notes:* A loud metallic *chung, chung;* also a harsh *wahk;* also a rapid, dry, and loud *chíkidik;* also a loud *kíyiyiying.*

Family TROGLODYTIDAE: Wrens

**Thryothorus castaneus castaneus:* Bay Wren.

"Rare" (Chapman). Collected March 22, 1926 (Van Tyne). A bird of thickets in most woodland and along stream edges. *Breeding:* In the Canal Zone, nest with egg found July 28 (Stone, 1918).

Thryothorus leucotis galbraithii: Buff-breasted Wren (Galbraith's).

Occasional in thickets around the clearing. A common species (collected at Frijoles) of moist thickets, in fairly open areas and the edge of clearings.[20]

---

[20] The plain wren (*T. modestus elutus*), common in larger clearings, may be expected to occur. It lacks the sharp black wing barring and is less buffy on the breast.

Thryothorus fasciato-ventris albigularis: Black-bellied Wren.

Occasional in the thickets at the edge of the clearing.

**Troglodytes musculus inquietus:* Southern House Wren (Panama).

A pair generally can be found around the laboratory and sometimes at one of the houses along the shore of the island. *Notes:* Most of them sufficiently resemble those of the northern *T. aedon* to be readily recognized. *Breeding:* Egg dates, early January through August (Chapman, Van Tyne, Skutch, Eisenmann).

**Henicorhina leucosticta pittieri:* White-breasted Wood Wren (Sclater's).

Uncommon; collected by Van Tyne (who identifies it as this race) and also by Chapman. A bird of forest undergrowth and fallen treetop tangles.

**Cyphorhinus phaeocephalus lawrencii:* Song Wren (Lawrence's Musician).

Fairly common in the forest in thickets, occasional at the edge of the clearing. *Notes:* Call, a guttural *cútta, cútta, cútta.* Song, a variety of whistles usually intermixed with *cutta* notes, *per-cutta wheet, per-cutta whoot, per-cutta wheet, per-cutta whoot; per-cutta-cuttle wheet whoot; per-cutta whoot whoot* (Harrower). Two sleeping nests with four or five occupants February-March 1935 (Skutch).

**Microcerculus philomela philomela:* Nightingale Wren.

A little-known forest species. Collected March 23, 1926 (Van Tyne). Seen December 30, 1930 (Chapman, Skutch). May 14-23, 1933, a total of six found singing in various parts of the island (Carleton).

Family MIMIDAE: Mockingbirds and Thrashers

Dumetella carolinensis: Catbird.

"Rare winter visitant" (Chapman). Recorded from Panamá October 24-April 23.

Family TURDIDAE: Thrushes

**Turdus grayi casius:* Clay-colored Robin (Bonaparte's).

A pair or two can generally be found in the clearing. *Notes:* Its song and most of its calls are much like those of the American robin

(*T. migratorius*), but it has a distinctive, whining call, often interminably repeated, sounding like *chee-weé-va* or *kee-eé-wuh,* sometimes *wáyewoo. Breeding:* Egg dates in the Canal Zone and adjacent Panamá range from February-August (Hallinan, Harrower, Eisenmann; Stone, 1918).

Hylocichla mustelina: Wood Thrush.

Rare winter visitant; seen December 29, 1926 (Chapman), March 21, 1935 (Skutch).

**Hylocichla ustulata swainsonii:* Swainson's Thrush (Olive-backed).

Migrant. Collected April 17, 1927 (Van Tyne), seen April 4, 5, 6, 1935 (Skutch), April 17, 1942 (Imhof), October 14, 1944 (Allen). Fairly common migrant through Panamá October 7-November 9 and March 17-May 1.

Family SYLVIIDAE: Warblers, Gnatcatchers, and their Allies

**Polioptila plumbea bilineata:* Tropical Gnatcatcher (Lawrence's).

Not common; a bird of light second-growth and scrubby areas. *Notes:* A thin nasal *tzeet, tzeet;* a nasal twang.

**Ramphocaenus melanurus rufiventris:* Long-billed Gnatwren (Antwren).

Fairly common in thickets in the lighter woods. *Breeding:* In Panama City, nest with two newly hatched young, July 15, 1950 (Eisenmann).

Family CYCLARHIDAE: Pepper-shrikes

Cyclarhis gujanensis: Rufous-browed Pepper-shrike.

Seen singing March 9-10, 1950, near the laboratory (Wetmore). Previously unreported from the Canal Zone, and known in Panamá only from open woodland and scrub on the Pacific slope. Length, 5.6 inches. Above olive-green, with brownish cap, rufous superciliaries, gray sides of head; below largely yellow, fading to white on abdomen.

Family VIREOLANIIDAE: Shrike-vireos

**Smaragdolanius pulchellus viridiceps:* Green Shrike-vireo.

A forest bird of the treetops, very hard to see, but probably not uncommon. *Notes:* Whistles a monotonous "'*one-two three*', all on the same note, with a tireless persistence" (Chapman). Length, 5.3

inches. Entirely brilliant green, with a yellow throat and blue hindneck.

Family VIREONIDAE: Vireos

Vireo flavifrons: Yellow-throated Vireo.

Seen March 12, 1935 (Skutch). Uncommon winter visitant in Panamá, November 3-March 12.

Vireo olivaceus: Red-eyed Vireo.

"Migrant" (Chapman). A common migrant and occasional winter visitant in Panamá, August 14-May 1, but chiefly seen in September and October, March and April.

Vireo flavoviridis flavoviridis: Yellow-green Vireo.

Very common in the treetops in the forest and at the edge of the clearing. Panamá-breeding birds are sometimes separated under the name *insulanus. Notes:* Calls are like those of *V. olivaceus;* song is also similar, but the phrases are shorter, drier, and more monotonous, and the utterance is less continuous. *Breeding:* In the Canal Zone, March 26 (Imhof).

**Hylophilus decurtatus pusillus:* Gray-headed Greenlet (Pachysylvia).

Not uncommon in the lighter woods, generally moving in small groups among the lower trees; sometimes seen at the edge of the clearing. *Notes:* A rapid, emphatic, whistled *cheetsacheét,* repeated at intervals of about 5 seconds; sometimes the note sounds more like *itsachéyit. Breeding:* In the Canal Zone, young collected June 25 (Stone, 1918).

Family COEREBIDAE: Honeycreepers

**Coereba flaveola columbiana:* Bananaquit.

Common in the clearing among the smaller trees and flowering shrubs. *Notes:* A buzzy, high, unmusical *zízi-zízi-zízi-zízi-ziz,* sometimes accelerating to *zizizizi. Breeding:* Nests, January 20, 1935, February-April 1935 (Skutch); August 30, 1947 (Eisenmann); November 20, 1939 (building), December 29, 1930 (Skutch). Old nests are often used for sleeping, and sleeping nests are also built.

**Dacnis cayana ultramarina:* Blue Dacnis (Ultramarine).

Common in and around the clearing and trees of the lake shore. *Notes: tseet. Breeding:* Two juvenals being fed July 28, 1947 (C. A. Moore).

Dacnis venusta venusta: Scarlet-thighed Dacnis.

Seen February 8, 1951, 2 males and 2 females at Fuertes House (Collias); June 26, 27, 1951, male and female at south edge of laboratory clearing (Eisenmann). A species rarely recorded in the Canal Zone. Length, 4.75 inches. *Male:* Turquoise blue above, including sides of head; black forehead, wings, tail, and underparts; thighs scarlet. *Female:* Olive above; bluish-green sides of head and neck; buffy underparts; thighs tinged with red.

**Cyanerpes cyaneus carneipes:* Blue Honeycreeper.

Usually very common in and around the clearing—at least in June and July; 20 individuals (mostly adult males) on June 27, 1951, in one tree; not noted in August 1945, September 1938 (Eisenmann), or in October 1943 (Allen). *Notes: st, st* or *tsst, tsst;* also *zzee. Breeding:* Feeding juvenal, April 6, 1937 (Gilliard).

Cyanerpes lucidus isthmicus: Shining Honeycreeper.

July 1, 2, 3, 6, 11, 1950, 1 to 3 individuals of both sexes seen at close range in and around the clearing (Eisenmann); March 17, 1951, pair (Scholes). Length, 4 inches. *Male:* General color deep blue, becoming azure on the crown; black throat, wings, and tail; legs bright yellow. *Female:* Greenish above, becoming grayish-blue on the head; underparts whitish, the chest streaked with blue, the sides with greenish; legs greenish.

**Chlorophanes spiza arguta:* Green Honeycreeper.

Common in and around the clearing, particularly in the tall trees. *Notes: pst, pst;* also a short nasal grunt *uhr,* given by the male. *Breeding:* July 7, 1950, female gathering nesting material (Eisenmann).

Family PARULIDAE: Wood Warblers

Mniotilta varia: Black-and-white Warbler.

Fairly common winter visitant; late date, March 18, 1933 (Carleton). Recorded in Panamá August 24-March 26.

**Protonotaria citrea:* Prothonotary Warbler.

Fairly common winter visitant, especially along the lake shore; November 24, 1939 (Skutch)–March 14, 1933 (Carleton). Recorded in Panamá August 1–March 14.

Helmitheros vermivorus: Worm-eating Warbler.

Seen February 26, 1935 (Skutch). A winter visitant recorded in Panamá December 15–March 16.

Vermivora chrysoptera: Golden-winged Warbler.

Winter visitant (Chapman); September 19, 1951 (Bourliere). Recorded in Panamá October 24–April 16.

Vermivora peregrina: Tennessee Warbler.

Fairly common migrant and winter visitant; October 23, 1944 (Allen)–March 24, 1950 (Cottrell). Recorded in Panamá October 17–April 1.

**Dendroica petechia aestiva:* Yellow Warbler.

Common winter visitant. Collected April 17, 1927, May 4, 1926 (Van Tyne). Seen September 12, 1938 (Eisenmann)–April 23, 1935. Recorded in Panamá August 17–May 4. Barro Colorado sight records may not all be this subspecies, but they relate to the northern birds treated until recently as the species *D. aestiva.*

**Dendroica pensylvanica:* Chestnut-sided Warbler.

Common winter visitant, October 25, 1944 (Allen)–April 15, 1935 (Skutch). Recorded in Panamá September 22–April 15.

Dendroica fusca: Blackburnian Warbler.

Seen March 20, 1950 (Cottrell). Recorded in Panamá as migrant September 27–November 17, March 5–April 28.

**Dendroica castanea:* Bay-breasted Warbler.

Fairly common migrant and winter visitant, October 22, 1944 (Allen)–April 5, 1927 (Van Tyne). Recorded in Panamá October 22–April 27.[21]

---

[21] The blackpoll warbler (*Dendroica striata*) is the subject of two sight reports, which are remarkable as this species migrates through the West Indies and has apparently never been recorded in Central America. Dr. A. A. Allen writes that November 6, 1944, he observed one "close enough so that I had no trouble seeing the light-colored legs and white under tail coverts." Mrs. G. G. Fry writes that on February 8 and 9, 1940, she heard a song, which she recognized as that of this species, and that one of the members of her party, Mrs. L. J. Francke, saw the bird and said it was a male in spring plumage.

Seiurus aurocapillus: Ovenbird.

Winter visitant. Reported singing February 19, 20, 1940 (Mrs. Fry). Late date, March 18, 1933 (Carleton). Recorded in Panamá November 26–April 15.

**Seiurus noveboracensis notabilis:* Small-billed Waterthrush (Northern).

Common winter visitant along forest streams and lake shore. Six specimens taken by Van Tyne March 11, 1926–May 4, 1926, April 17, 1927, are identified by him as this race. Other forms probably occur. Seen October 25, 1944 (Allen)–May 4, 1926 (Van Tyne). Recorded in Panamá September 18–May 4.

**Seiurus motacilla:* Louisiana Waterthrush.

Collected March 12, 1926 (Van Tyne). Recorded in Panamá August 24–March 18.

Oporornis formosus: Kentucky Warbler.

Uncommon winter visitant. Late date, March 28, 1935 (Skutch). Recorded in Panamá September 8–March 28.

Oporornis philadelphia: Mourning Warbler.

Uncommon winter visitant (Chapman, Skutch). Recorded in Panamá September 24–April 14.[22]

Wilsonia citrina: Hooded Warbler.

Male seen September 24, 1951 (Bourliere). Rare migrant and winter visitant in Panamá.

Wilsonia canadensis: Canada Warbler.

Migrant, September 24, 1951 (Bourliere); October 20, 1944 (Allen); March 25, 1950 (Cottrell); April 16, 20, 1935 (Skutch). Recorded in Panamá September 21–October 20, March 25–May 19; sometimes winters.

Setophaga ruticilla: American Redstart.

Winter visitant, January 18, 1931 (Skutch), February 1940 (Mrs. Fry). Recorded in Panamá August 17–April 28.

---

[22] The yellowthroat (*Geothlypis trichas*) is mentioned in Chapman's 1929 (but not in his 1938) list. As the only reported Panamá specimen is a migrant collected in western Chiriquí, the later omission may have been intentional.

**Basileuterus delatrii mesochrysus:* Chestnut-capped Warbler (Sclater's).

Collected June 18, July 27, 1927 (Van Tyne). According to Chapman, "not uncommon along clearing borders," but I have not seen it on any of my visits. It favors second-growth thickets and scrub. *Notes:* Calls include a simple *chit,* a *zeep-zeep* or *dzit-dzit;* song is a rather rapid, dry, chittering *chit-cha-chup-cha-chuweép,* with variations. *Breeding:* In Panamá near the Canal Zone, juvenal being fed June 25 (Eisenmann).

Family ICTERIDAE: Blackbirds, Troupials, and Allies

**Zarhynchus wagleri ridgwayi:* Chestnut-headed Oropéndola (Wagler's).

Small bands are frequently seen around the clearing and in the forest; location of breeding colonies not presently known. *Notes:* A slashing, liquid croak, *grwáckoo, grwáckoo, grwak, grwak;* often *grwáckoo* alone; also a series of gurgling notes like the sound of dripping water, *plup, plup, plup, plúp-loo-úpoo;* also *plup* alone. *Breeding:* In the former colony near the laboratory nest-building regularly began the first or second week of January, egg laying began in late January and continued to April, and by the end of June the young had left (Chapman); June 27, 1925, a few young still in nest (Gross).

**Cacicus cela vitellinus:* Yellow-rumped Cacique (Lawrence's).

A local colonial nester, favoring trees with open surroundings or towering above their neighbors. *Breeding:* A colony of 16 nests attached to a bush growing on a dead trunk in water of the estero west of Salud Point, April–May 1935, destroyed by a snake (Skutch).

Amblycercus holosericeus holosericeus: Yellow-billed Cacique (Prevost's).

Seen February 19, 1940, at edge of the clearing (Mrs. Fry). A common thicket bird in more open country. *Notes:* The male utters mellow whistles, answered by the female with a long dry *churr* (Skutch). *Breeding:* Not colonial, nest with eggs in the Canal Zone, April 24 (Hallinan).

Psomocolax oryzivorus violeus: Giant Cowbird (Colombian Rice Grackle).

Frequents breeding colonies of *Zarhynchus* and *Cacicus,* in whose nests it lays its egg. After the breeding season it gathers in flocks, feeding in fields and often attending cattle.

Icterus galbula: Baltimore Oriole.

Winter visitant, February 11, 1929 (Chapman); February 8, 1940, male and female (Mrs. Fry); March 24, 1950 (Cottrell). Recorded in Panamá October 2–April 20.

Icterus spurius: Orchard Oriole.

Winter visitant, February 19, 1937 (Chapman); February 22, 1948 (Wetmore); March 20, 1950, male and female (Cottrell). Recorded in Panamá August 2–March 20.

Icterus mesomelas salvinii: Yellow-tailed Oriole (Salvin's).

Infrequently noted near the laboratory. April 17, 1942 (Imhof); March 12, 1946, March 8 and May 3, 1949 (Wetmore).

Icterus chrysater giraudii: Yellow-backed Oriole (Giraud's).

Common in and around the clearing and often along the lake shore. *Notes:* Song is a rather hesitant, disconnected series of 6 to 14 loud, clear whistles, moving irregularly up and down scale, and ending in an inconclusive manner. Another common call goes *teéa, cheep-cheep-cheep tee,* the first and last notes whistled, the middle ones nasal; often the last note is suppressed.

Family THRAUPIDAE: Tanagers

**Tanagra fulvicrissa:* Fulvous-vented Euphonia.

Regular in small groups, feeding on mistletoe berries.

Tanagra laniirostris crassirostris: Thick-billed Euphonia.

"Not common" (Chapman). In the clearing, April 1935 (Skutch).

**Tangara inornata languens:* Plain-colored Tanager.

Very common in small groups around the clearing. *Notes:* When feeding, a low *tst tst tst;* when flying off, *tsrrr. Breeding:* Nests found in mango and lime trees near the laboratory, April and May 1935 (Skutch). In Canal Zone, fledgling being fed, August 17 (Harrower, Arbib).

Tangara lavinia lavinia: Rufous-winged Tanager (Lavinia's).

Seen July 22, 1933 in the clearing (Arbib). A little-known forest species.[23]

---

[23] The rather similar green tanager, *T. gyrola deleticia* (not mentioned by Sturgis), has also been recorded in the Canal Zone; it lacks the rufous wings and has a blue rump.

Tangara larvata franciscae: Golden-masked Tanager (Mrs. Wilson's).

Rather common in small groups around the clearing. *Breeding:* Nests found in orange and avocado trees near the laboratory, February–May, 1937 (Skutch); collecting nesting material, July 13, 1947 (Mrs. Hobson).

**Thraupis episcopus diaconus:* Blue-gray Tanager (Blue).

Very common in the clearing, and found in other open situations. *Notes:* Song is a fast, sibilant, twittering *tsu tsu tseéwee tsu-tseéwee tsu-tseéwee tseéwee tseéwee,* with variations. Calls are *chup;* also *chueép;* also *seeee. Breeding:* Nests, January (Chapman), May 10, 1935 (Skutch); building nest, July 4, 1948 (Longenecker, Eisenmann). In the Canal Zone, nests with eggs, April 13 and May 6 (Hallinan); in Panamá City, feeding young in nest, June 23 (Eisenmann).

**Thraupis palmarum atripennis:* Palm Tanager.

Very common in the clearing. *Notes:* Song somewhat like that of the preceding species, but with a distinct "r" sound: *súsuri súsuri, sree sree sree, súsuri súsuri súsuri,* with variations. Calls are *see-ee* with a rising or questioning inflection, and *see-you* with a falling inflection. *Breeding:* In natural and artificial crannies, late in January 1926 (Chapman); February 28, 1935, in coco palm (Skutch); June 1, 1935, young hatched, nest in cranny in top of dead trunk (Skutch).

**Ramphocelus dimidiatus isthmicus:* Crimson-backed Tanager.

Irregular, but sometimes fairly common in the clearing. A bird of thickets and small trees in open country. *Breeding:* February and April, 1935; second nest destroyed and same pair raised another brood in May (Skutch). In the Canal Zone, nests with eggs found March 3 (Stone 1918), May 10 and 24 (Hallinan), June 11 (Stone, 1918).

Ramphocelus icteronotus: Yellow-rumped Tanager.

Irregular, but sometimes not uncommon around the edge of the clearing. A bird of thickets at the edge of humid forest. *Breeding:* In the Canal Zone, nests with eggs found April 30 and May 14 (Stone, 1918).

**Piranga rubra rubra:* Summer Tanager.

Regular winter visitant, November 1939 (Skutch)–March 24, 1933 (Carleton), and March 24, 1950 (Cottrell). Recorded in Panamá September 3– April 16.

**Piranga olivacea:* Scarlet Tanager.

Male collected April 5, 1936 (Niedrach). In Panamá an uncommon migrant recorded March 25–April 5.

**Habia fuscicauda erythrolaema:* Dusky-tailed Ant-tanager.

Not uncommon in thickets in the forest. *Notes:* Song is a beautiful flutelike warble. Call is a harsh wrenlike scold. *Breeding:* In the Canal Zone, nest with eggs found May 14 (Stone, 1918). Some authorities consider this form a race of the red-throated ant-tanager, *H. gutturalis.*

Tachyphonus rufus: White-lined Tanager (Boddaert's).

Irregular about the clearing; a bird of thickets at the edge of woodland. *Breeding:* In the Canal Zone, nest with eggs found May 7 (Stone, 1918).

**Tachyphonus luctuosus panamensis:* White-shouldered Tanager.

Not uncommon in the clearing and in lighter woods; a bird of forest edge. *Notes: tsip, tsip.*

Heterospingus rubrifrons: Sulphur-rumped Tanager.

Seen (4 birds) November 20, 1939, in the tree-tops in the forest near the tower (Skutch). A little-known species. *Male:* Above sooty-slate with yellow rump; below slate-gray, tinged with yellow on abdomen, with white patch on each side of breast; white under wing coverts. *Female:* Duller and less yellow on abdomen. Length, 6 inches. Considered by Hellmayr a "hen-feathered" race of *H. xanthopygius.*

**Eucometis penicillata cristata:* Gray-headed Tanager (Gray-crested).

Fairly common in light woodland and occasional at the edge of the clearing. A bird of shrubbery and low trees. *Notes: chewp, chewp;* also a sharp *chip. Breeding:* March 29, 1935 (Skutch); July 1, 1948, nest with one egg being incubated at Snyder-Molino trail O, hatched July 11 (Longenecker, Eisenmann).

**Rhodinocichla rosea eximia:* Rose-breasted Thrush-tanager (Panama).

One at border of clearing winter of 1936–1937; found dead February 17, 1937 (Chapman, Weber). A bird of dense thickets, most common on the Pacific slope. *Notes:* A rich, very loud, rather hollow, whistled *chó-ho,* repeated over and over, and sometimes varied to *cheéa-wo, cho-wéy.*

Family FRINGILLIDAE: Finches, Grosbeaks, and Allies

**Saltator maximus intermedius:* Buff-throated Saltator.

Occasional in thickets around the clearing. *Breeding:* Carrying nesting material April 15, 1935; nest with nestling in lime tree May 9, 1935 (Skutch). In the Canal Zone, nests with eggs found April 1 (Hallinan) and April 30 (Stone, 1918).

**Saltator albicollis isthmicus:* Streaked Saltator.

Occasional in the thickets around the clearing; common in open country. *Notes:* A loud, whistled *cheé-oo, cheé-oo, cheé-oo, cheéeee-oo;* or *choo, cheé-oo, cheé-oo, cheéee-oo,* varied at times to *chip-cheé-up, chip-cheé-up, chup-cheé-oo;* also a sharp *tseek. Breeding:* In the Canal Zone, nests with eggs found April 7, May 10 (Hallinan), August 10 (Harrower).

**Pitylus grossus saturatus:* Slate-colored Grosbeak.

Common in the forest, particularly near the clearing; more often heard than seen. *Notes:* A variety of high, whistled phrases, *wítchee-weéoo, cheéoo;* also *wee-ee, wítchoo cheéoo cheer;* also *hoó-ee, weéoo-wíhoo-wéyoo.* Call is a metallic *chip.*

**Cyanocompsa cyanoides cyanoides:* Blue-black Grosbeak (Panama Blue).

Common in thickets at the edge of the clearing and in the lighter woodland. *Notes:* Song a series of loud, clear, deliberate whistles *do-do, deh, dee, deh, do,* often followed by a soft, irregular twitter; sometimes there are only five whistled notes, corresponding very well with the solmization "do do re mi re." Also uttered is a sharp scolding *kee-eey. Breeding:* Nest with eggs, July 1947 (C. A. Moore). In the Canal Zone, nest with two fresh eggs, July 27, 1933 (Harrower).

Spiza americana: Dickcissel.

Seen twice in winter (Chapman). In Panamá a winter visitant, numerous locally on migration, September 11–May 10, one specimen June 16.

**Sporophila aurita aurita:* Variable Seedeater (Hicks's).

Very common in the clearing. *Notes:* A sweet, rapid, twittering, somewhat canarylike *tsíwee tsíwee tsíwee, chee chee chee, twee-twee-twee-twee, chirr chirr chirr chirr* with variations, the *chirrs* often omitted. Call is a sweet questioning *chíwee* or *tsíwee;* also *cheep. Breeding:* Nests with fresh eggs, June, July, August, September (Gross, Eisenmann); young left nest as early as June 26, 1951 (Laughlin, Eisenmann), and there were young in the nests as late as second week of October 1927 (Gross). In the Canal Zone, nests with eggs found as early as last week of May, but eggs are laid chiefly June–August (*fide* Gross).

Sporophila nigricollis nigricollis: Yellow-bellied Seedeater.

One seen in the clearing March 19, 1933 (Carleton). A common open-country species, often noted at Frijoles. *Notes:* Song is sweet, but ends usually with two buzzy phrases, *seéwee-seéwee-seéwee-seéwee soósoo, bzeéwee-bzeéwee;* another song is *zeéoo, zeéoo, bzü, bzü;* a third is *wit-seéoo, tsitseéoo, tsee. Breeding:* In the Canal Zone and Panama City, nests with eggs, July 13 (Harrower, Arbib), July 17 (Eisenmann).

**Volatinia jacarina splendens:* Blue-black Grassquit.

Adult male collected April 27, 1927 (Van Tyne). On the mainland an abundant bird of grassy areas. *Notes:* An explosive *bzeé-eep* given by the male as it jumps a foot in the air, often repeating the performance every 10 to 15 seconds for a half-hour or more. *Breeding:* In the Canal Zone and nearby Panamá, occupied nests, July 2 (eggs) (Stone, 1918); July 6 (2 eggs) hatched July 7, July 13 (3 young), July 14 (1 young and 1 egg) (Eisenmann).

Oryzoborus funereus: Thick-billed Seed-finch (Rice Grosbeak).

Occasional in the clearing. An open-country species. *Notes:* Song is a sweet warble, given from the top of a small tree or other elevation. *Breeding:* In the Canal Zone, nest with eggs found April 11 (Hallinan).

Arremonops conirostris striaticeps: Green-backed Sparrow (Lafresnaye's).

Occasional in thickets of the clearing; a bird of more open country. *Notes:* Song, a loud, clear note, repeated at first slowly then gradually faster and faster, *cho, cho, cho, cho cho cho cho-cho-chochocho.*

Calls, *whit-cho;* also a whistled *whit* or *white* (like the *white* in the bob-white call); also *whup;* also *checoo, cheéoo;* also *chep-chep-chep. Breeding:* July 10, 1950, juvenal with adult (Eisenmann). In the Canal Zone and Panama City, nests with eggs, April 18, June 2, June 11 (Stone, 1918), July 16 (Harrower, Arbib); nests with young, June 20, July 17 (Eisenmann, I. R. Eisenmann, Jr).

REFERENCES

Aldrich, J. W., and Bole, B. P.

1937. The birds and mammals of the western slope of the Azuero Peninsula (Republic of Panama). Sci. Publ. Cleveland Mus. Nat. Hist., vol. 7, pp. 1-196.

Allee, W. C.

1926a. Measurement of environmental factors in the rain-forest of Panama. Ecology, vol. 7, No. 3, pp. 273-302.

1926b. Distribution of animals in a tropical rain-forest with relation to environmental factors. Ecology, vol. 7, No. 4, pp. 445-468.

Arbib, R. S., and Loetscher, F.

1935. Some notes from the Panama Canal Zone—summer 1934. Auk, vol. 52, p. 326.

Beard, J. S.

1944. Climax vegetation in tropical America. Ecology, vol. 25, No. 2, pp. 127-158.

Chapman, F. M.

1928. The nesting habits of Wagler's oropendola (*Zarhynchus wagleri*) on Barro Colorado Island. Bull. Amer. Mus. Nat. Hist., vol. 58, pp. 123-166.

1929. My tropical air castle. New York.

1935. The courtship of Gould's manakin (*Manacus vitellinus vitellinus*) on Barro Colorado Island. Bull. Amer. Mus. Nat. Hist., vol. 68, pp. 471-525.

1938. Life in an air castle. New York.

Cleaves, H. H.

1944. Panama ant-thrush (*Formicarius analis panamensis*). Wilson Bull., vol. 56, No. 2, pl. 2.

Eisenmann, E., and Poor, H. H.

1946. Suggested principles for vernacular nomenclature. Wilson Bull., vol. 58, No. 4, pp. 210-213.

Enders, R. K.

1935. Mammalian life histories from Barro Colorado Island, Panama. Bull. Mus. Comp. Zool., vol. 78, No. 4, pp. 385-502.

Friedmann, H., Griscom, L., and Moore, R. T.

1950. Distributional check-list of the birds of Mexico. Pacific Coast Avifauna, No. 29, pt. 1.

Greenway, J. C., Jr.

1934. *Panyptila cayenensis* (Gmelin) nesting in a house. Auk, vol. 51, pp. 377-379.

Griscom, Ludlow.

1935. The ornithology of the Republic of Panama. Bull. Mus. Comp. Zool., vol. 78, No. 3, pp. 261-382.

Gross, A. O.

1927. Barro Colorado Island biological station. Ann. Rep. Smithsonian Inst. 1926, pp. 327-342.

1930a. A jungle laboratory. Nature Mag., vol. 15, pp. 11-15.

1930b. Rainbows on wings: the Massena trogons of the Tropics. Nature Mag., vol. 15, pp. 249-250.

1930c. That bird the toucan. Nature Mag., vol. 15, pp. 291-294.

1950. Nesting of the streaked flycatcher in Panama. Wilson Bull., vol. 62, pp. 183-193.

Gross, A. O., and Van Tyne, J.

1929. The purple gallinule (*Ionornis martinicus*) of Barro Colorado Island, Canal Zone. Auk, vol. 46, pp. 431-446.

Hallinan, T.

1924. Notes on some Panama Canal Zone birds, with special reference to their food. Auk, vol. 41, pp. 304-326.

Harrower, D. E.

1936a. The habits of the passerine birds of Central America, with particular reference to their breeding. Cornell Univ. Dept. Ornithology, Doctoral Dissertation (ms.).

1936b. Nesting of *Oncostoma* in the Canal Zone. Auk, vol. 63, p. 337.

Haverschmidt, Fr.

1948. Observations on *Nyctibius grandis* in Surinam. Auk, vol. 65, pp. 30-32.

Heath, R. E.

1932. Notes on some birds of Barro Colorado Island, Canal Zone. Ibis (1932), pp. 480-487.

Hellmayr, C. E.

1924-1949. Catalogue of birds of the Americas. Field Mus. Nat. Hist., Zool. Ser. 13, pts. 1-11. (Begun by C. B. Cory and completed by B. Conover.)

Hobson, D. M.

1948. An annotated list of birds seen in the Canal Zone and Panama. Indiana Audubon Soc. Year Book, 1948, pp. 304-326.

Imhof, T. A.

1950. Additional bird records for Panama. Auk, vol. 67, pp. 255-257.

Jewel, L. L.

1913. Some North American birds in Panama. Auk, vol. 30, pp. 422-429.

Kenoyer, L. A.

1929. General and successional ecology of the lower tropical rain forest of Barro Colorado Island, Panama. Ecology, vol. 10, No. 2.

Lehmann, F. C.

1943. El genero *Morphnus*. Caldasia, vol. 7, pp. 165-179.

Moore, C. M.

1948. Choosing a bird for special study on Barro Colorado Island. Indiana Audubon Soc. Year Book, 1948, pp. 24-26.

Peters, J. L.

1931-1951. Check-list of birds of the world, vols. 1-7. Harvard Univ. Press, Cambridge, Mass.

Quaintance, C. W.
1949. Vignettes of Barro Colorado life. Turtox News, vol. 27, pp. 74-78.
Ridgway, Robert.
1901-1950. Birds of North and Middle America. U. S. Nat. Mus. Bull. 50, pts. 1-11. (Continued by H. Friedmann.)
Rogers, C. H.
1939. The swifts of Panama. Auk, vol. 56, pp. 81-83.
Skutch, A. F.
1931. Life history of Rieffer's hummingbird. Auk, vol. 48, pp. 481-500.
1934. A nesting of the slaty antshrike on Barro Colorado Island. Auk, vol. 51, p. 9.
1935. Helpers at the nest. Auk, vol. 52, pp. 252-273.
1940. Social and sleeping habits of Central American wrens. Auk, vol. 57, pp. 293-312.
1943. The family life of Central American woodpeckers. Sci. Month., vol. 56, pp. 358-364.
1945. On the habits and nest of the antthrush *Formicarius analis.* Wilson Bull., vol. 57, pp. 122-128.
1946. Life histories of two Panamanian antbirds. Condor, vol. 48, pp. 16-28.
1949. Life history of the yellow-thighed manakin. Auk, vol. 66, pp. 1-24.
1950a. The nesting seasons of Central American birds in relation to climate and food supply. Ibis (1950), pp. 185-222.
1950b. An adventure with toucans. Nature Mag., vol. 43, pp. 410-413, 440.
1951a. Congeneric birds nesting together in Central America. Condor, vol. 53, pp. 3-15.
1951b. Life history of the boat-billed flycatcher. Auk, vol. 68, pp. 30-49.
Standley, P. C.
1933. The flora of Barro Colorado Island, Panama. Contr. Arnold Arb., Harvard Univ., vol. 5, pp. 1-178.
Stone, Witmer.
1918. Birds of the Panama Canal Zone, with special reference to a collection made by Mr. Lindsay L. Jewel. Proc. Acad. Nat. Sci. Philadelphia, vol. 70, pp. 239-280.
Sturgis, B. B.
1928. Field book of birds of the Panama Canal Zone. New York.
Sutton, G. M.
1951. Mexican birds. Univ. Oklahoma Press, Norman, Okla.
Van Tyne, J.
1926. The nest of *Automolus ochrolaemus pallidigularis* Lawrence. Auk, vol. 43, p. 546.
1929. The life history of the toucan *Ramphastos brevicarinatus.* Univ. Michigan Mus. Zool., Misc. Publ. No. 19.
1930. The Barro Colorado laboratory as a station for ornithological research. Wilson Bull., vol. 42, p. 229.
1937. South American pied-billed grebe in the Canal Zone. Auk, vol. 54, p. 379.
1944. The nest of the antbird *Gymnopithys bicolor bicolor.* Univ. Michigan Mus. Zool., Occ. Pap. No. 491.
1950. Bird notes from Barro Colorado Island, Canal Zone. Univ. Michigan Mus. Zool., Occ. Pap. No. 525.

WETMORE, ALEXANDER.

1946. The birds of San José and Pedro Gonzales Islands, Republic of Panamá. Smithsonian Misc. Coll., vol. 106, No. 1.

1950. An additional form of pepper-shrike from western Panamá. Proc. Biol. Soc. Washington, vol. 63, p. 62.

YOUNG, C. C.

1928. Ornithology of the coastland of British Guiana. Ibis (1928), p. 763.

ZETEK, J.

1948. Report on the Canal Zone Biological Area for the year ended June 30, 1947. Ann. Rep. Smithsonian Inst. 1947, pp. 126-151.

1951. Report on the Canal Zone Biological Area for the year ended June 30, 1950. Ann. Rep. Smithsonian Inst. 1950, pp. 133-144.

ZIMMER, J. T.

1948. Studies of Peruvian birds. No. 53. The family Trogonidae. Amer. Mus. Nov. No. 1380, pp. 25-26.

1950. Studies of Peruvian birds. No. 55. The hummingbird genera *Doryfera, Glaucis, Threnetes,* and *Phaethornis.* Amer. Mus. Nov. No. 1449, pp. 19-29.

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 117, NUMBER 6

THE SCAPHOPOD MOLLUSKS COLLECTED BY THE FIRST JOHNSON-SMITHSONIAN DEEP-SEA EXPEDITION

(WITH ONE PLATE)

BY

WILLIAM K. EMERSON
Allan Hancock Foundation
University of Southern California

(PUBLICATION 4059)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
FEBRUARY 26, 1952

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

THE SCAPHOPOD MOLLUSKS COLLECTED BY THE FIRST JOHNSON-SMITHSONIAN DEEP-SEA EXPEDITION[1]

By WILLIAM K. EMERSON

Allan Hancock Foundation
University of Southern California

(With One Plate)

A small but significant collection of scaphopods was obtained in 1933 by the First Johnson-Smithsonian Deep-Sea Expedition to the Puerto Rican Deep, sponsored by the late Eldridge R. Johnson, of Philadelphia. Although only one new species was found, examples were obtained of several species that had been represented previously by unique specimens or by very few individuals. A better taxonomic understanding of several formerly little-known species has been made possible owing to the acquisition of numerous examples of these species. The expedition procured a total of 17 species, 2 of which are questionably identified. The species are listed both systematically and by station. The station data shed little light upon the natural associations of the species because of the great vertical depth range encompassed by many of the hauls. The specimens are all in the collection of the division of mollusks of the United States National Museum.

No attempt has been made to compile a complete synonymy of the species. The reader is referred to the excellent monograph of the eastern American scaphopods by John B. Henderson.[2] Reference is made to the original descriptions and to Henderson for the complete synonymies and descriptions. The classification used is essentially that of Henderson.

The author wishes to express his appreciation to Dr. Harald A. Rehder, curator, division of mollusks, United States National Museum, for having extended to him the use of the laboratory facilities

---

[1] Contribution No. 62 of the Allan Hancock Foundation, University of Southern California. Previous papers on the scientific results of this expedition were published in Smithsonian Misc. Coll., vol. 91. This report on the scaphopod mollusks was not completed in time to be included in that volume.

[2] Henderson, John B., A monograph of the east American scaphopod mollusks, U. S. Nat. Mus. Bull. 111, pp. i-vi, 1-177, pls. 1-20, 1920.

SMITHSONIAN MISCELLANEOUS COLLECTIONS, VOL. 117, NO. 6

and collections in making this study, and to the administration of the Allan Hancock Foundation for material aid in its completion.

Family DENTALIIDAE

Genus DENTALIUM Linné, 1758

Dentalium LINNÉ, Syst. Nat., ed. 10, p. 785, 1758.
Dentalium MONTFORT, Conchyl. Syst., vol. 2, p. 23, 1810.

Genotype by subsequent designation, Montfort 1810, *Dentalium elephantium* Linné, 1758; Recent, Amboina and Philippine Islands.

DENTALIUM (DENTALIUM) GOULDII PORTORICENSE Henderson, 1920

Dentalium (*Dentalium*) *gouldii portoricense* HENDERSON, U. S. Nat. Mus. Bull. 111, p. 30, pl. 2, fig. 5, 1920 (Mayagüez Harbor, Puerto Rico).

Remarks.—A large series of over 100 specimens of this rare shell was taken at one station. Only five individuals were known previously. The material lacks the well-developed intercostal longitudinal striae of the typical subspecies. The hexagonal tip is simple, there being no slit or notch. Fresh specimens have a vitreous shell that has a glazed appearance.

Records.—Station 10, 18°29′20″ N., 66°05′30″ W., 120-160 fathoms (4). Station 26, 18°30′20″ N., 66°22′05″ W., 33-40 fathoms (1). Station 104, 18°30′40″ N., 66°13′20″ W., 80-120 fathoms (100±).

Subgenus COCCODENTALIUM Sacco, 1896

Coccodentalium SACCO, Boll. Mus. Univ. Torino, vol. 11, p. 98, 1896.
Coccodentalium SACCO, Moll. Terr. Terz. Piedmonte e della Liguria, pt. 22, p. 110, 1897.

Subgenotype by original designation, *Dentalium radula* Schroeter, 1784; Miocene, Piedmont of Italy.

DENTALIUM (COCCODENTALIUM) CARDUUS Dall, 1889

Dentalium carduus DALL, Bull. Mus. Comp. Zool., vol. 18, pt. 2, p. 423, pl. 27, fig. 3, 1889 (off Santa Lucia).
Dentalium (*Dentalium*) *carduus*, HENDERSON, U. S. Nat. Mus. Bull. 111, p. 33, pl. 3, figs. 4, 5, 7, 1920 (Little Bahama Bank; off Grenada).

Remarks.—A fragment representing the anterior portion of this rare species was collected. This specimen appears to be the sixth record, as Henderson (1920) states the species to be known from only five examples. This species is here placed in the subgenus *Coccoden-*

talium because of the possession of surface sculpture similar to *Dentalium radula* Schroeter, the subgenotype.

Record.—Station 100, 18°38′45″ N., 64°53′45″ W., 100-300 fathoms (1).

Subgenus DENTALE Da Costa, 1778[3]

Dentale DA COSTA, Hist. Nat. Test. Brit., p. 24, 1778.
Antalis HERRMANNSEN, Indicis Generum Malacoz., vol. 1, p. 63, 1846.
Antalis PILSBRY and SHARP, Man. Conch., vol. 17, p. 37, 1897.

Subgenotype by monotypy, *Dentale vulgare* Da Costa 1778; Recent, Mediterranean and Adriatic Seas, Atlantic Ocean from Spain to Belgium, etc.; Tertiary of Belgium and Italy.

DENTALIUM (DENTALE) BARTLETTI Henderson, 1920

Dentalium (*Antalis*) *bartletti* HENDERSON, U. S. Nat. Mus. Bull. 111, p. 55, pl. 8, figs. 2, 7, 1920.

Remarks.—Only one lot containing five examples of this fragile deep-water species was taken. Henderson's (1920) West Indian records include specimens from off Havana, St. Vincent, and Martinique, in 357 to 464 fathoms.

Record.—Station 93, 18°38′00″ N., 65°09′30″ W., 350-400 fathoms, "cement-like mud" (5).

DENTALIUM (DENTALE) CERATUM Dall, 1881

Dentalium ceratum DALL, Bull. Mus. Comp. Zool., vol. 9, p. 38, 1881.
Dentalium (*Antalis*) *ceratum*, HENDERSON, U. S. Nat. Mus. Bull. 111, p. 49, pl. 7, figs. 2, 4, 5, 6, 7, 1920.

Remarks.—Henderson divided this extremely variable species into several subspecies of doubtful validity. Though the few specimens obtained are poorly preserved, they appear to represent two of Henderson's subspecies, his "typical" and his southern "geographical race" from Barbados, *Dentalium ceratum tenax*.

Records.—Station 102, 18°50′30″ N., 64°43′00″ W., 90-500 fathoms (4). Station 104, 18°30′40″ N., 66°13′20″ W., 80-120 fathoms (2).

Subgenus LAEVIDENTALIUM Cossmann, 1888

Laevidentalium COSSMANN, Ann. Soc. Roy. Malacol. Belgique, vol. 23, p. 7, 1888.
Laevidentalium HENDERSON, U. S. Nat. Mus. Bull. 111, p. 73, 1920.

Subgenotype by original designation, *Dentalium incertum* Deshayes, 1825; Eocene of the Paris Basin.

---

[3] For the extensive synonymy of *Dentale*, see Emerson, Nautilus, vol. 64, p. 17, 1951.

DENTALIUM (LAEVIDENTALIUM) CALLIPEPLUM Dall, 1889

Dentalium callipeplum Dall, Bull. Mus. Comp. Zool., vol. 18, p. 419, pl. 27, fig. 12(b), 1889.
Dentalium (*Laevidentalium*) *callipeplum*, Henderson, U. S. Nat. Mus. Bull. 111, p. 74, pl. 12, fig. 5, 1920.

Remarks.—A good series of well-preserved specimens representing this rather uncommon species was taken. The specimens range in size from fragments of the small, narrow, needlelike anterior portions to large, entire individuals, one of which is apparently the longest specimen known, measuring nearly 75 mm. in length. The specimens in a good state of preservation show clearly the development of microscopic incremental rings. These rings are in close association posteriorly and become progressively farther apart anteriorly for approximately one-third the length of the shell, after which they become irregularly spaced or nearly completely obscure in the remaining portion. The annulations are produced by slightly oblique incised lines. In adult specimens, the posterior orifice generally has a shallow, subtriangular notch on the concave face.

Records.—Station 23, 18°32′15″ N., 66°17′45″ W., 260-360 fathoms (8). Station 25, 18°32′15″ N., 66°22′10″ W., 240-300 fathoms (4). Station 62, 19°25′45″ N., 69°09′00″ W., 350 fathoms (10). Station 94, 18°37′45″ N., 65°05′00″ W., 300-470 fathoms (1).

DENTALIUM (LAEVIDENTALIUM) ?PERLONGUM Dall, 1881

Dentalium perlongum Dall, Bull. Mus. Comp. Zool., vol. 5, No. 6, p. 61, 1878 [name only].
Dentalium perlongum Dall, Bull. Mus. Comp. Zool., vol. 9, p. 36, 1881.
Dentalium (*Laevidentalium*) *perlongum*, Henderson, U. S. Nat. Mus. Bull. 111, p. 75, pl. 9, fig. 1, 1920.

Remarks.—A few small, glossy, needlelike fragments which may represent the posterior tips of this species were taken. The largest fragment measures only 12 mm. in length.

Record.—Station 13, 18°31′05″ N., 66°02′15″ W., 200-300 fathoms (7).

Subgenus EPISIPHON Pilsbry and Sharp, 1897

Episiphon Pilsbry and Sharp, Man. Conch., vol. 17, p. 117, 1897.
Episiphon Suter, Man. New Zealand Moll., p. 821, 1913.

Subgenotype by subsequent designation, Suter, 1913, *Dentalium sowerbyi* Guilding, 1834; Recent, southeastern United States and West Indies.

DENTALIUM (EPISIPHON) JOHNSONI Emerson, new species

Pl. 1, fig. 2

Diagnosis.—Shell slender, thin but not fragile, slightly but uniformly curved, strongly compressed laterally to form an ovate section; section more ovate posteriorly than anteriorly. Juvenile specimens slowly and regularly increasing in diameter, apex attenuated to a needlelike orifice, generally with no indication of a pipe; apex in adult stage often truncated with a very thin, rounded inner tube situated slightly off center toward the convex face and projecting from the orifice. Apical portion of mature individuals filled except for the space occupied by the tube. Aperture of truncated specimens only slightly larger in diameter than the apical orifice. Shell white, vitreous, semitransparent or translucent where clouded by semiopaque growth rings. Surface glossy, essentially smooth, broken only by occasional irregular growth rings, without longitudinal sculpture. Measurements of the holotype: length, 24 mm.; diameter of apical orifice, 1 mm.; diameter of aperture, 1.3 mm. Mature specimens range from 17 to 28 mm. in length.

Remarks.—This relatively large species is one of the largest members of a subgenus composed primarily of small forms. However, it meets the other requirements of the group. The degree of curvature varies slightly with individuals, a few being moderately curved.

Comparisons.—No representative described from the Atlantic Ocean reaches the large size of this species. *Dentalium* (*Episiphon*) *sowerbyi,*[4] from off the Florida coast and in the West Indies, is a minute species characterized by prominent, coarsely developed growth rings and a circular outline. The most closely related form among the fossil species of the Caribbean region appears to be the Miocene species, *Dentalium* (*Episiphon*) *macilentum,*[5] which is a much smaller, more compressed species.

Type locality.—Off Puerto Rico, Station 25, 18°32′15″ N., 66°22′ 10″ W., 240-300 fathoms.

Type depository.—Holotype, U.S.N.M. No. 603543, Station 25, 18°32′15″ N., 66°22′10″ W., 240-300 fathoms. Paratypes, U.S.N.M. No. 429714, Station 25, 18°32′15″ N., 66°22′10″ W., 240-300 fathoms (72).

Other records.—Station 12, 18°31′00″ N., 66°00′15″ W., 200-300 fathoms, blue mud (1). Station 13, 18°31′05″ N., 66°02′15″ W.,

---

[4] Guilding, Trans. Linn. Soc. London, vol. 17, p. 35, pl. 3, fig. 7, 1834.

[5] Pilsbry, Proc. Acad. Nat. Sci. Philadelphia, vol. 63, pp. 166-167, fig. 1-2, 1911 (Bowden, Jamaica).

200-300 fathoms, blue mud (12). Station 14, 18°31′00″ N., 66°04′10″ W., 240-340 fathoms (3). Station 23, 18°32′15″ N., 66°17′45″ W., 260-360 fathoms (4). Station 32, 18°25′50″ N., 67°14′55″ W., 200-280 fathoms (1). Station 67, 18°30′12″ N., 65°45′48″ W., 180-280 fathoms, mud (3). Station 84, 18°32′30″ N., 65°18′30″ W., 300-350 fathoms (1). Station 93, 18°38′00″ N., 65°09′30″ W., 350-400 fathoms, mud (30). Station 94, 18°37′45″ N., 65°05′30″ W., 300-470 fathoms (1).

Subgenus BATHOXIPHUS Pilsbry and Sharp, 1897

Bathoxiphus PILSBRY and SHARP, Man. Conch., vol. 17, p. 121, 1897.
Bathoxiphus BOISSEVAIN, *Siboga* Exped., vol. 54, Scaphopoda, p. 48, 1906.

Subgenotype by subsequent designation, Boissevain 1906, *Dentalium ensiculus* Jeffreys, 1877; Recent, Atlantic Ocean, in deep water.

DENTALIUM (BATHOXIPHUS) ENSICULUS Jeffreys, 1877

Dentalium ensiculus JEFFREYS, Ann. Mag. Nat. Hist., ser. 4, vol. 19, p. 154, 1877.
Dentalium (*Bathoxiphus*) *ensiculus*, HENDERSON, U. S. Nat. Mus. Bull. 111, p. 81, pl. 14, figs. 1, 4, 5, 7, 9, 1920.

Remarks.—One lot containing 50 specimens was dredged in 350 to 400 fathoms. The character of these specimens substantiates Henderson's findings that the Antillean material tends to be somewhat more slender than the northern representatives. The largest specimen measures 30 mm. in length. This deep-water species apparently has an extensive geographical range, having been previously reported from off the New England coast to St. Bartholomew, W. I., and in the eastern Atlantic off the coasts of Portugal, Ireland, etc.

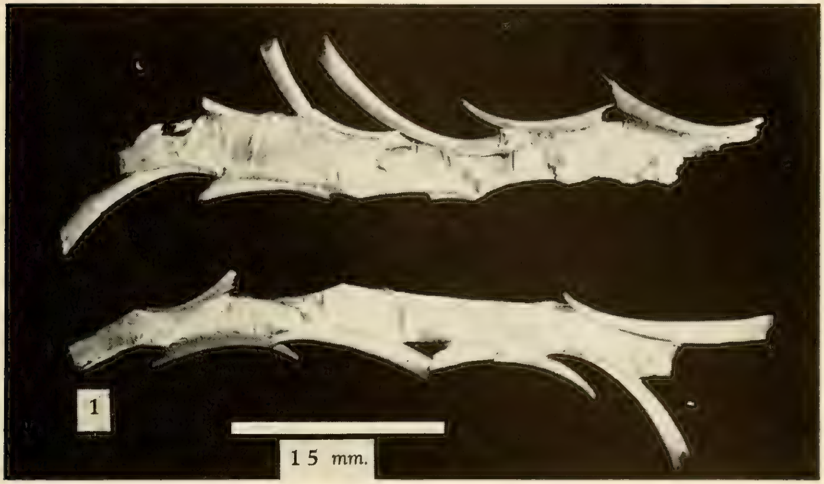
Record.—Station 93, 18°38′00″ N., 65°09′30″ W., 350-400 fathoms, "cement-like mud" (50).

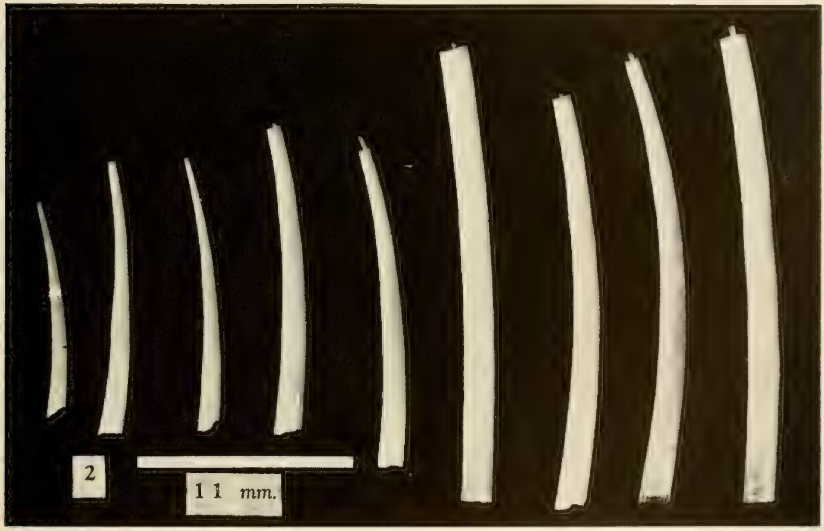
Subgenus COMPRESSIDENS Pilsbry and Sharp, 1897

Compressidens PILSBRY and SHARP, Man. Conch., vol. 17, p. 123, 1897.

Type by original designation, *Dentalium pressum* Pilsbry and Sharp, 1897; Recent, West Indies to the Florida Keys region.

Remarks.—The western Atlantic representatives of this group may actually be members of the Siphonodentaliidae of the subgenus *Pulsellum.* However, since the soft parts are not available for study, the classification of Henderson (1920) is being followed.





SCAPHOPOD MOLLUSKS

1, Specimens of *Entalina platamodes* (Watson) shown attached to the membranous tubes of a polychaetous worm. 2, A series of *Dentalium* (*Episiphon*) *johnsoni*, new species, showing various stages of development and individual variation; specimen at extreme right is the holotype, the remaining specimens are paratypes.

DENTALIUM (COMPRESSIDENS) PRESSUM Pilsbry and Sharp, 1897

Dentalium compressum WATSON, Journ. Linn. Soc. Zool. London, vol. 14, p. 516, 1879 [not Orbigny, 1850].
Dentalium (*Compressidens*) *pressum* PILLSBRY and SHARP, Man. Conch., vol. 17, p. 124, pl. 7, fig. 11; pl. 22, figs. 50-52, 1897.
Dentalium (*Compressidens*) *pressum*, HENDERSON, U. S. Nat. Mus. Bull. 111, p. 83, pl. 14, figs. 3, 6, 8, 1920.

Remarks.—Only one small specimen of this Antillean-continental slope species was found. It ranges north within the Gulf Stream to the Florida Keys.

Record.—Station 67, 18°30′12″ N., 65°45′48″ W., 180-280 fathoms, mud (1).

DENTALIUM (COMPRESSIDENS) OPHIODON Dall, 1881

Dentalium ophiodon DALL, Bull. Mus. Comp. Zool., vol. 9, p. 38, 1881.
Dentalium (*Compressidens*) *ophiodon*, HENDERSON, U. S. Nat. Mus. Bull. 111, p. 84, pl. 14, fig. 2, 1920.

Remarks.—A representative series of this Antillean-continental slope species was taken. It is a smaller, more slender species with a much less degree of compression than *Dentalium* (*Compressidens*) *pressum* Pilsbry and Sharp, which has a similar range.

Records.—Station 13, 18°31′05″ N., 66°02′15″ W., 200-300 fathoms, "blue mud" (5). Station 25, 18°32′15″ N., 66°22′10″ W., 240-300 fathoms, "soft mud" (6).

Family SIPHONODENTALIIDAE

Genus ENTALINA Monterosato, 1872

Entalina MONTEROSATO, Notizie intorno alle Conch. Fossile di Monte Pellegrino e Ficarazzi, p. 27, 1872.
Entalina SACCO, Moll. Terr. Terz. Piedmonte e della Liguria, pt. 22, p. 114, 1897.

Genotype by subsequent designation, Sacco, 1897, *Dentalium tetragona* Brocchi, 1814 (= ?*Dentalium quinquangulare* Forbes, 1843); Miocene, northern Italy.

ENTALINA PLATAMODES (Watson), 1879

Siphodentalium [sic] *platamodes* WATSON, Journ. Linn. Soc. Zool. London, vol. 14, p. 519, 1879.
Entalina platamodes, HENDERSON, U. S. Nat. Mus. Bull. 111, p. 87, pl. 15, figs. 1, 4, 5, 7, 1920.

Entalina quadrata HENDERSON, U. S. Nat. Mus. Bull. 111, p. 88, pl. 15, figs. 2, 3, 6, 10, 1920.

Remarks.—Five lots totaling over 200 specimens of this unusual species were taken. A number of dead specimens were found attached to the sides of membranous tubes apparently belonging to a polychaetous annelid of the genus *Nothria*[6] (see pl. 1, fig. 1). This appears to be the first record of such an association.

Watson (1879) described *Entalina platamodes* (off Culebra Island, West Indies), from a poorly preserved specimen as indicated by his remarks, "neither end is fresh enough for description." However, the general characters of the shell were clearly defined by his statement, "shell five sided, with four sharp corners, which are nearly right angles, and one very obtuse angle along the concave curve . . . there are a few longitudinal striae . . . strongest near the angles, more or less obsolete as they recede from these." Henderson (1920) described *Entalina quadrata* from one well-preserved specimen which possesses a continuous quadrate section and many longitudinal riblets. The material at hand shows that the concave face varies considerably in the degree of medial keel development. Most specimens appear to be five-sided, owing to the presence of this ridge. However, some appear to have four sides when the ridge is not well developed. While the arrangement and number of the longitudinal riblets is more constant in most specimens, the pattern is often interrupted by wear. Apparently Watson's type specimens were badly worn, with the result that the riblets were less discernible, while Henderson's type specimen of *E. quadrata* chanced to be a well-preserved individual showing the complete arrangement of the riblets. Since the intergrading specimens appear to connect the two forms, the species are here considered to be conspecific.

This species is closely related to *Entalina quinquangularis* (Forbes) from the Mediterranean-Aegean Seas, and the northwestern Atlantic Ocean.

Records.—Station 13, 18°31′05″ N., 66°02′15″ W., 200-300 fathoms, blue mud (25). Station 23, 18°32′15″ N., 66°17′45″ W., 260-360 fathoms, mud (40±). Station 25, 18°32′15″ N., 66°22′10″ W., 240-300 fathoms, mud (60). Station 35, 18°23′40″ N., 67°16′45″ W., 180-280 fathoms (3). Station 67, 18°30′12″ N., 65°45′48″ W., 180-280 fathoms, mud (100±).

---

[6] Provisionally identified by Dr. Olga Hartman, Allan Hancock Foundation, University of Southern California.

Genus CADULUS Philippi, 1844

Cadulus Philippi, Enumeratio Molluscorum Sicilae, vol. 2, p. 209, 1844.

Genotype by monotypy, *Dentalium ovulum* Philippi, 1844 (=*Cadulus* (*Cadulus*) *ovulum* Philippi); Recent, Mediterranean Sea.

CADULUS (CADULUS) CONGRUENS Watson, 1879

Cadulus curtus congruens Watson, Journ. Linn. Soc. Zool. London, vol. 14, p. 527, 1879.

Cadulus (*Cadulus*) *congruens,* Henderson, U. S. Nat. Mus. Bull. 111, p. 142 pl. 20, fig. 10, 1920.

Remarks.—One lot containing 18 specimens, which apparently represent this species, was dredged in fairly deep water. This species was not previously represented in the United States National Museum collection.

The types were collected by the *Challenger* off Culebra Island, West Indies, in 390 fathoms with a pteropod-oöze bottom.

Record.—Station 67, 18°30′12″ N., 65°45′48″ W., 180-280 fathoms, mud (18).

CADULUS (CADULUS) EXIGUUS Watson, 1879

Cadulus exiguus Watson, Journ. Linn. Soc. Zool. London, vol. 14, p. 528, 1879.

Cadulus (*Cadulus*) *exiguus,* Henderson, U. S. Nat. Mus. Bull. 111, p. 145, pl. 20, fig. 9, 1920.

Remarks.—Three lots totaling 32 specimens were taken. This species was previously represented by only two specimens in the United States National Museum collection.

The type locality is off Culebra Island, West Indies, in 390 fathoms.

Records.—Station 13, 18°31′05″ N., 66°02′15″ W., 200-300 fathoms, blue mud (4). Station 35, 18°23′40″ N., 67°16′45″ W., 180-280 fathoms (5). Station 67, 18°30′12″ N., 65°45′48″ W., 180-280 fathoms (23).

CADULUS (CADULUS) ?TERSUS Henderson, 1920

Cadulus (*Cadulus*) *tersus* Henderson, U. S. Nat. Mus. Bull. 111, p. 149, pl. 20, fig. 4, 1920 (Barbados).

Remarks.—One fragment which may represent this species was dredged.

Record.—Station 67, 18°30′12″ N., 65°45′48″ W., 180-280 fathoms, mud (1).

Subgenus GADILOPSIS Woodring, 1925

Gadilopsis Woodring, Carnegie Inst. Washington Publ. 366, p. 206, 1925.

Subgenotype by original designation, *Ditrupa dentalina* Guppy, 1873 (=*Cadulus* (*Gadilopsis*) *dentalinus* (Guppy)); Miocene, Jamaica.

CADULUS (GADILOPSIS) ACUS Dall, 1889

Cadulus acus Dall, Bull. Mus. Comp. Zool., vol. 18, p. 432, pl. 27, fig. 11, 1889.
Cadulus (*Gadila*) *acus*, Henderson, U. S. Nat. Mus. Bull. 111, p. 140, pl. 20, figs. 11, 13, 1920.

Remarks.—Five lots of this uncommon species were taken. In this shallow-water species the oblique growth rings are developed moderately. There is a slight variation in width among individuals.

Records.—All Samaná Bay, Dominican Republic. Station 55, 19° 10′12″ N., 69°27′03″ W., 17 fathoms (15). Station 56, 19°10′15″ N., 69°27′20″ W., 17 fathoms (35±). Station 57, 19°10′20″ N., 69°28′35″ W., 18 fathoms, mud (2). Station 58, 19°10′20″ N., 69° 29′15″ W., 18 fathoms, mud (4). Station 59, 19°10′25″ N., 69°30′05″ W., 18-19 fathoms, mud (2).

Subgenus PLATYSCHIDES Henderson, 1920

Platyschides Henderson, U. S. Nat. Mus. Bull. 111, p. 104, 1920.

Subgenotype by original designation, *Cadulus grandis* Verrill, 1884; Recent, west Atlantic, north of Hatteras.

CADULUS (PLATYSCHIDES) ELEPHAS Henderson, 1920

Cadulus (*Platyschides*) *elephas* Henderson, U. S. Nat. Mus. Bull. 111, p. 107, pl. 17, fig. 10, 1920.

Remarks.—Six specimens were obtained that can be referred unquestionably to this species. It was previously known only from the unique, which was dredged in 464 fathoms off St. Vincent.

This large ivory-white shell appears to have a simple posterior orifice. The largest specimen measures 16 mm. in length, 1.5 mm. less than the type. In these additional specimens the hemisphere on the concave face is slightly more bulbous than in the type.

Records.—Station 25, 18°32′15″ N., 66°22′10″ W., 240-300 fathoms, mud (4). Station 67, 18°30′12″ N., 65°45′48″ W., 180-280 fathoms, mud (2).

CADULUS (PLATYSCHIDES) ?BUSHII Dall, 1889

Cadulus carolinensis bushii DALL, Bull. Mus. Comp. Zool., vol. 17, p. 430, 1889 (Barbados).

Cadulus (*Platyschides*) *bushii,* HENDERSON, U. S. Nat. Mus. Bull. 111, p. 125, pl. 19, fig. 10, 1920.

Remarks.—The one lot collected is questionably referred to this species. While the specimens are about the same size and have an outline similar to *Cadulus bushii,* they are heavy, rather opaque shells in which the oral aperture is quite constricted.

This may prove to be a new species.

Record.—Station 21, 18°30′20″ N., 66°10′30″ W., 140-200 fathoms (8).

LIST OF SPECIES COLLECTED, ARRANGED BY STATIONS[7]

Station 10. Lat. 18°29′20″ N. Long. 66°05′30″ W. February 2, 1933
Lat. 18°30′24″ N. Long. 66°04′15″ W.
Off San Juan, Puerto Rico, in 120-160 fathoms, tangle:
Dentalium (*D.*) *gouldii portoricense.*

Station 12. Lat. 18°31′00″ N. Long. 66°00′15″ W. February 2, 1933
Lat. 18°30′30″ N. Long. 66°01′45″ W.
Off Punta Maldonado, Puerto Rico, in 200-300 fathoms, beam trawl, blue mud:
Dentalium (*Episiphon*) *johnsoni.*

Station 13. Lat. 18°31′05″ N. Long. 66°02′15″ W. February 2, 1933
Lat. 18°30′30″ N. Long. 66°04′05″ W.
Off Punta Maldonado, Puerto Rico, in 200-300 fathoms, beam trawl, blue mud:
Dentalium (*Laevidentalium*) *?perlongum.*
Dentalium (*Episiphon*) *johnsoni.*
Dentalium (*Compressidens*) *ophiodon.*
Entalina (*E.*) *platamodes.*
Cadulus (*C.*) *exiguus.*

Station 14. Lat. 18°31′00″ N. Long. 66°04′10″ W. February 2, 1933
Lat. 18°30′30″ N. Long. 66°03′15″ W.
Off Punta Maldonado, Puerto Rico, in 240-340 fathoms, beam trawl:
Dentalium (*Episiphon*) *johnsoni.*

Station 21. Lat. 18°30′20″ N. Long. 66°10′30″ W. February 4, 1933
Lat. 18°31′15″ N. Long. 66°12′20″ W.
Off Putna Salinas, Puerto Rico, in 140-200 fathoms, beam trawl:
Cadulus (*Platyschides*) *?bushii.*

---

[7] Bartsch, Paul, Station Records of the First Johnson-Smithsonian Deep-Sea Expedition, Smithsonian Misc. Coll., vol. 91, No. 1, pp. 1-31, 1 map, 1933.

Station 23. Lat. 18°32'15" N. Long. 66°17'45" W. February 4, 1933
Lat. 18°32'00" N. Long. 66°21'15" W.
Off Punta Cerro Gordo, Puerto Rico, in 260-350 fathoms, otter trawl:

Dentalium (Laevidentalium) callipeplum.
Dentalium (Episiphon) johnsoni.
Entalina (E.) platamodes.

Station 25. Lat. 18°32'15" N. Long. 66°22'10" W. February 7, 1933
Lat. 18°32'05" N. Long. 66°22'10" W.
Off Punta Cerro Gordo, Puerto Rico, in 240-300 fathoms, dredge, mud:

Dentalium (Laevidentalium) callipeplum.
Dentalium (Episiphon) johnsoni.
Dentalium (Compressidens) ophiodon.
Entalina (E.) platamodes.
Cadulus (Platyschides) elephas.

Station 26. Lat. 18°30'20" N. Long. 66°22'05" W. February 7, 1933
Lat. 18°30'30" N. Long. 66°23'05" W.
Off Punta Cerro Gordo, Puerto Rico, in 33-40 fathoms, dredge, rock, etc.:

Dentalium (D.) gouldii portoricense.

Station 32. Lat. 18°25'50" N. Long. 67°14'55" W. February 9, 1933
Lat. 18°23'50" N. Long. 67°17'35" W.
Off Punta Jiguero, Puerto Rico, in 200-280 fathoms, dredge:

Dentalium (Episiphon) johnsoni.

Station 35. Lat. 18°23'40" N. Long. 67°16'45" W. February 9, 1933
Lat. 18°24'45" N. Long. 67°14'15" W.
Off Punta Jiguero, Puerto Rico, in 180-280 fathoms, beam trawl:

Entalina (E.) platamodes.
Cadulus (C.) exiguus.

Station 55. Lat. 19°10'12" N. Long. 67°27'03" W. February 16, 1933
Lat. 19°10'15" N. Long. 69°27'10" W.
Samaná Bay, Dominican Republic, in 17 fathoms, dredge:

Cadulus (Gadilopsis) acus.

Station 56. Lat. 19°10'15" N. Long. 69°27'20" W. February 16, 1933
Lat. 19°10'15" N. Long. 69°28'05" W.
Samaná Bay, Dominican Republic, in 17 fathoms, dredge:

Cadulus (Gadilopsis) acus.

Station 57. Lat. 19°10'20" N. Long. 69°28'35" W. February 16, 1933
Lat. 19°10'20" N. Long. 69°29'00" W.
Samaná Bay, Dominican Republic, in 18 fathoms, dredge, mud:

Cadulus (Gadilopsis) acus.

Station 58. Lat. 19°10′20″ N. Long. 69°29′15″ W. February 16, 1933
Lat. 19°10′25″ N. Long. 69°30′05″ W.
Samaná Bay, Dominican Republic, in 18 fathoms, dredge, mud:
Cadulus (*Gadilopsis*) *acus*.

Station 59. Lat. 19°10′25″ N. Long. 69°30′05″ W. February 16, 1933
Lat. 19°10′35″ N. Long. 69°30′40″ W.
Samaná Bay, Dominican Republic, in 18-19 fathoms, dredge, mud:
Cadulus (*Gadilopsis*) *acus*.

Station 62. Lat. 19°25′45″ N. Long. 69°09′00″ W. February 18, 1933
Lat. 19°27′45″ N. Long. 69°14′45″ W.
Off Punta Pescadores, Dominican Republic, in 350 fathoms, dredge:
Dentalium (*Laevidentalium*) *callipeplum*.

Station 67. Lat. 18°30′12″ N. Long. 65°45′48″ W. February 23, 1933
Lat. 18°32′18″ N. Long. 65°46′12″ W.
Off Punta Picua, Puerto Rico, in 180-280 fathoms, dredge, mud:
Dentalium (*Episiphon*) *johnsoni*.
Dentalium (*Compressidens*) *pressum*.
Entalina (*E.*) *platamodes*.
Cadulus (*C.*) *congruens*.
Cadulus (*C.*) *exiguus*.
Cadulus (*C.*) *?tersus*.
Cadulus (*Platyschides*) *elephas*.

Station 84. Lat. 18°32′30″ N. Long. 65°18′30″ W. February 26, 1933
Lat. 18°39′00″ N. Long. 65°17′00″ W.
North of Culebra Island, in 300-350 fathoms, otter trawl:
Dentalium (*Episiphon*) *johnsoni*.

Station 93. Lat. 18°38′00″ N. Long. 65°09′30″ W. March 2, 1933
Lat. 18°37′45″ N. Long. 65°05′00″ W.
North of St. Thomas, Virgin Islands, in 350-400 fathoms, dredge, mud:
Dentalium (*Dentale*) *bartletti*.
Dentalium (*Episiphon*) *johnsoni*.
Dentalium (*Bathoxiphus*) *ensiculus*.

Station 94. Lat. 18°37′45″ N. Long. 65°05′00″ W. March 2, 1933
Lat. 18°39′00″ N. Long. 65°03′30″ W.
North of St. Thomas, Virgin Islands, in 300-470 fathoms, dredge:
Dentalium (*Laevidentalium*) *callipeplum*.
Dentalium (*Episiphon*) *johnsoni*.

Station 100. Lat. 18°38′45″ N. Long. 64°52′45″ W. March 4, 1933
Lat. 18°40′15″ N. Long. 64°50′15″ W.
North of St. Thomas, Virgin Islands, in 100-300 fathoms, otter trawl:
Dentalium (*Coccodentalium*) *carduus*.

Station 102. Lat. 18°50′30″ N. Long. 64°43′00″ W. March 4, 1933
Lat. 18°51′00″ N. Long. 64°33′00″ W.
Northwest of Anegada Island, in 90-500 fathoms, otter trawl:
Dentalium (*Dentale*) *ceratum*.

Station 104. Lat. 18°30′40″ N. Long. 66°13′20″ W. March 8, 1933
Lat. 18°30′10″ N. Long. 66°13′50″ W.
Off Punta Boca Juana, Puerto Rico, in 80-120 fathoms, oyster dredge, mud:
Dentalium (*D.*) *gouldii portoricense*.
Dentalium (*Dentale*) *ceratum*.

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 117, NUMBER 7

HOST RELATIONSHIPS OF MOTHS OF THE GENERA DEPRESSARIA AND AGONOPTERIX, WITH DESCRIPTIONS OF NEW SPECIES

BY
J. F. GATES CLARKE
U. S. Bureau of Entomology and Plant Quarantine

(Publication 4083)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
APRIL 23, 1952

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

HOST RELATIONSHIPS OF MOTHS OF THE GENERA DEPRESSARIA AND AGONOPTERIX, WITH DESCRIPTIONS OF NEW SPECIES

By J. F. GATES CLARKE
U. S. Bureau of Entomology and Plant Quarantine

(With Six Plates)

In 1932 I began collecting larvae of the species of *Depressaria* and *Agonopterix* (Lepidoptera: Oecophoridae) for the purpose of rearing the moths and gaining some knowledge of their habits and distribution and with the hope that unknown species might be discovered. It soon became evident that undescribed species of these genera were numerous and that many of their habits were both intriguing and informative. Although interrupted, sometimes for several years, these investigations have continued sporadically over the past two decades with moderate success.

During the summer of 1950, by means of a grant-in-aid made by the American Philosophical Society which defrayed some of the expense of an extended trip through several western States, I was able to resume my explorations in this field.[1] My purpose, essentially, was to determine if possible whether the long-suspected host specificity of many species of *Depressaria,* particularly those attached to plants of the genus *Cicuta,* really existed. Unfortunately, only a few species of this genus of plants were found, and so the project was enlarged to include species of moths attached to other umbelliferous plants.

In the course of the summer's field work plants were examined at 80 localities, as shown in the list beginning on page 5. Infestations

---

[1] I wish to express my gratitude to the American Philosophical Society for the grant-in-aid that made these investigations possible and to the Smithsonian Institution for administering the grant. Also, I have many times been indebted to my friend Dr. Lincoln Constance, Department of Botany, University of California, for determinations of plants and for his stimulating company in the field. During the summer of 1950, in connection with the present studies, I again received his generous help, and again I thank him. I am indebted to Harry F. Clements for furnishing the photograph for plate 5, figure 2; all other photographs and drawings herein are of my own making. Unless otherwise indicated, all material for this paper was collected and reared by me.—J. F. G. C.

SMITHSONIAN MISCELLANEOUS COLLECTIONS, VOL. 117, NO. 7

do not occur throughout the plants' ranges, the distribution of the moths being affected by other factors. In all, 34 species of umbels were examined. For the most part these food plants were situated along highways and so were readily accessible. I have used this method of roadside collecting for many years and have found that larvae can thereby be collected rapidly and with much saving of time.

On the westward journey I made observations and collections at several localities, but it was not until we reached Washington and Oregon that serious collecting really began. A brief discussion of some of the localities, with illustrations of the habitats and some of the food plants, seems appropriate in order to acquaint the reader with the diverse conditions under which these umbelliferous plants flourish.

The Umbelliferae are found throughout the continent from the seashore to the high altitudes of the Rocky, Cascade, and other mountains, in swamps, and in the deserts and prairies. By following the advent of spring from the lowlands to the high altitudes, it is possible to enjoy profitable collecting from March to August. Even in the lowlands of the Midwest and eastern United States and Canada, certain species of larvae will be found well into August.

After crossing the Rocky Mountains, going west, one encounters the Intermountain Area between the Rocky and Cascade Mountains. Throughout this inland empire Umbelliferae abound, and it is here that we find a vast number of species of *Lomatium.* One species of *Lomatium* is found as far east as Missouri; the rest are western. Perhaps the commonest species is *L. dissectum,* which covers vast areas from Alberta to British Columbia, Montana, Idaho, Washington, and Oregon to Colorado and California. This is host to *Depressaria leptotaeniae.*

In central Washington and Oregon, desert conditions, which extend north into southern British Columbia and south into California, prevail. In somewhat restricted, sandy habitats within this area will be found *Pteryxia terebinthina foeniculacea,* the host to *D. yakimae* (pl. 1, figs. 1, 2). In Ten Sleep Canyon, Wyo., another variety of this plant, *P. t. calcarea,* is host to *Depressaria pteryxiphaga,* described on page 16.

Continuing west to the eastern slopes of the Cascade Mountains one encounters a great array and succession of umbelliferous plants that are hosts to a considerable number of species of *Depressaria* and *Agonopterix.* One of the commonest species of these plants is *Cicuta occidentalis,* which is found in marshy areas and along creeks, rivers, and irrigation ditches. On plate 2, figure 1, is illustrated a typical habitat at Rock Creek, Oreg., where Oregon State Highway 82 crosses it, in which the *Cicuta* grows in association with grasses, tule, and *Typha.* This particular stand of *C. occidentalis* was heavily infested with *D. juliella.* On plate 2, figure 2, are illustrated uninfested specimens of this plant at Carlton, Wash.

As one leaves the desert and arid spaces of the Intermountain Area and ascends the eastern slopes of the Cascade Mountains he passes through the Timbered Transition Zone. In this zone, usually on the open, rocky slopes, *Lomatium triternatum macrocarpum,* host to *D. betina,* is found. Also in this zone one encounters *Osmorhiza occidentalis* and *O. chilensis.* Both of these species are attacked by *Agonopterix rosaciliella,* but I have never found a *Depressaria* attached to either of these plants. *O. occidentalis* is found most abundantly at altitudes of 5,000 to 6,000 feet, and *O. chilensis* usually grows at lower altitudes and in the Humid Transition Zone of the west side of the Cascades. *O. chilensis* is not normally infested; in fact, the only infestation I have ever found was at Billy Goat, Okanogan County, Wash., where the host was attacked by *Agonopterix rosaciliella.*

The alpine meadows, which one encounters after passing through the foothills of the Cascade Range and the high ridges above them, provide the habitats for a great variety of umbels. At Harts Pass, which forms the boundary between Whatcom and Okanogan Counties, Wash., and Slate Peak, in the former county (pl. 3), there are no fewer than twelve species of Umbelliferae. These are: *Osmorhiza occidentalis, O. chilensis, Heracleum lanatum, Angelica arguta, Ligusticum purpureum, Lomatium dissectum, L. brandegei, L. geyeri, L. ambiguum, Angelica lyalli* Wats., *Lomatium gormani* (Howell) C. & R., and *L. triternatum* (Pursh) C. &. R., the last three being recorded by Muenscher.[2] In addition, *L. angustatum,* from which I have reared *D. angustati,* will be found on some of the high ridges such as Skyline Ridge, Mount Baker District, Whatcom County, Wash.

Proceeding westward, after passing through the alpine meadows and the Arctic Highland ridges, we enter the forested Hudsonian, Canadian, and Humid Transition Zones in that order. In the first two there is little of interest for one devoted to the study of the insects being discussed, but in the Humid Transition there is a wide variety of Umbelliferae.

Oenanthe sarmentosa (pl. 5, fig. 1), the host of *D. nervosa,* is

---

[2] Muenscher, W. C., The flora of Whatcom County, State of Washington, pp. 108-110, 1941.

abundant in practically every swale, swamp, marsh, and roadside ditch, and although *nervosa* is not found throughout the range of the host it is widespread in Oregon and Washington and undoubtedly will be found in British Columbia. I obtained *nervosa* in quantity on the American side of the international boundary at Blaine, Wash. On the dry prairies of the Humid Transition Zone, on the dry, gravelly slopes of some of the San Juan Islands, and along the seashore at Bellingham and Birch Bays, *Lomatium utriculatum,* host to *D. besma,* and *L. nudicaule* abound. *Sium suave, Cicuta douglasii,* and *Osmorhiza chilensis* are also found abundantly, *C. douglasii* being an occasional host of *D. nervosa.* In this zone also *Angelica arguta, A. lucida,* and *A. hendersonii* are encountered. *A. lucida* grows in the marshy, tidewater areas of the Siletz River, Oreg., and *A. hendersonii* (pl. 4, figs. 1, 2) is found along the rocky bluffs of the seashore of the Oregon coast. Both of these plants, together with *Ligusticum apiifolium* and *Conioselinum chinense,* are hosts to *A. rosaciliella* and *A. oregonensis.*

Throughout all these zones, with the exception of the Arctic, we are apt to find *Daucus carota, Heracleum lanatum,* and *Conium maculatum. H. lanatum* is frequently infested with *D. heracliana,* and the other two sometimes show injury, but I have not yet reared an oecophorid from either one.

The species of *Depressaria* adhere rather closely to a pattern of attack in which the young umbels are webbed by the larva or several larvae. Pupation takes place in a hollow stalk of the host or in debris at or near the base of the plant. Some exceptional variations are discussed under the pertinent species.

On plate 5, figure 1, are figured characteristic examples of umbels of *Oenanthe sarmentosa* in which the rays are drawn together and the inflorescence is distorted by the larvae of *Depressaria nervosa.* In figure 2 of the same plate is an illustration of an umbel of *Lomatium dissectum multifidum* webbed and damaged by larvae of *D. leptotaeniae.* When this photograph was taken the fruits were maturing, but the typical damage is well illustrated.

The larvae of *Agonopterix* species are chiefly leafrollers, but occasionally they web the rays and feed in the fruits. As far as I know the larvae never pupate in a hollow stalk.

Above I have discussed the more important plants, of a rather limited region of the continent, attacked by larvae of the two genera under consideration and have indicated some of the places where they may be found. Obviously I have not shown the extent of the entire ranges of the plants, nor have I recorded all the exact localities from which the plants have been collected.

LIST OF LOCALITIES WHERE FOOD PLANTS (UMBELLIFERAE) OF DEPRESSARIA AND AGONOPTERIX WERE COLLECTED

["x" indicates infestations of larvae and/or collections that produced adults; "o" indicates no occurrence of the insects.]

Localities	Food plants *	Larvae	Adults
1. Oelwein, Iowa	*Zizia aurea* (L.) Koch	x	o
2. Quinn, S. Dak.	*Lomatium* sp.	x	o
3. Ten Sleep, Wyo.	*Pteryxia terebinthina calcarea* (M. E. Jones)	x	x
4. Deer Lodge, Mont.	*Lomatium dissectum multifidum* (Nutt.) M. & C.	x	x
5. Alberton, Mont.	*Lomatium ambiguum* (Nutt.) C. & R.	x	x
	Lomatium macrocarpum (H. & A.) C. & R.	x	x
6. Hooper, Wash.	*Cicuta occidentalis* Greene	o	o
	Conium maculatum L.	o	o
7. Washtucna, Wash.	do.	o	o
8. 8 miles west of Moses Lake, Wash.	*Pteryxia terebinthina foeniculacea* (T. & G.) Math.	x	x
9. 10 miles east of Burke, Wash.	do.	x	x
10. Pomona, Yakima County, Wash.	*Lomatium* sp.	o	o
11. Cliffdell, Kittitas County, Wash.	*Lomatium triternatum macrocarpum* (C. & R.) Math.	x	x
	Osmorhiza occidentalis (Nutt.) Torr.	o	o
12. Sawmill Flat, Kittitas County, Wash.	*Lomatium triternatum macrocarpum*	x	x
13. Marietta, Whatcom County, Wash.	*Oenanthe sarmentosa* Presl.	o	o
14. Lake Samish, Whatcom County, Wash.	do.	x	x
15. Bellingham, Wash.	do. (Numerous observations)	o	o
16. Lawrence, Whatcom County, Wash.	*Oenanthe sarmentosa*	x	x
17. Blaine, Wash.	do.	x	x
	Heracleum lanatum Michx.	o	o
18. Ferndale, Wash.	*Oenanthe sarmentosa*	o	o
19. Birch Bay, Whatcom County, Wash.	do.	x	x
	Lomatium nudicaule (Pursh) C. & R.	o	o
20. Hamilton, Skagit County, Wash.	*Oenanthe sarmentosa*	x	x
21. Vogler Lake, Skagit County, Wash.	do.	o	o
	Osmorhiza chilensis Hook. & Arn.	o	o
22. Toad Lake, Whatcom County, Wash.	do.	o	o
	Heracleum lanatum	o	o
	Oenanthe sarmentosa	x	x

---

* Botanical authority is given only after the first occurrence of the name.

Localities	Food plants *	Larvae	Adults
23. Fazon Lake, Whatcom County, Wash.	*Oenanthe sarmentosa*	o	o
	Cicuta douglasii (DC.) C. & R.	x	x
24. Olympia, Wash.	*Oenanthe sarmentosa*	o	o
25. Centralia, Wash.	do.	o	o
26. Chehalis, Wash.	do.	o	o
27. Kelso, Wash.	*Daucus carota* L.	o	o
28. Oregon City, Oreg.	*Oenanthe sarmentosa*	o	o
	Osmorhiza chilensis	o	o
	Heracleum lanatum	o	o
29. Molalla, Oreg.	*Oenanthe sarmentosa*	o	o
30. Wilhoits Springs, Oreg.	do.	x	x
31. Clackamas River, Oreg.	*Ligusticum apiifolium* (Nutt.) A. Gray	x	x
32. Depoe Bay, Oreg.	*Angelica hendersonii* C. & R.	x	x
	Conioselinum chinense (L.) BSP	x	x
	Daucus pusillus Michx.	o	o
	Oenanthe sarmentosa	o	o
	Heracleum lanatum	o	o
33. Hogarty Creek, Oreg.	*Oenanthe sarmentosa*	o	o
34. Whale Cove, Depoe Bay, Oreg.	*Conioselinum chinense*	x	x
	Oenanthe sarmentosa	o	o
35. Beverly Beach, Oreg.	do.	o	o
36. Agate Beach, Oreg.	do.	o	o
37. Siletz River, Oreg.	*Angelica lucida* (L.)	x	x
38. Toledo, Wash.	*Oenanthe sarmentosa*	o	o
39. Tumwater, Wash.	do.	o	o
40. 3 miles west of Monroe, Wash.	*Angelica arguta* Nutt.	o	o
41. Tye River, U. S. Highway 2, Wash.	do.	o	o
	Heracleum lanatum	o	o
42. Rayrock Springs, Stephens Pass, Wash.	*Angelica arguta*	x	x
	Osmorhiza chilensis	o	o
43. Winton, Wash.	*Angelica canbyi* C. & R.	o	o
	Cicuta douglasii	o	o
	Heracleum lanatum	o	o
44. Azwell, Wash.	No umbels found	o	o
45. Carlton, Wash.	*Cicuta occidentalis*	o	o
46. Billy Goat, Okanogan County, Wash.	*Osmorhiza occidentalis*	x	x
47. 2 miles south of Billy Goat, Wash.	*Osmorhiza chilensis*	x	x
48. Eight Mile Creek Guard Station, Okanogan County, Wash.	*Angelica arguta*	o	o
49. Sherman Guard Station, Okanogan County, Wash.	do.	o	o
50. Winthrop, Wash.	*Cicuta occidentalis*	o	o
51. Robinson Creek, Okanogan County, Highway 16, Wash.	do.	o	o

---

* Botanical authority is given only after the first occurrence of the name.

Localities	Food plants *	Larvae	Adults
52. Harts Pass, Okanogan County, Wash.	*Lomatium brandegei* (C. & R.) F. Macbr.	o	o
	Lomatium geyeri (S. Wats.) C. & R.	o	o
	Lomatium ambiguum	o	o
	Osmorhiza occidentalis	o	o
	Angelica arguta	o	o
53. Lower Harts Pass, Okanogan County, Wash.	*Heracleum lanatum*	o	o
	Angelica arguta	o	o
	Ligusticum sp.	o	o
54. Slate Peak, Whatcom County, Wash.	*Lomatium ambiguum*	x	x
	Lomatium geyeri	o	o
	Lomatium brandegei	x	x
	Lomatium dissectum (Nutt.) Math. & C.	o	o
55. Ingalls Creek, Blewett Pass, Wash.	*Angelica arguta*	o	o
56. Peshastin Creek, Blewett Pass, Wash.	do.	o	o
57. Touchet, Wash.	*Daucus carota*	o	o
58. Freewater, Oreg.	*Cicuta occidentalis*	o	o
59. Langdon Lake, Oreg.	*Angelica arguta*	o	o
60. 16.5 miles north of Elgin, Oreg.	do.	o	o
61. 10 miles north of Elgin, Oreg.	do.	o	o
62. Minam, Oreg., Wallowa River	*Cicuta occidentalis*	o	o
63. Rock Creek, Highway 82, Oreg.	do.	x	x
64. Joseph, Oreg.	*Heracleum lanatum*	o	o
65. Wallowa Lake, Oreg.	do.	o	o
	Angelica arguta	o	o
66. Aneroid Lake Trail, Oreg.	do.	o	o
	Osmorhiza occidentalis	o	o
	Ligusticum sp.	o	o
	Heracleum lanatum	o	o
67. Oregon City, Oreg.	*Oenanthe sarmentosa*	o	o
	Osmorhiza chilensis	o	o
68. Bridal Veil Falls, Oreg.	*Lomatium angustatum* (Coult. & Rose) St. John	x	o
	Lomatium triternatum macrocarpum	o	o
	Lomatium dissectum multifidum	o	o
	Heracleum lanatum	x	x
	Angelica sp.	o	o
	Daucus carota (injury only detected)	o	o
	Oenanthe sarmentosa	o	o
	Osmorhiza chilensis	o	o
69. Oneonta Gorge, Oreg.	*Lomatium angustatum*	o	o
70. Lake Padden, Whatcom County, Wash.	*Cicuta douglasii*	x	x
	Sium suave Walt.	o	o

---

* Botanical authority is given only after the first occurrence of the name.

Localities	Food plants *	Larvae	Adults
71. Waterville, Wash.	*Cicuta occidentalis*	x	x
72. Coeur d'Alene Lake, Idaho	*Lomatium dissectum multifidum*	o	o
73. Denna Mora Creek, U. S. Highway 10, Mont.	*Ligusticum canbyi* C. & R. *Angelica arguta*	o o	o o
74. Clinton, Mont.	*Sium suave*	o	o
75. McDonald Pass, Mont.	*Angelica arguta* *Heracleum lanatum* *Osmorhiza occidentalis*	x o	x o
76. Jackson Lake, Wyo.	*Ligusticum filicinum* S. Wats.	o	o
77. Togwotte Pass, Wyo.	do.	x	o
78. 25 miles southeast of Lander, Wyo.	*Lomatium* sp.	o	o
79. 13 miles east of North Platte, Nebr.	*Cicuta maculata* L.	x	x
80. Lucas, Iowa	do.	x	x

* Botanical authority is given only after the first occurrence of the name.

As pointed out at the beginning of this discussion, the object of the field work undertaken was to endeavor to induce larvae to accept substitute foods, and to rear the moths. On page 9 is a chart in which I have tabulated the food plants and the species of *Depressaria* and *Agonopterix* that have been reared to date. It will be noticed at once that the differences in feeding habits between the species of the two genera follow different patterns. The three species of *Agonopterix* are definitely polyphagous, one species feeding on no less than 14 species of umbels. The species of *Depressaria,* on the other hand, show a *distinct* monophagous tendency, although three species feed on more than one plant. Even so, the range of acceptance is very narrow and, indeed, though not lethal, may be accidental.

The first attempt to induce larvae to feed on substitute food was made in 1933 when larvae of *Depressaria multifidae* were offered, in place of *Lomatium grayi,* the normal food, *L. dissectum multifidum,* which they refused. In 1946,[3] however, a series of moths was reared from *L. columbianum* which are indistinguishable from a long series of *multifidae.*

In the summer of 1950 numerous attempts at substitution of foods were made, but without success. Larvae of *D. betina* found on *L. triternatum macrocarpum,* the normal food plant, were offered *Osmorhiza chilensis.* Most larvae refused this substitute, but some ate it voraciously; all died. Although *L. triternatum macrocarpum* is the normal food, occasionally scattered larvae from which moths were reared were found on *L. dissectum* and *L. columbianum.* All

---

[3] Clarke, J. F. Gates, Journ. Washington Acad. Sci., vol. 37, p. 13, 1947.

these species of *Lomatium* are frequently found growing in close association.

Depressaria nervosa was found in great abundance in the extreme western parts of Whatcom and Skagit Counties, Wash., and less commonly in one locality in Oregon, feeding on *Oenanthe sarmentosa.* Larvae of this moth feed on a species of *Oenanthe* in Europe and, undoubtedly, in Asia. At Fazon Lake and Lake Padden, both in Whatcom County, Wash., I found a few larvae on *Cicuta douglasii,* which was quite acceptable to them, and they completed their metamorphosis. The food plant at Lake Padden was growing intermingled with *Sium suave,* which the larvae did not infest and which was refused by them when offered as a substitute. Larvae of *nervosa* were

	DEPRESSARIA																				*AGONOPTERIX*		
	heracliana	*juliella*	*eleanorae*	*cinereocostella*	*whitmani*	*leptotaeniae*	*yakimae*	*multifidae*	*angustati*	*togata*	*constancei*	*betina*	*schellbachi*	*moya*	*besma*	*thustra*	*angelicivora*	*armata*	*pteryxiphaga*	*nervosa*	*oregonensis*	*rosaciliella*	*muricolorella*
Angelica arguta																	x					x	
hendersonii																					x	x	
lucida																					x		
Cicuta douglasii																				x			
maculata				x																			
occidentalis		x	x																				
Conioselinum chinense																						x	
Daucus carota	?																						
Eryngium vaseyi																					x		
Heracleum lanatum	x																						
Ligusticum apiifolium																					x	x	
Lomatium ambiguum																x							
angustatum									x														
brandegei																		x					
californicum											x												
caruifolium																					x		
columbianum								x				x											
dissectum												x											
dissectum multifidum						x																	
grayi								x															x
macdougali													x										
macrocarpum					x																		x
marginatum																					x		
nudicaule																					x		
triternatum macrocarpum												x				x							
utriculatum															x						x		
vaginatum														x									
Oenanthe sarmentosa																				x	x	x	
Osmorhiza chilensis																						x	
occidentalis																						x	
Pastinacea sativa	x																						
Pteryxia terebinthina calcarea																			x				
terebinthina foeniculacea							x																
Sanicula bipinnata																					x		
bipinnatifida																					x		
laciniata																					x		
nevadensis																					x		
tuberosa																					x		

offered umbels of *Angelica arguta* and *Cicuta occidentalis,* which also were refused.

At Slate Peak, Whatcom County, Wash., a large quantity of larvae of an undescribed species of *Depressaria* was collected on *Lomatium brandegei.* Six larvae were offered *Oenanthe sarmentosa,* six more *Osmorhiza chilensis,* but all refused these substitutes and died. One larva accepted *L. angustatum,* from the Columbia River Gorge, Oreg., but died.

Other larvae collected at Slate Peak, feeding on *L. geyeri,* were offered *L. angustatum* and *O. chilensis,* which were refused, and all the larvae died.

Larvae of *D. juliella* were found on the usual food plant, *Cicuta occidentalis,* where Oregon State Highway 82 crosses Rock Creek, Oreg., a tributary of the Wallowa River. Four of these larvae were offered *Angelica arguta,* but they refused to eat it and remained inactive in the rearing tin.

Only one substitution in the genus *Agonopterix* was attempted and that for *A. rosaciliella.* Larvae collected on *Osmorhiza chilensis* were given *O. occidentalis,* which they readily accepted. All produced moths.

We can therefore infer that in *Depressaria* a high degree of host specificity exists and that, although larvae can develop on more than one food plant when once established, no tolerance exists for substitutes in diet. It is equally clear that no host specificity exists in *Agonopterix* and that there is a correspondingly high degree of tolerance for substitutes.

AGONOPTERIX MURICOLORELLA (Busck)

Depressaria muricolorella Busck, Proc. U. S. Nat. Mus., vol. 24, p. 741, 1902.

Type—U.S.N.M. No. 6125.

Type locality.—Golden, Colo.

Food plants.—*Lomatium grayi* C. & R.[4] and *L. macrocarpum.*

Remarks.—Of this species I now have two specimens from Alberton, Mont., reared from *Lomatium macrocarpum,* recorded here for the first time. Both specimens are males and emerged July 11-13, 1950. The larvae were found feeding in the immature fruits of the host.

---

[4] Authorities for botanical names are given only for those names not appearing in the list, p. 5 *et seq.*

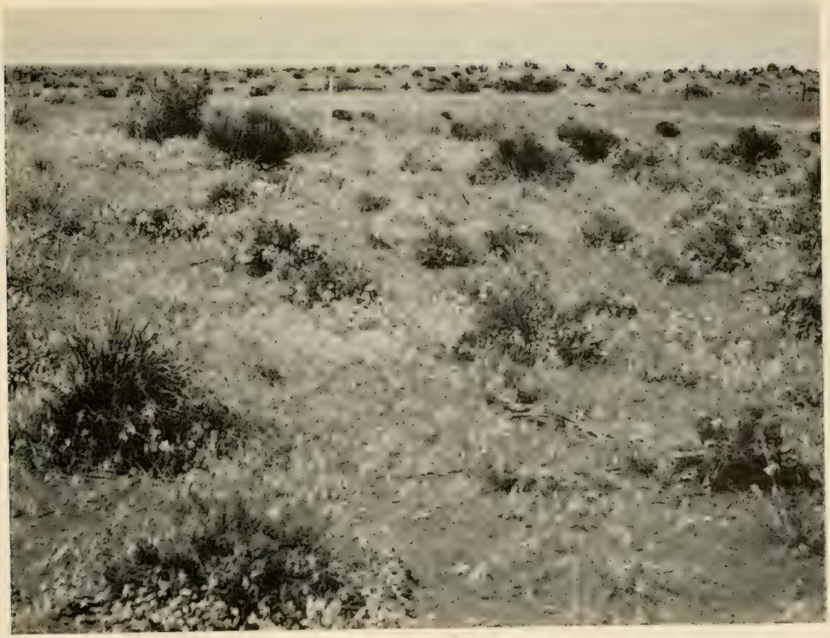


Fig. 1, upper: *Pteryxia terebinthina foeniculacea* growing in association with grasses, *Artemisia,* and *Chrysothamnus* 8 miles west of Moses Lake, Wash. Fig. 2, lower: *Pteryxia terebinthina foeniculacea,* same locality.

Fig. 1, upper: *Cicuta occidentalis* growing in association with tule, grasses, and *Typha* at Rock Creek, Oreg., at the junction with State Highway 82. Fig. 2, lower: *Cicuta occidentalis,* uninfested, at Carlton, Wash.

Fig. 1, upper: Slate Peak, Whatcom County, Wash. Four species of *Lomatium* are found on the slopes shown in the center of the photograph. These are *L. ambiguum, L. brandegei, L. dissectum,* and *L. geyeri.* Fig. 2, lower: The same locality as above but farther east. On the steep shale slopes in the upper part of the illustration the same four species of *Lomatium* listed above are found.

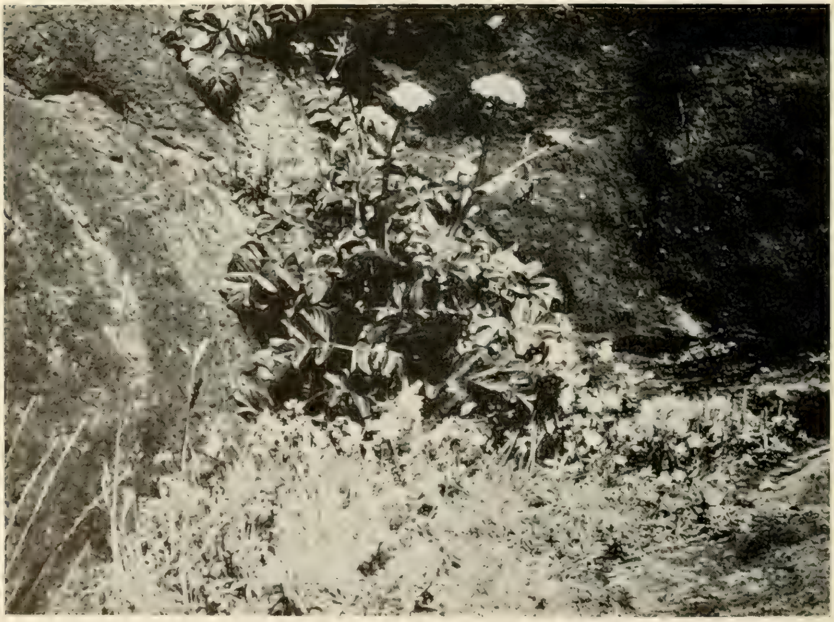
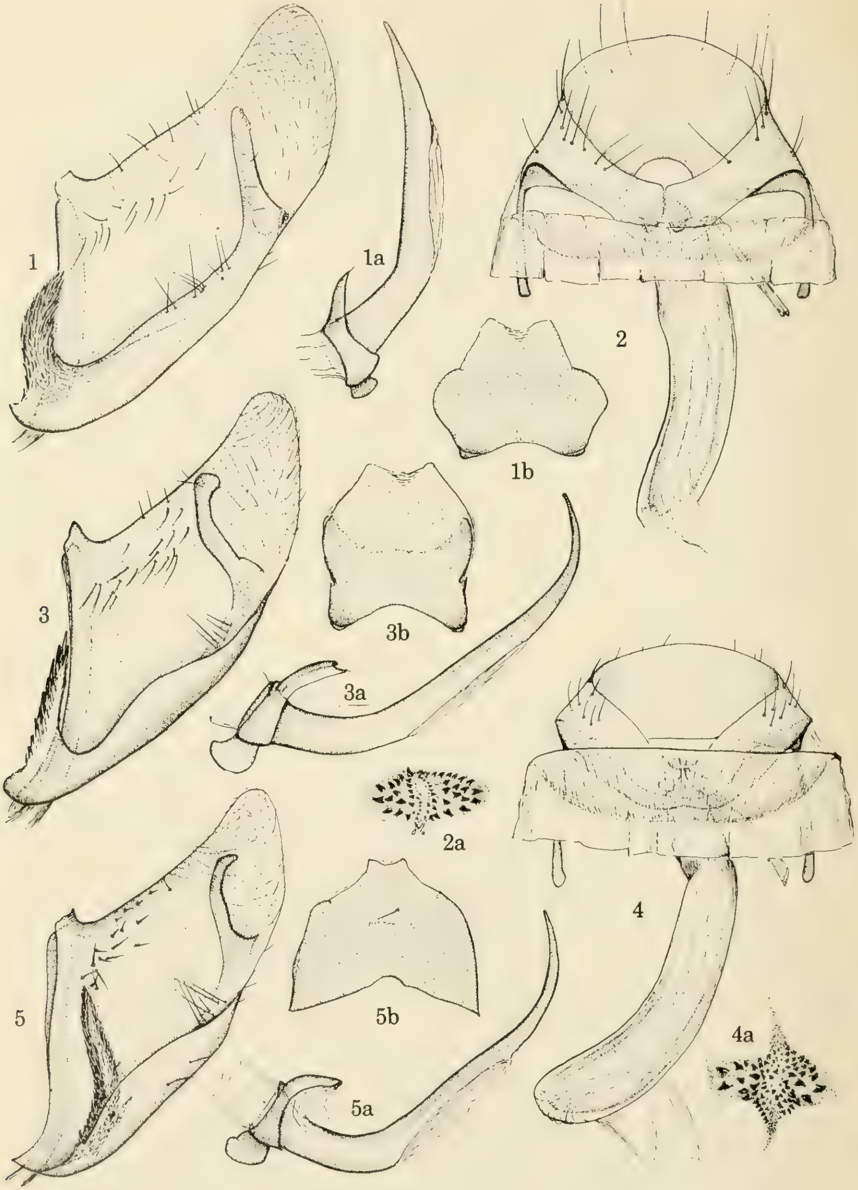


Fig. 1, upper: *Angelica hendersonii* growing along the rocks of the Oregon coast at Finistere Lodges, Depoe Bay. On the ground above *Conioselinum chinense* and *Heracleum lanatum* are abundant. Fig. 2, lower: *Angelica hendersonii* in the same locality as above.

Fig. 1, upper: *Oenanthe sarmentosa* growing in association with ferns, *Lysichiton, Mimulus,* and grasses at Lawrence, Whatcom County, Wash. Note three distorted umbels in center of photograph which are infested. Fig. 2, lower: *Lomatium dissectum multifidum* from Pullman, Wash. Note the characteristic damage and webbing done by larvae of *Depressaria leptotaeniae.*



Figs. 1-1b, *Depressaria angelicivora,* new species: 1, Right harpe; 1a, aedeagus; 1b, anellus. Figs. 2, 2a, *Depressaria angelicivora,* new species: 2, Female genitalia with ovipositor and bursa copulatrix removed; 2a, signum. Figs. 3-3b, *Depressaria pteryxiphaga,* new species: 3, Right harpe; 3a, aedeagus; 3b, anellus. Figs. 4, 4a, *Depressaria pteryxiphaga,* new species: 4, Female genitalia with ovipositor and bursa copulatrix removed; 4a, signum. Figs. 5-5b, *Depressaria armata,* new species: 5, Right harpe; 5a, aedeagus; 5b, anellus.

AGONOPTERIX OREGONENSIS Clarke

Agonopterix oregonensis Clarke, Proc. U. S. Nat. Mus., vol. 90, p. 65, 1941.

Type.—U.S.N.M. No. 52079.

Type locality.—Salem, Oreg.

Food plants.—*Angelica hendersonii, A. lucida, Eryngium vaseyi* C. & R., *Ligusticum apiifolium, Lomatium caruifolium* (H. & A.) C. & R., *L. marginatum* (Benth.) C. & R., *L. nudicaule* (Pursh) C. & R., *L. utriculatum* (Nutt.) C. & R., *Oenanthe sarmentosa, Sanicula bipinnata* H. & A., *S. bipinnatifida* Dougl., *S. laciniata* H. & A., *S. nevadensis* S. Wats., and *S. tuberosa* Torr.

Remarks.—Only four of the food plants listed above, *A. hendersonii, A. lucida, Ligusticum apiifolium,* and *Oenanthe sarmentosa,* are recorded here for the first time; the others, recorded previously by me,[5] are entered for completeness.

The localities for the specimens reared in 1950 are as follows: Oregon: Depoe Bay, 5 ♂♂, 2 ♀♀ (July 26-28, 1950); Siletz River, 2 miles east U. S. Highway 101, 2 ♂♂ (August 3, 1950). Washington: Lawrence, Whatcom County, ♀ (July 22, 1950); Toad Lake, Whatcom County, ♂ (July 21, 1950).

AGONOPTERIX ROSACILIELLA (Busck)

Depressaria rosaciliella Busck, Proc. U. S. Nat. Mus., vol. 27, p. 763, 1904.

Type.—U.S.N.M. No. 7815.

Type locality.—"Camp Watson," Oreg.

Food plants.—*Angelica arguta, A. hendersonii, Conioselium chinense, Ligusticum apiifolium, Oenanthe sarmentosa, Osmorhiza chilensis,* and *O. occidentalis.*

Remarks.—In my revision of this family (p. 84) [6] I recorded the food plant of this species as *Osmorhiza occidentalis* and stated that the larvae of *rosaciliella* were not found on *O. chilensis.* On a preceding page of the present paper I have indicated that the species is found on both plants. I have before me 19 specimens of *rosaciliella* reared during the summer of 1950 from the above list of hosts. These show a wide degree of variation, including specimens that match the Blue Mountains material recorded previously (p. 84) [6] and also moths that are of the exact color and contrasting markings as the series

---

[5] Clarke J. F. Gates, Journ. Washington Acad. Sci., vol. 37, p. 3, 1947.

[6] Clarke, J. F. Gates, Revision of the North American moths of the family Oecophoridae, with descriptions of new genera and species. Proc. U. S. Nat. Mus., vol. 90, pp. 33-286, pls. 1-48, 1941.

of 90 specimens I recorded from Skyline Ridge, Whatcom County, as *A. r. echinopanicis,* which were reared on *Echinopanax horridum* (p. 86) and which I described as a food-plant race of *rosaciliella.* There is no doubt that all these color variations represent entities of a single species. There appears to be no justification for the racial designation of *echinopanicis,* although those who wish to use this name for the population feeding on *E. horridum* may do so for this contrastingly marked form.

The localities for the moths reared in 1950 are as follows: Oregon: Clackamas River, 15 miles east of Estacada, 2 ♂♂ (July 28, 1950), ♀ (July 27, 1950); Depoe Bay, 3 ♂♂ (July 27-August 2, 1950), 5 ♀♀ (July 28-August 2, 1950). Washington: Billy Goat, Okanogan County, 2 ♂♂, 4 ♀♀ (July 29-August 2, 1950); Lawrence, Whatcom County, ♀ (July 24, 1950); Rayrock Springs, Stephens Pass, ♀ (August 2, 1950).

DEPRESSARIA CINEREOCOSTELLA Clemens

Depressaria cinereocostella Clemens, Proc. Ent. Soc. Philadelphia, vol. 2, p. 422, 1864.

Type.—In the Academy of Natural Sciences of Philadelphia.

Type locality.—"Virginia."

Remarks.—In my revision I listed three food plants for this species, *Carum carvi* L., *Sium lineare* Michx., and *Ligusticum scoticum* L. It is impossible to check the identities of the plants from which the specimens are supposed to have been reared, but it seems certain that there has been some confusion regarding some of the identifications of the plants made many years ago, before the Umbelliferae were properly revised by Mathias and Constance. One of the plants listed above, *S. lineare,* is a synonym of *S. suave* Walt., as is also *S. cicutaefolium* Benth. & Hook. I have before me a series of *cinereocostella* labeled "Rf. *Sium cicutaefolium,*" which I collected at the junction of South River and U. S. Highway 50, Maryland. These bear emergence dates of August 11-20, 1939. The identity of this plant has not been verified by competent authority.

In August 1950 larvae of *cinereocostella* were encountered commonly in several places in Nebraska and Iowa, feeding in the umbels of *Cicuta maculata.* I have before me a series of 12 males and 12 females from 13 miles east of North Platte, Nebr., and 7 males and 6 females from Lucas, Iowa. Emergence dates range from August 8-21, 1950.

The larvae of the South River specimens pupated in the hollow stalks of the host, a habit found commonly among Depressariae. The larvae of the Nebraska and Iowa specimens, however, pupate in a tightly webbed umbel. Actually the rays of the umbels are left free, but the flowers are webbed into a compact mass.

Despite these differences in habits I can find no structural or colorational differences that suggest specific separation.

DEPRESSARIA NERVOSA Haworth

Depressaria nervosa HAWORTH, Lepidoptera Britannica, vol. 3, p. 560, 1811.

Type.—In the British Museum (Natural History).

Type locality.—London, England.

Food plants.—*Oenanthe crocata* L., *O. sarmentosa,* and *Cicuta douglasii.*

Remarks.—Walsingham[7] recorded this species from "Southern Oregon" in 1881, but there has always been some doubt about the accuracy of his identification, and the name of the European *nervosa* has been dropped from the North American lists. Busck[8] believed that Walsingham's specimens were probably referable to *D. juliella* Busck, and the name *nervosa* was omitted from Busck's revision of the family.[9] The similarity between *nervosa* and *juliella* is apparent, but the latter is much brighter and lighter than the former and their food plants are different.

In England *D. nervosa* larvae feed in the umbels of *Oenanthe crocata* and in western North America in the umbels and on the leaves of *O. sarmentosa* and *Cicuta douglasii.* Despite these differences in the food plants there is no doubt that the American specimens are referable to *nervosa,* although the Washington and Oregon series might warrant subspecific designation.

I have before me a reared series of 173 specimens as follows: Oregon: Clackamas County, Wilhoits Springs, 3 ♂♂, 3 ♀♀. Emergence dates, July 25-29, 1950. Washington: Skagit County, Hamilton, ♂, 4 ♀♀; Whatcom County, Birch Bay, 3 ♂♂, 6 ♀♀; Blaine, ♂; Fazon Lake, ♂, 2 ♀♀; Lake Padden, 2 ♂♂, ♀; Lawrence, 72 ♂♂, 57 ♀♀; Samish Lake, 5 ♂♂, 8 ♀♀; Toad Lake, 2 ♂♂, ♀. In addition to the above there are 24 specimens deposited in the British Museum (Natural History).

The emergence dates range from July 17 to August 18, 1950. The August dates are for specimens collected at Lake Padden and reared from *Cicuta douglasii.*

---

[7] Proc. Zool. Soc. London, 1881, p. 317.

[8] Proc. Ent. Soc. Washington, vol. 9, p. 91, 1908.

[9] Proc. U. S. Nat. Mus., vol. 35, pp. 187-207, 1908.

I am indebted to John Bradley, of the British Museum, who has kindly compared some of the American specimens with the European series in the British Museum collections and who has confirmed my identification. The European specimens in the U. S. National Museum are lighter and more olivaceous than the moths from Oregon and Washington, but the latter vary from olivaceous to rather bright red although the majority are predominantly brownish red.

DEPRESSARIA WHITMANI Clarke

Depressaria whitmani CLARKE, Proc. U. S. Nat. Mus., vol. 90, p. 182, pl. 36, figs. 200, 200a; pl. 48, fig. 286, 1941.

Type.—U.S.N.M. No. 52083.

Type locality.—Snake River, Whitman County, Wash., opposite Clarkston.

Food plant.—*Lomatium macrocarpum.*

Remarks.—In addition to the type series, I now have a female, reared from the normal food plant, from Montana. The larva was collected 3 miles east of Alberton, on U. S. Highway 10, feeding in the fruits of the host on June 15 and the moth emerged July 7, 1950. The food plant was growing on rocky ground in association with pine, grasses, and balsam root. The occurrence of this species in Montana extends the range over 200 miles east of the type locality.

DEPRESSARIA YAKIMAE Clarke

Depressaria yakimae CLARKE, Proc. U. S. Nat. Mus., vol. 90, p. 185, 1941.

Type.—U.S.N.M. No. 52073.

Type locality.—Yakima, Yakima County, Wash.

Food plant.—*Pteryxia terebinthina foeniculacea.*

Remarks.—When I described this species I predicted that the larva would be found on some species of *Lomatium,* but I have now found *yakimae* attached to *Pteryxia,* a closely related genus.

I now have six reared specimens that were obtained from pupae, the larval stage having passed by mid-June. The pupae were collected at a point 8 miles west of Moses Lake, Wash., on U. S. Highway 10, and also 10 miles east of Burke, Grant County, Wash., on U. S. Highway 10. The dates were June 17 and 21, 1950, respectively. Moths began to emerge June 18 and the last appeared June 23, 1950.

The larva of this species spins a tough though rather loose cocoon between the rays of the flowers where pupation takes place. This is a departure from the usual habit for pupation in this group and is parallel only to *cinereocostella* among the known species. The pupa is always found with the ventral surface down and the caudal end elevated, sometimes almost to the vertical position.

DEPRESSARIA ANGELICIVORA, new species

Plate 6, figures 1-1b, 2-2a

Description.—Alar expanse, 25-27 mm.

Labial palpus with second segment creamy white strongly tinged with pink inwardly, with scattered fuscous scales outwardly and the brush suffused with fuscous; third segment fuscous sparsely irrorate with pink scales and with pink tip. Antenna fuscous except underside of scape, which is pink, and underside of about one-third of shaft, which is pink to cream color. Head and thorax whitish ocherous with admixture of fuscous on vertex and anteriorly on thorax and tegula. Forewing with basal third blackish fuscous shading to paler fuscous at apex, streaked with blackish fuscous along veins in some specimens and costa edged with pink, the whole with a washed, faded appearance; from costa at middle an inwardly oblique whitish ocherous line to middle of cell continuing as an outwardly oblique though more indefinite line of the same color to middorsum; from slightly beyond inception of the above line a similar, outwardly oblique line to apical fourth at center of wing, thence inwardly oblique to slightly before tornus; these two lines are shaded and streaked with pale-brownish scaling and outline a more or less diamond-shaped area in center of wing; at end of cell a whitish ocherous spot; from apical third of costa around termen to middorsum a somewhat broken blackish fuscous line; cilia fuscous basally, lighter distally with some pinkish suffusion. Hindwing whitish basally shading to fuscous around margins; cilia pale yellowish fuscous with fuscous basal line and suffused with pink. Legs whitish ocherous banded and suffused with fuscous and pink. Abdomen whitish ocherous suffused with fuscous above and with blackish fuscous longitudinal lateral band beneath.

Male genitalia.—Similar to other members of this group, but the basal process of sacculus about as long as half the width of harpe at base and the clasper straight, digitate.

Female genitalia.—Genital plate narrow and anterior pockets shallow; sclerotized section of ductus bursae very short, about one-fourth total length.

Type.—U.S.N.M. No. 61133.

Type locality.—McDonald Pass, 14 miles west of Helena, Mont. (6,100 feet).

Food plant.—*Angelica arguta.*

Remarks.—Described from the type ♂, 5 ♂ and 3 ♀ paratypes, all from the type locality. Emergence dates August 9-12, 1950. Paratypes in the U. S. National Museum and the British Museum (Natural History).

The food plant of this species is widespread, but the only examples found infested were the specimens from which this series of moths was reared. The plants were growing in moist ground at a spring with its resulting drainage, and were growing in association with *Heracleum, Mimulus, Epilobium, Alnus,* and other species comprising a lush growth.

The larva of this species attacks the young umbels before they have opened completely and causes great distortion and discoloration of the inflorescence. Pupation occurs in the leaf bracts near the main stalk of the host. This is a departure from the usual habit of members of this group, which almost always pupate in debris near the base of the plant or in the hollow stalks. As many as five pupae were found in a single bract, each larva having constructed a heavy web before pupation.

In the key to species in my revision, this species runs to *betulella* by reason of the longitudinal stripes on the ventral side of the abdomen. However, *angelicivora* belongs in the *angustati-multifidae* complex and can be separated from all the species of this group by the washed-out, faded appearance of the forewing. The male genitalia of *angelicivora* place it nearest *schellbachi,* but it differs from the latter by the shorter basal process of the sacculus, which is a little more than half the length of that in *schellbachi,* and by the straight clasper as compared to the curved clasper of *schellbachi.* The aedeagus of *angelicivora* is more like those of *leptotaeniae* and *yakimae.* The female genitalia are similar to *thustra,* but the sclerotized section of the ductus bursae is slightly more than half as long.

DEPRESSARIA PTERYXIPHAGA, new species

Plate 6, figures 3-3b, 4-4a

Description.—Alar expanse, 18-20 mm.

Labial palpus with second segment ocherous-white, suffused with pinkish in most specimens, marked with fuscous and pink-tipped fuscous scales exteriorly and in the brush; third segment blackish fuscous, apex ocherous-white. Antenna scape blackish fuscous, shaft grayish fuscous with paler annulations. Head and thorax ocherous-white to ocherous with a strong pinkish suffusion in most specimens;

thorax anteriorly, and tegula basally, edged with fuscous. Forewing blackish fuscous basally shading to fuscous apically; extreme edge of costa ocherous-white to ocherous suffused with pinkish; slightly before middle of costa and at apical third of costa large blotches of the same color with similar, smaller spot at base of costa; at end of cell an ocherous-white to ocherous discal spot followed by a slender black dash; at basal third, on vein 11, a black spot followed by an oblique dash of the same color on vein 10; from apical third of costa, around termen to tornus, an indistinct series of small black spots; cilia grayish fuscous, darker basally. Hindwing whitish basally shading to pale fuscous around margins; cilia light buff to grayish around apex with narrow, pale-fuscous subbasal line; sometimes cilia suffused with pinkish. Legs ocherous-white marked and banded with fuscous and paler areas sometimes pinkish. Abdomen ocherous-white suffused with grayish above and strongly marked fuscous beneath, especially laterally.

Male genitalia.—Similar to the *angustati-multifidae* group but with straight basal process from sacculus with few dentate processes and with distal end of clasper dilated.

Female genitalia.—Genital plate narrow and strongly sclerotized along anterior edge; anterior pocket narrow; ductus bursae sclerotized for about one-third its length.

Type.—U.S.N.M. No. 61134.

Type locality.—Ten Sleep, Wyo.

Food plant.—*Pteryxia terebinthina calcarea.*

Remarks.—Described from the type ♂, 2 ♂ and 4 ♀ paratypes, all from the type locality. Emergence dates July 5-9, 1950. Paratypes in the U. S. National Museum and the British Museum (Natural History).

The food plant of this species is common in the Ten Sleep Canyon, just east of Ten Sleep, Wyo., and the actual locality in which the larvae of this species were collected was at the foot of the canyon alongside U. S. Highway 16 at 4,600 feet. Here the plant grows in association with *Artemisia, Balsamorhiza,* and grasses on the steep slopes of the sides of the canyon.

The larva of *pteryxiphaga* feeds on the leaves of the food plant and webs them together. Larvae were collected June 13, 1950, and pupation began June 16, 1950.

A brief color description follows: Larva pale yellowish green with dorsal and broad subdorsal longitudinal stripes gray-green; tubercles pale whitish green with brown at insertion of setae. Head pale yellowish brown with sparse brown mottling posteriorly and the sutures dark brown. Thoracic shield yellowish narrowly edged with brown laterally; on each side, dorsolaterally, a few dark-brown spots. Anal plate yellowish green.

In my key this species runs to the *yakimae-leptotaeniae* couplet but is easily distinguished from both by the pale costal blotches. Occasional specimens of *pteryxiphaga* lack the pink costal edge, in which cases the examples would run to the *angustati-multifidae* couplet. In such examples the genitalia must be used for identification. In all cases, as a matter of fact, the genitalia should be used in determination of species of this complex.

The genitalia of this species suggest a close affinity with *multifidae* on the one hand and *thustra* on the other. The twisted basal process of the sacculus of *thustra* immediately separates *pteryxiphaga* from it, and the latter can be distinguished from *multifidae* by the straight basal process of sacculus. The female of *pteryxiphaga* can be separated from *multifidae* by the narrow genital plate and shallow anterior pocket and from *thustra* by the strongly sclerotized anterior edge of the genital plate and the shorter sclerotized section of ductus bursae.

DEPRESSARIA LEPTOTAENIAE Clarke

Depressaria leptotaeniae Clarke, Can. Ent., vol. 65, p. 87, pl. 4, 1933.

Type.—U.S.N.M. No. 44742.

Type locality.—Pullman, Wash.

Food plant.—*Leptotaenia dissectum multifidum* (Nutt.) M. and C.

Remarks.—Larvae of this species were collected on the host on a hillside 11 miles northwest of Deer Lodge, Mont., on June 15. Pupation began the following day, and the moths, one male and two females, emerged July 8-9, 1950. The food plant was growing in association with sagebrush, balsamroot, grasses, and other prairie plants on open ground.

This species has not been recorded previously in Montana, and the distribution is thus extended eastward considerably.

DEPRESSARIA THUSTRA Clarke

Depressaria thustra Clarke, Journ. Washington Acad. Sci., vol. 37, p. 15, figs. 7-7a, 14, 1947.

Type.—U.S.N.M. No. 58009.

Type locality.—Gilmer, Klickitat County, Wash.

Food plants.—*Lomatium triternatum macrocarpum* and *L. ambiguum.*

Remarks.—Originally I described this species from the first-named food plant from a low altitude. I have before me, however, a single specimen from *L. ambiguum,* from Slate Peak, Whatcom County, Wash., 6,500 feet, which is indistinguishable from the original series. The twisted basal process of the sacculus is characteristic and distinguishes *thustra* from all other described species.

The Slate Peak specimen emerged August 4, 1950; larva collected July 18, 1950.

The food plant (*ambiguum*) of this species was found at Harts Pass and on the rocky slopes of Slate Peak (pl. 3), but larvae were found only at the latter place where they were observed tying and feeding in the umbels.

When the supply of the original food plant became exhausted I substituted *L. angustatum* and *O. chilensis,* but both of these substitutes were refused and the larvae died.

DEPRESSARIA ARMATA, new species

Plate 6, figures 5-5b

Description.—Alar expanse, 17 mm.

Labial palpus with second segment light buff with moderate grayish-fuscous scaling in brush; exteriorly and interiorly shining silvery fuscous; third segment grayish fuscous, buff-tipped. Antenna fuscous; underside of scape and proximal third of shaft shining silvery fuscous. Head and thorax buff mixed with grayish fuscous; anterior edge and posterior tip of thorax and basal third of tegula grayish fuscous. Forewing grayish fuscous becoming considerably lighter toward apex; at basal third, in cell, a longitudinal blackish dash followed, at end of cell, by a blackish-edged whitish-buff spot; at three-fifths of costa an obscure blackish subquadrate spot; from apical fifth of costa, around termen to tornus, a series of obscure blackish spots; cilia grayish with a darker basal band. Hindwing very pale basally shading to light grayish fuscous at apex; cilia grayish with darker subbasal band. Legs whitish buff shaded and banded with grayish fuscous.

Male genitalia.—Basal process armed with fine, spinulate spines except at base where they are shorter and coarser. Anellus very broad, broader than long.

Female genitalia.— Female unknown.

Type.—U.S.N.M. No. 61135.

Type locality.—Slate Peak, Whatcom County, Wash., 6,500 feet.

Food plant.—Lomatium brandegei.

Remarks.—Described from the unique type male. The adult emerged August 4, 1950.

This species is nearly related to *angustati,* and keys to the same place in my key, but there are abundant points of difference between them. The costal spot and the lack of any transverse fasciae on the forewing of *armata* immediately distinguish it from *angustati.* The basal process of the sacculus of *armata* is turned away from the cucullus and that of *angustati* is turned toward it. The habits of the two are also different, the larva of *angustati* feeding in the leaves and the larva of *armata* inhabiting the umbels.

The larvae of *armata* were found abundantly at between 6,400 and 6,700 feet, being absent at Harts Pass at 6,200 feet and absent above 6,700 feet.

Although a considerable quantity of larvae were collected, only one moth was obtained owing to lack of sufficient food plant and to substitution attempts. Larvae were offered *Oenanthe sarmentosa* and *Osmorhiza chilensis,* which they refused, and all died. Others were offered *L. angustatum,* but only one accepted this substitute and all died.

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 117, NUMBER 8

THE SAND CRAB EMERITA TALPOIDA (SAY) AND SOME OF ITS RELATIVES

BY
R. E. SNODGRASS

(Publication 4086)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
APRIL 15, 1952

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

THE SAND CRAB EMERITA TALPOIDA (SAY) AND SOME OF ITS RELATIVES

By R. E. Snodgrass

CONTENTS

INTRODUCTION

Emerita talpoida (Say) of the Atlantic coast of the United States, and several related species found elsewhere, are small anomuran crabs of the family Hippidae, which are of particular interest because of their total adaptation to a special way of living and to what is probably, among the arthropods, a unique method of feeding. The Emeritas bury themselves with the head end up, "facing" the ocean, in the wet sand of sloping beaches covered by the wash of the waves. Here they extend their long, plumose antennae to collect from the descending water over them whatever food material may be carried in suspension, which is then transferred to the mouth parts by a ventral flexing and folding of the antennae, which in turn are enclosed by the large platelike meropodites of the third maxillipeds. The mandibles are much reduced and are entirely functionless as organs of feeding. The antennal method of food gathering by *Emerita* was first described by Weymouth and Richardson (1912) for the west-coast species *analoga.*

Smith (1877) in his study of *Emerita* (*Hippa*) *talpoida* of the Atlantic coast did not recognize the feeding function of the antennae, which he thought were used for cleaning the legs; finding the stomach full of sand, he concluded that the crabs swallowed sand for whatever nutritive matter it might contain. The essential likeness in structure of the several *Emerita* species, however, can leave no doubt that they all feed in the same manner. Their habits alone would suggest that the antennae are food-collecting organs, and the mouth is so closely shut in by the maxilliped plates that a direct ingestion of sand would hardly be possible.

It is surprising to find that no other members of the hippid family are equipped for antennal feeding, though they are all sand burrowing in their habits. In the two other principal genera of the family, *Hippa* and *Mastigocheirus,* the mandibles are even more reduced than in *Emerita,* but the second antennae have short, simple flagella in no way adapted to food gathering. In both these genera, however, the inner lobes of the first maxillae are developed into a pair of strong, toothed jaws closing beneath the mouth. Evidently, then, the functional loss of the mandibles by the hippids has been compensated in two ways: in *Hippa* and *Mastigocheirus* by the formation of substitute jaws from the maxillulae; in *Emerita* by the development of the antennal flagella into food-gathering organs. One is tempted to wonder why the adult hippids lost their mandibles in the first place, and how they fed while making adjustments to their present structure. The nature of the food and the feeding method of *Hippa* and *Mastigocheirus,* however, are still unknown. The members of the related family Albuneidae, which likewise live in sand, have well-developed, functional mandibles, and strongly chelate first pereiopods.

Both *Emerita talpoida* and *E. analoga* are commonly found in great numbers between tide marks on sandy beaches, where they will be covered by the inflowing waves. As the crabs are exposed by the receding water they quickly back themselves into the wet sand in a slanting position with the ventral surface toward the ocean. Here they await the return wave, and when the downflow begins they spread the antennae out before them against the current. According to the tides, the crabs move up or down the beach. MacGinitie (1938) says of *E. analoga* that a "general migration with the tide takes place in mass movement" and is done so quickly that to an observer "it appears that a portion of the beach comes up, moves either up or down, and then disappears. . . . On a gently sloping beach this migration usually occurs at a time when the sand crab colony is covered with from two to six inches of water." When the movement of the water begins to slacken, the crabs quickly orient themselves facing the ocean and dig into the sand. Wharton (1942) says of *E. talpoida* that the crabs "will follow a shallow wave towards the water and a deep wave up the beach." The usual stimulus for proper orientation, according to MacGinitie, is the water flowing over the crabs from behind, and if a stream of water from a hose is made to flow over them away from the ocean, "they will immediately reverse their position in the sand and face toward the land, even if they must move uphill to do so." Under natural conditions, MacGinitie says, "the stimulus of the current appears to be much stronger than the stimulus of sight," though when the current is at a minimum, if a large black screen is placed between the crabs and the ocean, they will face landward.

The mating of the sexes of *Emerita analoga* on the California coast is said by MacGinitie (1938) to take place late in spring and early in summer. The males, generally several at a time, bury themselves in the sand at the side of a female and attach to her under surface packets of spermatozoa in a thick adhesive mucus. According to Wharton (1942), the very young males of *E. talpoida,* with a carapace length of 3 mm., which appear in August at Beaufort, N. C., are sexually mature, and attach themselves to year-old females for mating, as many as seven of the miniature males having been found on a single large female. The spermatophores are attached between the coxopodites of the fourth legs of the female. From the time of their first appearance in August until the following June, the small males increase in length of the carapace from an average of about 3 mm. to about 7 mm.

I. GENERAL STRUCTURE OF EMERITA TALPOIDA

The material on which the anatomical part of this paper is based has been furnished by the Division of Marine Invertebrates of the United States National Museum.

A specimen of *Emerita talpoida* as ordinarily seen (fig. 1 B), when freshly dug up out of the sand, or in museum collections, has the general appearance of a small, symmetrically egg-shaped object, the largest females being about 30 mm. in length, the males half as long. A pair of short antennules (*1Ant*) and two slender eyestalks project from the anterior end, and on the sides at the posterior end are two paddlelike uropods (*Urpd*). The rest of the appendages are closely folded against the underside of the body, where the legs, except those of the first pair, are further concealed by lateral extensions of the carapace, and by the long telson (*Tel*) bent forward below them. The color is a uniform pale yellowish brown. When buried in soft wet sand the crabs are thus well protected from their granular environment; their only problem is that of respiration, but the antennules projecting into the water above the sand together form a respiratory tube.

When an *Emerita* is stretched out at full length (fig. 1 C) it is seen to be a complete crab. A smooth, rounded, shell-like carapace covers the gnathothoracic region of the body, a 6-segmented abdomen bears an extremely long, pointed telson (*Tel*), at the base of which project the relatively large uropods (*Urpd*). On the under surface, the region of the mouth and the feeding organs, and the flagella of the second antennae, unless the latter are extended, are completely covered by a pair of large valvelike plates, which are the meropodites of the third maxillipeds (fig. 3 A, *Mrpd*). At the sides of the latter are two elongate pterygostomial plates (fig. 1 B, *Ptst*) flexibly attached to the edges of the carapace. The maxilliped plates open ventrally like a pair of trap doors, and if they are lifted the long plumose flagella of the second antennae will be seen looped upon each other immediately above them (fig. 3 B). When the antennae are artificially extended, the flagella project in curves outward and posteriorly (fig. 1 A). Following the maxillipeds are five pairs of legs, the first pair of which are directed forward against the maxilliped plates, the second, third, and fourth pairs usually folded under the carapace, and the slender fifth pair bent upward and forward into the branchial chambers. The abdomen of the female has three pairs of slender pleopods in addition to the uropods.

In its postembryonic development *Emerita talpoida,* according to Smith (1877), goes through four zoea stages and a megalops stage. The first zoea stage was not observed by Smith, but in the other stages the zoea has a long rostral spine and two lateral spines on the carapace, large eyes on short peduncles, and an abdomen of five segments bent forward beneath the thorax. The telson is a broad plate, with a wide, rounded distal margin. The mandibles in all the zoea stages appear to be functional organs. In the second stage the appendages include, besides the mandibles, two pairs of maxillae, two pairs of maxillipeds, and the uropods. The third maxillipeds

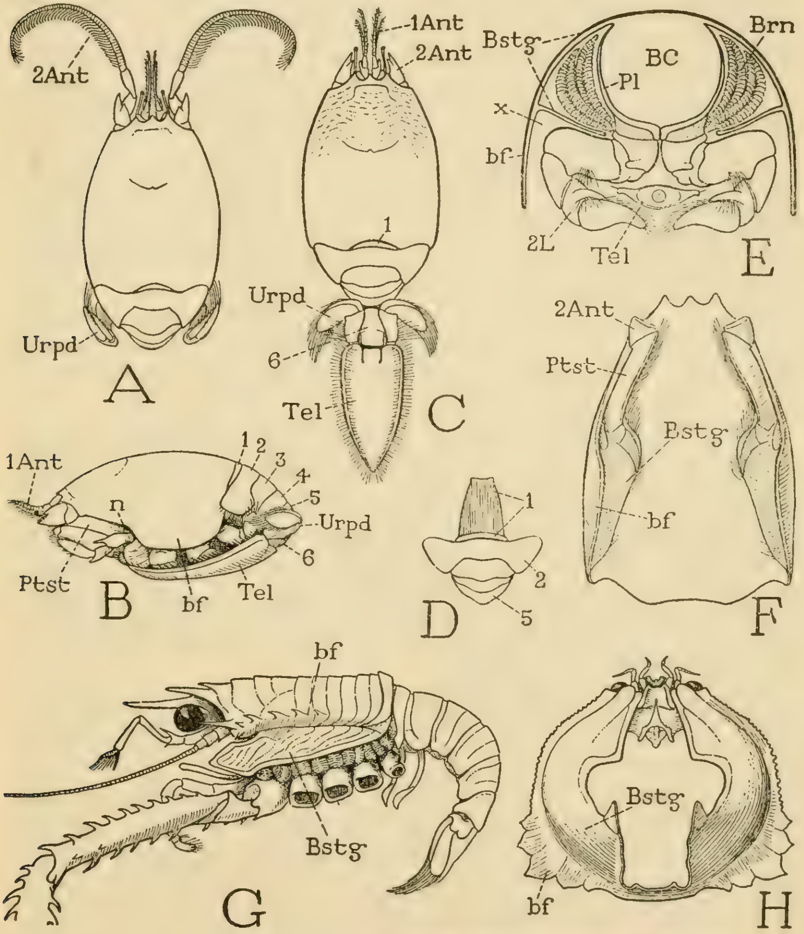


Fig. 1.—External features of *Emerita, Galathea,* and *Calappa.*

A, *Emerita talpoida* (Say), female, with antennae extended, dorsal. B, same with antennae concealed, left side. C, same, abdomen artificially extended, dorsal. D, same, abdomen detached, showing long apodemal plate of first tergum, dorsal. E, same, cross section of body behind second legs. F, same, carapace, pterygostomial plates, and branchiostegites, ventral. G, *Galathea californiensis* Benedict, female. H, *Calappa flammea* (Herbst), carapace, ventral.

and the legs are still unsegmented rudiments. In the third zoea the legs are better developed, and those of the fifth pair appear; the gills are now represented by slender processes above the first four legs. In the fourth stage the full number of gills (nine on each side) is present, the uropods have two apical lamellae, but the telson preserves the broad form of earlier stages. The megalops at once takes on in many ways the form and habits of the adult. The second antennae, Smith says, have assumed all the important features of the adult antennae, including the mechanism for folding beneath the body, but there are still fewer annulations in the flagella. The mandibles have been reduced to the adult condition, the third maxillipeds form large opercular plates, the abdomen and telson resemble these parts in the adult. At Woods Hole the young Emeritas in the megalops stage, according to Smith, may be taken at the surface of the water in the towing net during late August and the early part of September. Specimens in aquaria swim rapidly at the surface, but in a shallow dish of sea water with sand on one side, they at once back themselves into the sand "with an evident satisfaction and with an ease and agility that could not have been excelled by their sand-loving parents after months or years of practice."

The first zoea stage of *Emerita talpoida* is said by Wharton (1942) to lack the lateral spines of the carapace. The megalops, according to Wharton, are amphibious like the adults, being well adapted for both swimming and burrowing. In swimming, the megalops keeps the abdomen extended, while the young adults swim with the abdomen flexed. The ventral pleopods of the megalops are used as swimmerets, there being four pairs in the megalops stage, differing in form from those of the adult.

It is customary to describe the body of a decapod crustacean as divided into two parts, a cephalothorax covered by the carapace, and a free abdomen, or pleon. However, there is a distinct head structure in front of the carapace, or beneath its projecting anterior end, which bears the eyestalks, the two pairs of antennae, and the labrum. It is not intimately united with the body, except in Palinuridae, and should be regarded as the true *head* of the animal. The region covered partly or wholly by the carapace includes the segments of the mandibles, the maxillae, the maxillipeds, and the legs, and is hence really a *gnathothoracic* tagma, or section of the body. The *abdomen,* then, constitutes a third part carrying the pleopods and the telson. This concept of a triple division of the decapod will be followed in the description of *Emerita.*

II. THE HEAD AND ITS APPENDAGES

The head of most of the malacostracan Crustacea represents the simplest type of head structure found among the arthropods, and therefore, in an evolutionary sense, the first known stage of head development. For this reason the writer (1951) has termed it the *protocephalon.* A more complex secondary type of head structure results from the addition of two or more postoral segments to the protocephalon, as in the amphipods, isopods, myriapods, and insects, in which the head bears, in addition to the eyes and antennae, the appendages concerned with feeding.

The head.—The head of *Emerita* is a typical protocephalon; though it is not so well sclerotized or so strongly developed as that of a crayfish or a lobster, it can be separated as a discrete head unit from beneath the anterior end of the carapace (fig. 2 A, C). On the dorsal surface (A) is a V-shaped ocular plate (*e*) supporting the eyestalks (*ES*), and behind it a larger, weakly sclerotized postocular plate (*m*) flexibly connected with the base of the under lamella of the projecting rostral part of the carapace. The small first antennae (*1Ant*) arise anteriorly beneath the edge of the ocular plate, and at the sides are the bases of the large second antennae (*2Ant*). On the ventral surface (C), the head presents a broad calcified region, the epistome (*Epst*), between and behind the bases of the antennules, with lateral extensions to the bases of the antennae and irregular postantennal wings (*k*). Supported on the posterior margin of the epistome is the triangular labrum (*Lm*), which projects forward inverted against the epistomal surface. If the labrum is turned posteriorly (D, *Lm*) it will be seen to have covered a noncalcified area of the epistome from which arise a pair of small setigerous processes. In most decapods the postantennal wings of the epistome (*k, k*) extend laterally to the bases of the inner lamellae of the carapace folds, but in *Emerita* the intervening regions are not calcified. At the basal angles of the labrum are the small mandibles (E, *Md*) solidly united with the adjoining edges of the epistomal wings, and behind the labrum is the mouth (*Mth*) flanked by a pair of small paragnaths (*Pgn*). The mandibles and the paragnaths, however, do not belong to the head.

The crustacean protocephalon is an anatomical fact, but its segmental composition is an uncertainty. The origin of the second antennae of the adult from the protocephalon might suggest that the protocephalon contains the second antennal segment. The second antennae, however, are postoral in their embryonic origin, and acquire their definitive preoral position secondarily. The idea that the mouth has migrated posteriorly from a more anterior position seems hardly tenable if it is implied that it has pushed clear through one or more segments. More probably, the ventral parts of the invaded segments are simply folded forward around the sides of the mouth. That something of this nature has taken place is indicated by the finding of Tiegs (1940, p. 133), in his study of the development of a symphylan, that much of the roof of the preoral cavity of the head is derived from the premandibular (second antennal) segment. However, in the adult arthropod, no remnant of a postoral arc of even the second antennal segment has been anatomically identified as such. The identity of the dorsal arc of this segment is equally elusive in the adult. The origin of dorsal muscles of the second antennae in

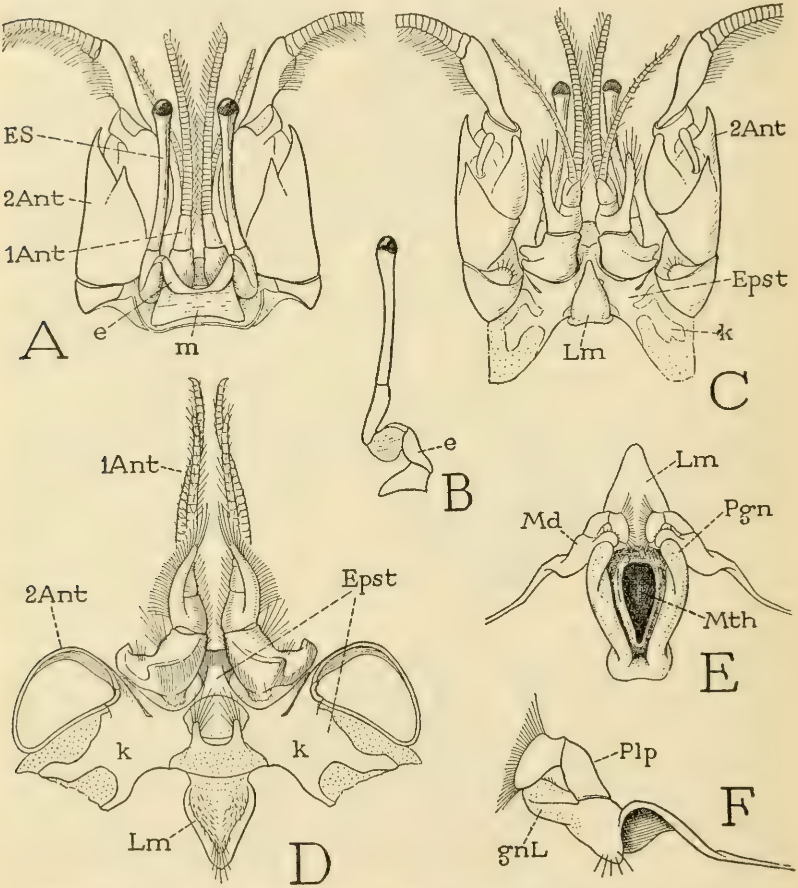


FIG. 2.—*Emerita talpoida* (Say), head, mandibles, and mouth region.

A, head (protocephalon) bearing eyestalks and first and second antennae, dorsal. B, left eyestalk, and supporting plate of head (*e*), dorsal. C, head, ventral, labrum normally turned forward beneath epistome. D, epistome, first antennae, and bases of second antennae, ventral, labrum artificially turned posteriorly. E, mouth region with associated labrum, mandibles, and paragnaths, ventral. F, right mandible, dorsal.

the decapods on the anterior part of the carapace might suggest that the rostral area of the carapace includes the dorsum of the second antennal segment; yet in the adult anostracan branchiopod there is clearly no segment between the protocephalic head and the mandibular segment. Recently it has been asserted (Henry, 1948) that there is no second antennal segment. It would indeed simplify matters very much to have this segment abolished, but unfortunately there is too much evidence of its existence, at least in works on arthropod embryology.

The eyestalks.—The slender eyestalks of *Emerita* (fig. 2 B) are 3-segmented, with the small eyes on the ends of the long distal segments. The second segments are abruptly and flexibly elbowed on the mostly membranous basal segments, which are borne on the ends of the ocular plate (*e*) of the head, so that the eyestalks can be freely protracted and retracted in a lengthwise direction.

The first antennae.—The relatively small first antennae, or antennules (fig. 2 A, *1Ant*), project forward between the eyestalks. Each antennule consists of a 3-segmented basal stalk, best seen from below (C, D), and a pair of multiarticulate flagella, of which the ventral one is more slender and a little shorter than the dorsal one. The large basal segment of the stalk is of irregular form and articulates below on the epistome; the second segment bears ventrally a large setigerous process. The flagella are fringed with short hairs and when the four of them are held together they enclose a narrow space between them, which is the usual exit canal of the respiratory system, but may become inhalant when the crab is buried in the sand. The antennular canal of *Emerita,* however, is not so well closed by setae as in some other sand-burrowing crabs.

The second antennae.—The second antennae are organs of vital importance to *Emerita* inasmuch as they are the food-collecting instruments of these crabs. Each appendage (fig. 3 F) consists of a 2-segmented basal stalk, of a middle part that contains two segments which constitute the flexing mechanism, and of a distal part including an elongate proximal segment, and the long, plumose terminal flagellum. The two basal segments are evidently the coxopodite (*Cxpd*) and the basipodite (*Bspd*). The second is produced laterally into a pointed lobe, but there is no true exopodite branch. The identity of the other segments is difficult to determine. Schmidt (1915) in his study of the antennal muscles of the crayfish accounts for seven antennal segments, making the flagellum the dactylopodite. There are, however, only five functional segments besides the flagellum in the antenna of *Emerita,* and the third and fourth are of irregular form.

The third antennal segment (fig. 3 F) is largely membranous, but its mesal part contains a strongly calcified convex plate supported on the inner angle of the basipodite. The fourth segment presents dorsally (B) a large, smooth, convex surface, but ventrally (F) it is represented only by a Y-shaped bar that supports the fifth segment, and articulates by each arm on the mesal plate of the third segment. The two articular points lie in an oblique line (*d-e*) extending proximally and laterally between the third and fourth segments, and it is on this line as an axis that the distal part of the antenna is flexed ventrally. The fourth segment, moreover, is braced laterally against the basipodite by a short rod (*f*) in the ventral wall of the third segment, which turns on the basipodite at a point in the axis of flexion. When, therefore, the distal part of the antenna bearing the flagellum is flexed ventrally on the oblique axis (*d-e*) between the third and fourth segments, it not only turns downward and posteriorly, but it goes over to the opposite side of the body, and the bar (*f*) braced against the fourth segment prevents any other movement. The two antennal flagella are thus assured of being symmetrically folded upon each other (B) ; in most specimens the left flagellum is below the right, but in some the right is below the left.

In the folded position of the antennae (fig. 3 B), the parts beyond the lines of flexion are entirely concealed within the large meropodite plates of the third maxillipeds (A, *Mrpd*), and the flagella are looped upon each other. According to Weymouth and Richardson (1912), *Emerita analoga* folds the antennae separately as the water runs off the beach. The flagella are first allowed to trail out with the current, and are then "folded up and withdrawn under cover of the third maxillipeds with such a rapid motion as to escape analysis." So closely are the antennae shut in above the maxilliped plates, however, that it would seem the plates must first open to receive them.

Inasmuch as the antennal flagella are specifically the food-collecting organs of *Emerita,* the details of their structure become a matter of special interest. Each flagellum of *Emerita talpoida* is cut into about 150 small rings by circular joints that impart a flexibility to the shaft as a whole. In cross section the shaft is rounded above and somewhat flattened below (fig. 3 E). The plumose character of the flagellum is due to the presence of eight rows of setae on the under surface, there being duplicate sets of four on each ring, so that in all there are about 1,200 setae on the entire flagellum. The setae of the outermost rows (E, *g*) are long, tapering filaments flaring outward with incurved tips; the concave margins are densely fringed with long slender hairs, giving these setae a featherlike structure. The setae of the second rows (*h*) are somewhat curved outward;

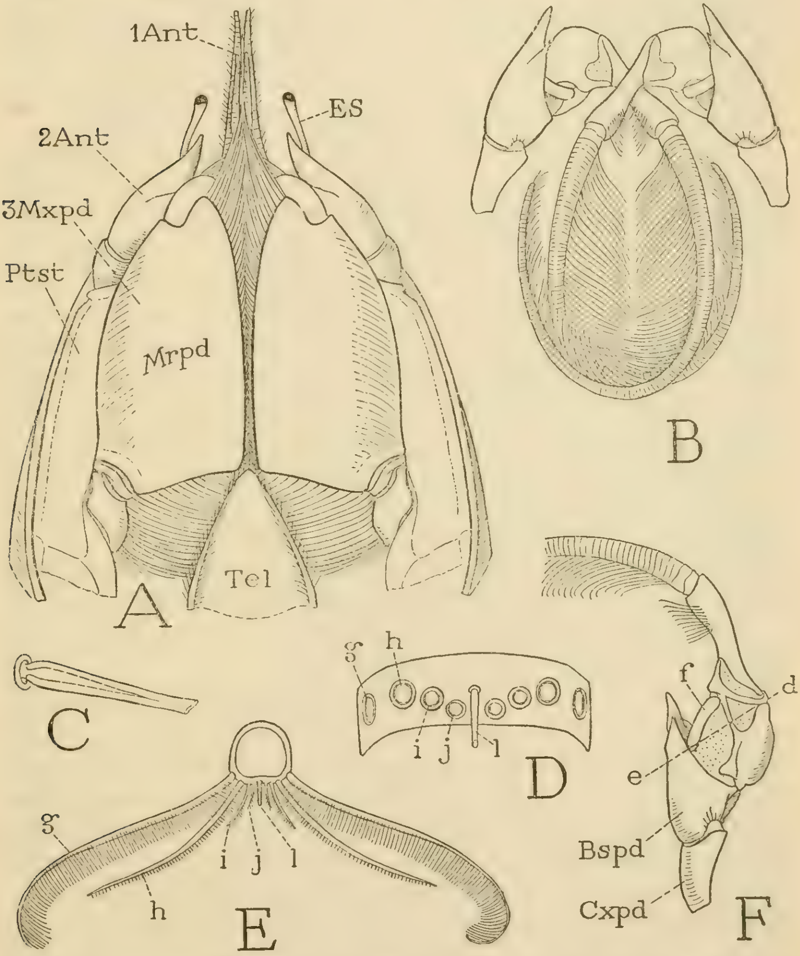


Fig. 3.—*Emerita talpoida* (Say), second antennae and third maxillipeds.

A, ventral surface of anterior part of body, second antennae folded above meropodite plates of third maxillipeds. B, second antennae in folded position, ventral. C, a median process of antennal flagellum (E, *l*). D, under surface of a flagellar ring, showing position of setae. E, cross section of flagellar ring, with setae. F, proximal part of right second antenna, showing folding mechanism, ventral.

their inner surfaces are armed with short, blunt, closely set processes like the teeth of a comb. The setae of the third and fourth rows (*i, j*) are short and simple with fine hairs on their inner margins.

Finally, along the midline of the flagellar shaft, between the innermost setae, is a row of slender, tapering processes (*l*), all slightly inclined toward the base of the flagellum. The tip of each of these median processes (C) is obliquely truncate and appears to contain a slight membranous depression. Weymouth and Richardson suggest that these structures in *E. analoga* may be sensory organs. At D of figure 3 are shown the relative positions of the several rows of setae and the median processes on a single ring of the flagellum.

When the antennae of a dead specimen of *Emerita talpoida* are extended (fig. 1 A) they project forward from the body and the flagella curve outward and posteriorly; in this position the marginal rows of setae are dorsal and ventral, with respect to the body. If, however, the antennae are turned horizontally away from the ventral surface as the crab stands vertically in the sand, or are carried into this position by the downflow of the water on the beach, the antennae will be rotated into a position in which the concave sides of the flagella are away from the ocean, and the setae will now be spread out against the descending current. Living specimens of *E. analoga*, buried in the sand in the feeding position, are said by Weymouth and Richardson to hold the antennae "directed forward" (presumably meaning oceanward) and laterally with the tips curved outward. In this position, these writers note, "the antennae thus present to the water flowing against the concave side a very efficient straining apparatus." In other words, the opposite rows of setae are spread out as a fine-meshed sieve against the downflowing water.

The stomach contents of *Emerita analoga* were found by Weymouth and Richardson to be always of the same kind of material, "chiefly shells of various diatoms, masses of brownish oily matter apparently derived from the diatoms, radiolarians, foraminifera, spicules of unrecognized origin, what were probably one-celled algae, and considerable amounts of sand—about what would be obtained by unselective straining of the water along the shore." From experimental feeding of *E. analoga* on suspensions of bacteria in liter jars of sea water, Zobell and Feltham (1937-38) found that the crabs can be sustained to a certain extent on bacteria alone, but that they do not thrive on a pure bacterial diet as well as does the mussel *Mytilus californianus,* and that they are not as efficient as the mussel in removing bacteria from the water. The antennae of *Emerita* in the folded position above the plates of the third maxillipeds are separated from the mouth by the second and first maxillipeds and the two pairs of maxillae; the method by which food material is transferred from the flagella to the mouth is, therefore, not open to observation.

III. THE GNATHOTHORAX

The gnathothoracic part of the body of *Emerita* is entirely covered above and on the sides by the carapace (fig. 1 A, B). The anterior dorsal margin of the carapace is produced into three small points over the head, the posterior lateral areas are extended downward in broad folds (B, *bf*) over the leg bases. In front of these folds on each side is an elongate plate (*Ptst*) reaching from the base of the second antenna to the base of the first leg, and flexibly attached to the margin of the carapace. This plate is known as the *pterygostomial plate* because it evidently represents the so-called pterygostomial region of the carapace of an astacuran decapod. The posterior end of the plate is not continued into the lateral fold (*bf*) of the carapace behind it, but goes beneath the latter to be continued into a soft, horizontal inner fold (F, *Bstg*) lying above the leg bases and closing the gill chamber from below (E). This soft inner fold is the true lower part of the branchiostegite (*Bstg*), the outer sclerotic fold (*bf*) is a secondary extension of the branchiostegite beyond the base of the inner fold. The branchiostegites themselves are folds of the thoracic walls projecting from the sides of the back; their inner lamellae are continuous dorsally with the mesal walls of the gill chambers, which are the true lateral walls of the thorax on which the legs are articulated (fig. 8 B). In carcinology the inner wall of the gill chamber is called either the epimeron or the pleuron, but for general usage *pleuron* is preferable because the gill-chamber wall of the crustacean evidently corresponds with the skeletal parts called the pleura in other arthropods.

In order to establish a basis for a consistent nomenclature, it will be of interest to follow the various modifications of the sclerotized dorsal part of the body wall that occur among the arthropods. In a simple, soft-bodied animal with ventrolateral rows of legs, such as an onychophoran (fig. 4 A), the circumference of the body is divided by the lines of the leg bases into a dorsum (*D*) above the appendages, and a venter (*V*) between them. A simple sclerotization of the body wall would then produce in each segment a dorsal plate, or *tergum,* and a ventral plate, or *sternum.* If the tergum comes down to the leg bases, the legs will be suspended from, or articulated on, its lower margins, a condition found in some arachnids. More commonly, however, as in the crustacean *Anaspides* (B), the dorsum of a thoracic segment contains a major tergal plate (*T*) covering the back, and on each side a small *pleural plate* (*Pl*) carrying the outer articulation (*a*) of the leg. Usually, however, the contour of the segment

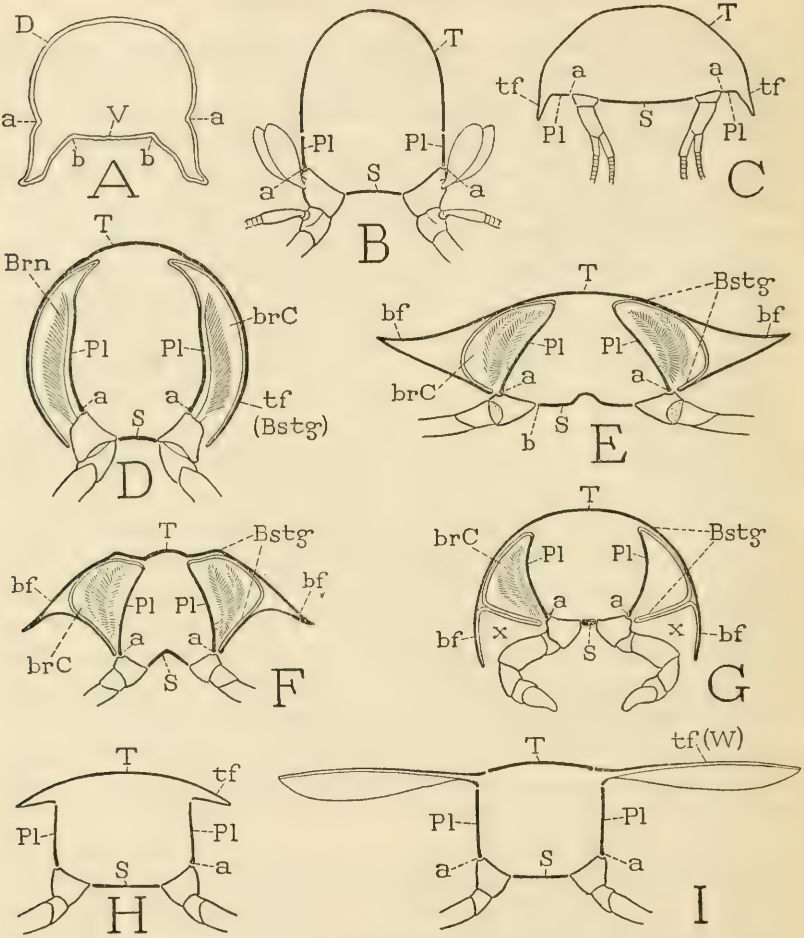


FIG. 4.—Diagrammatic cross sections of arthropods, showing various types of modification of the dorsal sclerotization.

A, dorsum entirely unsclerotized, as in an onychophoran. B, thorax of the crustacean *Anaspides,* dorsal sclerotization differentiated into a principal back plate, or *tergum* (*T*), and small laterotergal plates, or *pleura* (*Pl*), carrying lateral articulations of coxae. C, abdomen of an astacuran decapod, with small tergal folds (*tf*) projecting over pleura. D, thorax of an astacuran decapod, with tergal folds extended downward as gill covers, or branchiostegites. E, thorax of a crab, *Callinectes,* with branchiostegites produced into lateral folds (*bf*). F, thorax of a crab, *Calappa,* with branchiostegite folds depressed. G, thorax of *Emerita,* with branchiostegite folds (*bf*) extended downward over the legs, enclosing subbranchial canals (*x*). H, prothorax of an insect with short lateral folds (paranotal lobes) of tergum. I, alate segment of an insect, with tergal folds greatly extended horizontally and flexible at their bases, forming wings.

is not so simple as in *Anaspides*. In the decapod abdomen (C) the tergum is generally produced into short lateral folds (*tf*) overhanging the pleura (*Pl*). In the thorax (D) the pleura maintain a more or less vertical position as the lateral walls of the body cavity, while the tergal folds (*tf*) arise high up on the sides and descend as long branchiostegites (*Bstg*) over the gills to the bases of the legs. In most of the Brachyura (E, F) the outer walls of the branchiostegites (*Bstg*) are extended laterally into sharp-edged folds, but finally, in *Emerita* (G), the branchiostegite folds (*bf*) become thin ventral extensions of the carapace. A lesser development of branchiostegite folds is seen in the crab *Calappa* (fig. 1 H) in the form of flangelike projections from the sides of the back, and in the anomuran *Galathea* (G) there is a suggestion of the same thing in the presence of spiny ridges (*bf*) above the branchiostegites.

In all the decapod forms above discussed, it will be seen that the pleura form the true lateral walls of the thoracic segments, and carry on their lower margins the lateral articulations of the legs. The same is true for the thoracic segments of insects. In the insect prothorax there are usually short tergal folds (fig. 4 H, *tf*) overhanging the pleura; in the winged segments (I) the tergal folds are greatly extended, flexible at their bases, and become organs of flight. It is interesting to note, therefore, that the wings of an insect (I, *W*) may be regarded as structures topographically homologous with the branchiostegites of an astacuran decapod (D, *Bstg*).

The ventral surface of the gnathothorax of *Emerita* can be fully seen only after removal of the appendages, so, unless specimens are plentiful, it will be well to study first the mouth parts and legs, described in the next section. On the exposed ventral surface (fig. 5) there is to be noted an abrupt change in the sternal structure between the region of the maxillae and maxillipeds (A) and that of the pereiopods (B). The foramina of the legs (B, *1L-5L*) lie in regular rows at the sides of the narrow median sterna (*S*). The third maxillipeds (A, *3Mxpd*) arise lateral of the first legs (*1L*), and the three pairs of maxillipeds lie along oblique lines converging forward toward the mouth; the second maxillae (*2Mx*) again have lateral positions, and the first maxillae (*1Mx*) arise in membranous areas at the sides of the mouth. The sternal sclerotization of the maxillo-maxilliped region (A) is not segmentally divided; from the narrow metastomal area it expands posteriorly into a large, diamond-shaped plate between the bases of the maxillipeds in front of the first legs. The maxillary region is extended on each side in a strong bridge (*mxB*) to the base of the inner lamella, or doublure (*Dbl*), of the pterygostomial plate of the carapace. The maxillary bridges evidently represent the pleura of the second maxillary segment; they form the anterior limits of the branchial chambers. It is to be noted that the slender outer ends of the mandibles reach to the maxillary bridges, on which in the Anomura generally the mandibles have their outer articulations. The second maxillae have a lateral position because of the respiratory function of the scaphognathites, and the first and second maxillipeds are thrust forward between them, so that the second maxillae are immediately followed by the third maxillipeds.

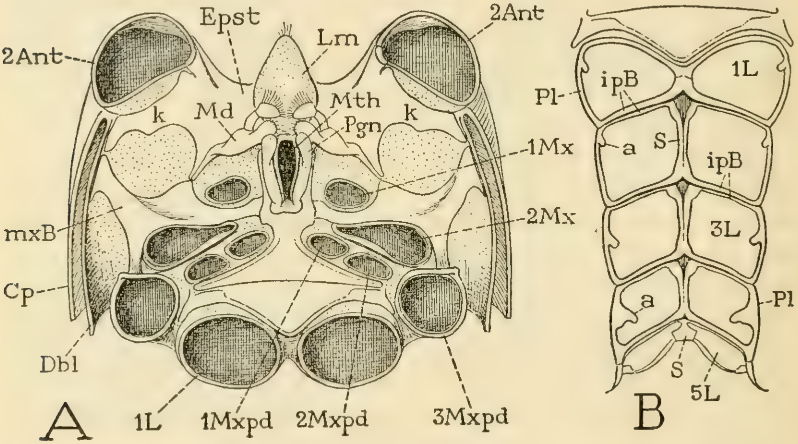


FIG. 5.—*Emerita talpoida* (Say), ventral skeleton of head and gnathothorax, exposed by removal of appendages.

A, ventral surface of head, mouth region, maxillary and maxilliped segments, anterior to first legs (*1L*). B, ventral surface of pereiopod segments.

In the region of the pereiopods (fig. 5 B) the ventral sclerotization at once assumes a regular pattern repeated in each of the five leg-bearing segments. Between each pair of legs is a narrow sternal plate or bar (*S*), which gives off laterally from its anterior end a pair of slender precoxal sternopleural arms, and from its posterior end a pair of similar postcoxal arms, which are continuous at their outer ends with the pleura of the same segment. The adjacent sternopleural arms of consecutive segments, however, are united to form a series of *interpedal brachia* (*ipB*), in which the intersegmental lines are marked by deep grooves.

The internal skeleton of *Emerita* consists of the usual intersegmental pleural and sternal apodemes of decapods. The sternal apodemes of the thorax are four pairs of plates or arms diverging forward and upward from the intersegmental grooves of the interpedal brachia, the fourth pair arising from the brachia between the fourth and fifth legs. The apodemes of the last two pairs are united at their bases, the others are narrowly separated over the sternal plates; in no case are they bridged by expansions of their inner ends as in the Astacura. A pair of divergent ridges in front of the first legs are probably intersegmental between the third maxillipeds and the first pereiopods. A pair of intermaxillary apodemes are united in a transverse bridge, the so-called "head apodeme" behind the mouth. The pleural apodemes are relatively small and are confined to the thorax; they arise on each side from the intersegmental grooves of the pleuron (fig. 8 B), and are Y-shaped, one arm joining the corresponding sternal apodeme, the other going back to the one following.

IV. THE GNATHOTHORACIC APPENDAGES

The segmental appendages of the gnathothorax are the mandibles, the first maxillae (maxillulae), the second maxillae (maxillae), the first, second, and third maxillipeds, and the five pairs of legs, or pereiopods. The mandibles and the two pairs of maxillae may be distinguished as the gnathal appendages; the maxillipeds are commonly regarded as thoracic, though in *Emerita* the first two pairs are entirely concerned with the feeding function.

The mandibles.—The mandibles of *Emerita talpoida* (fig. 2 F) are very small, though larger than in the other genera of Hippidae, and are immovably united with the posterior edges of the epistome. The basal part of each mandible (corpus mandibulae) is produced mesally into a weak gnathal lobe (*gnL*), and bears a relatively large 2-segmented palpus (*Plp*). The two diminutive jaws lie entirely in front of the mouth (E, *Mth*), with the gnathal lobes and the palpi underlapping the base of the labrum (*Lm*). Though the mandibles of *Emerita* clearly can have no use as biting or chewing organs, the palps may have a sensory function, or, together with the gnathal lobes, they perhaps serve to prevent the escape of food material from in front of the mouth. A pair of small paragnaths (*Pgn*) underlie the mandibular lobes.

In the zoea stages of *E. talpoida* the mandibles, as described by Smith (1877), are evidently functional organs, since they have broad, toothed gnathal lobes, though molar areas are absent. In the megalops stage, however, Smith says, "the mandibles have become thin and foliaceous and completely consolidated with the wall of the oral opening." A relatively large, indistinctly 2-segmented palpus is present, but the gnathal lobe is a small thin flap as in the adult.

The first maxillae.—The small, flat first maxillae (fig. 6 A) arise at the sides of the oral region and project mesally beneath the mouth. The body of each appendage contains a small basal plate and, proceeding from the latter, a pair of parallel bars, each of which supports a large free mesal lobe, while at the base of the more distal of these lobes there arises a small anterior lobe. The structure of the first maxilla of *Emerita* is similar to that in other decapods, and the small anterior lobe is commonly regarded as the endopodite, according to which interpretation the other two lobes are coxal and basal endites. It is of interest to note that the flat, weak, proximal mesal lobe of the maxillula of *Emerita* is developed in other hippid genera into a strong, toothed jaw (fig. 10 E).

The second maxillae.—These appendages (fig. 6 B, C) are larger than the first maxillae, but they have essentially the same structure, except for the presence of the huge scaphognathites (*Scpg*) attached laterally on their bases. Three mesal lobes of each maxilla arise from a common base and clearly correspond with the three lobes of the maxillula (A). The maxillary scaphognathite is generally interpreted as the exopodite of the appendage, but its position suggests that it might be a highly developed epipodite. The scaphognathites are the active organs in the maintenance of water currents through the gill chambers, as will be explained in the description of the respiratory system.

The first maxillipeds.—The first maxillipeds (fig. 6 D) are 2-branched appendages borne on a pair of small basal plates situated close to the midline of the body. The maxilliped branches are without doubt true exopodites and endopodites. The endopodites of the first maxillipeds are unsegmented; a sievelike arrangement of hairs on their concave mesal borders lies below the mouth. The exopodites are 2-segmented; the apical segments bear brushes of long hairs and converge against the sides of the labrum.

The second maxillipeds.—The maxillipeds of the second pair (fig. 6 E) resemble those of the first pair in that each consists of an endopodite and an exopodite supported on a small basal segment. Their bases are farther apart than those of the first maxillipeds, which latter in the figure (E) are seen between the basal segments of the outer maxillipeds. The exopodites of the second maxillipeds bear each an apical, brushlike segment similar to that of the first maxillipeds, but the endopodites are 4-segmented, with the two slender distal segments turned posteriorly. The long basal segments of the endopodites are fringed mesally with wide, comblike rows of setae directed

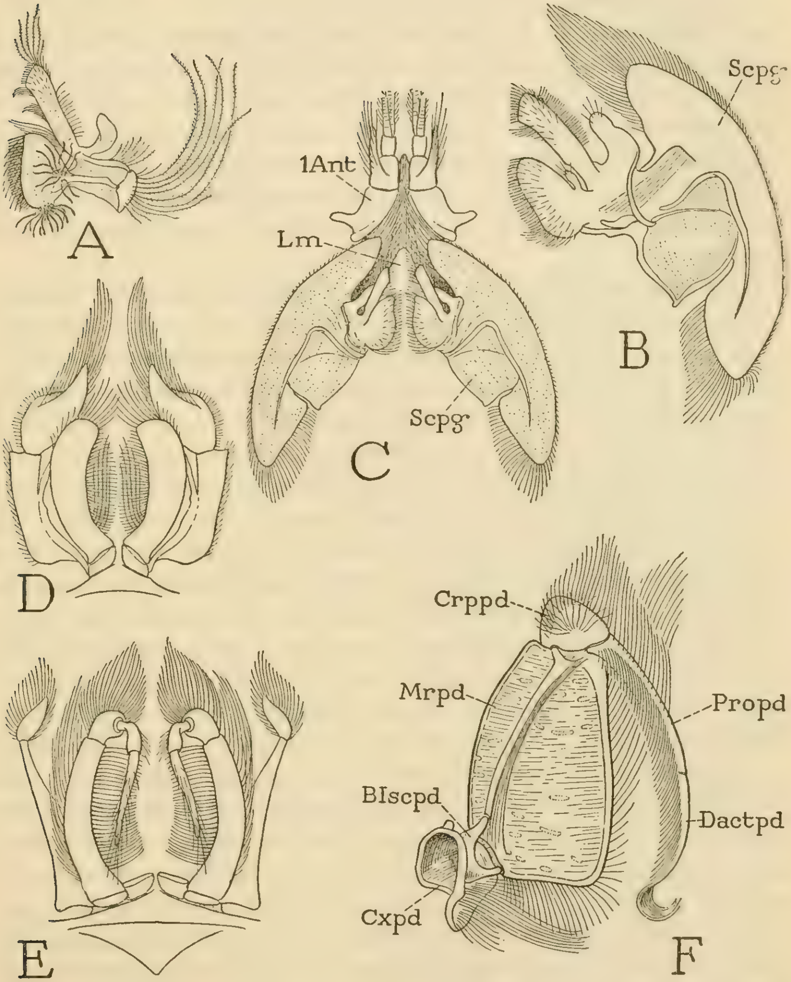


FIG. 6.—*Emerita talpoida* (Say), maxillae and maxillipeds.

A, left first maxilla, ventral (posterior). B, left second maxilla, flattened, ventral. C, second maxillae, with scaphognathites in natural position relative to the labrum and bases of first antennae, ventral. D, first maxillipeds, ventral. E, second maxillipeds, ventral. F, left third maxilliped, dorsal.

toward each other, and laterally with long hairs that blend with large setal brushes on the second segments.

The two pairs of maxillae and the first two pairs of maxillipeds lie horizontally between the mouth and the infolded antennal flagella, and the latter in turn are completely shut in ventrally by the plates of the third maxillipeds. Weymouth and Richardson (1912) say that "the mouth parts are admirably adapted for the manipulation of the minute organisms which the antennae have strained from the waves." Undoubtedly this is true, but it remains for some ingenious investigator to discover just how the various mouth-part appendages perform their function.

The third maxillipeds.—The third maxillipeds (fig. 6 F) have the same segmentation as the legs; each consists of the endopodite alone, there being no exopodite branch. The two appendages are widely separated at their bases (fig. 3 A), but the broad meropodites (*Mrpd*) come together mesally; the distal segments are turned posteriorly (fig. 6 F) and are ordinarily concealed above the meropodites. A short basal stalk of each appendage is formed by the coxopodite and the basi-ischiopodite (fig. 6 F, *Cxpd, BIscpd*). The large meropodite (*Mrpd*) is capped by a small carpopodite (*Crppd*), from which a long slender distal arm of the appendage, composed of the propodite (*Propd*) and the dactylopodite (*Dactpd*), turns posteriorly. The valvelike meropodites are opened and closed by an axial rotation of the appendages on their bases, but the mode of action by which they embrace and enclose the antennae has not been recorded. In the closed position (fig. 3 A), fringes of long hairs on the proximal parts of the appendages shut in the space behind the meropodites, covered medially by the anterior end of the telson (*Tel*), which lodges the posterior parts of the antennal loops (B). The narrow space between the meropodites, and the triangular opening at their divergent anterior ends are covered by overlapping setal fringes of the meropodites and the distal segments (fig. 6 F). The outer edges of the meropodites lie close against the pterygostomial plates (fig. 3 A, *Ptst*), and the large first legs are pressed against their ventral surfaces. Whatever food material the antennal flagella bring with them into the food chamber above the meropodites is thus effectively imprisoned for transference to the mouth.

The legs.—The legs of both the anomuran and the brachyuran crabs have generally only six disinct segments, while the typical decapod limb has seven, there being in the crabs only one apparent segment between the coxopodite and the meropodite. When a crab's leg is broken off, however, it leaves a small ring attached to the coxopodite, which may be supposed to be a much reduced basipodite (fig. 7 B, *Bspd*) detached from the ischiopodite. The functional second segment of the leg, therefore, is termed the basi-ischiopodite (D, *BIscpd*).

The legs of *Emerita,* together with the uropods, are principally organs for burrowing, though they must be used also for emergence from the sand. The uropods serve both for burrowing and for swimming. The burrowing activities of *Emerita* have been described by several writers. Smith (1877) notes merely that *E. talpoida* burrows backward by means of the thoracic legs and the uropods, while the telson is kept appressed to the under surface of the body. Concerning *E. analoga,* Mead (1917) says, "burrowing is accomplished by the combined action of the uropods and pereiopods, the latter being the more serviceable." Animals with clipped uropods could burrow, though more slowly than normally. MacGinitie (1938) gives only the statement that the crabs bury themselves rapidly in the sand by use of the anterior legs and the uropods. Weymouth and Richardson (1912) record more detailed observations on the use of the different appendages by *E. analoga.* The uropods, according to these writers, appear to be the most important digging implements; they strike upward and forward in unison, thus thrusting the body downward and backward if the sand is firm. The pereiopods take part in the burrowing in different ways; the second and third pairs thrust the body backward, those of the fourth pair push outward, and the large first legs are used to scull the body backward. "Under the combined action of all these appendages the animal is carried diagonally downward and backward until the anterior end of the carapace is just covered." According to Wharton (1942) *E. talpoida,* when preparing to burrow, backs up into the wet sand, and the uropods, rotating in unison, throw the sand dorsally, while the body is forced backward. The first legs work alternately pushing the sand laterally and anteriorly. The fourth legs, and also the third and the second legs, Wharton says, "move in unison laterally and posteriorly," but the posterior movement observed must be the relaxing stroke, since the statement follows that these legs "move the sand anteriorly and force the posterior end of the body into the sand."

The first legs of *Emerita* are large, thick, and strong, with broad, flat dactylopodites (fig. 7 A). As already noted, these legs project forward and are closely applied against the meropodite plates of the third maxillipeds, apparently serving to keep the plates tightly shut when they enclose the antennae. The wide, broadly fringed dactylopodites, however, adapt these legs also to their function in burrowing. The other legs take a more transverse position and are ordinarily mostly concealed beneath the branchiostegite folds of the carapace on the sides and by the telson below (fig. 1 B). The second and third legs (fig. 7 C, D) are similar in size and shape to each other. The dactylopodites have the form of short pruning hooks with broad bases and decurved tips. Each dactylopodite is firmly hinged ventrally by a double articulation on the end of the propodite, and when flexed upward its wide base overlaps the posterior surface of the propodite. Anteriorly the dactylopodite is braced against a strong projection from the propodite (G, *Propd*). In either the flexed or the extended position of the dactylopodite, therefore, the propodite and the dactylopodite of the second and third legs present a firm posterior surface for pushing backward against the sand. On the other hand, a forward push would appear to be more effective with the dactylopodites flexed against the propodites. Evidently, then, the second and third legs are constructed both for burrowing into the sand, and for emerging from it. In the female the openings of the oviducts are on the coxae of the third legs.

The smaller fourth legs (fig. 7 E) are turned posteriorly and upward, and furthermore, are twisted in such a manner that the posterior surfaces of the dactylopodites face outward. In *Emerita talpoida* the dactylopodites of these legs are simpler in shape than those of the second and third legs, but they are likewise articulated ventrally on the propodites and overlap the outer surfaces of the latter when flexed. There is no bracing process of the protopodite against the mesal surface of the dactylopodite, but the fourth legs, with the dactylopodites in the flexed position, are clearly constructed to push outward, as they are said to do by Weymouth and Richardson. In *E. talpoida* there is little difference in the structure of the fourth legs between the female (E) and the male (H).

According to MacGinitie (1938) the males of *E. analoga* "attach to the female by the dactyls of their fourth legs, which are equipped with a sort of sucker pad surrounded by stiff hairs. Sometimes they hold on with both dactyls, at other times with only one. As viewed under the microscope the sucking pad with its surrounding hairs does not look very efficient, but the ease with which the males cling to a female is surprising, for they have merely to place the dactyl against any part of the carapace or appendage of the female to attain a hold. However, the clinging is voluntary and not automatic." A similar habit has not been observed in the case of *E. talpoida,* but an examination of the end segments of a fourth leg of the male *analoga* reveals a structure (fig. 7 I) quite different from that of *talpoida* (H). The

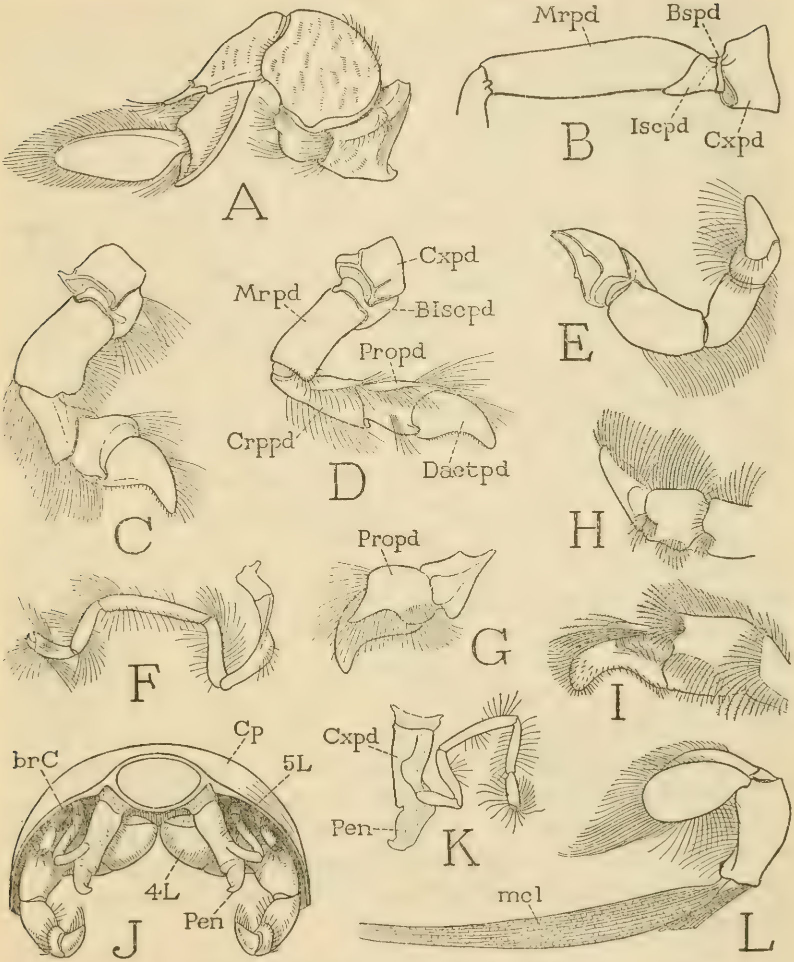


Fig. 7.—*Emerita talpoida* (Say) and *analoga* (Stimpson), pereiopods and uropod.

A, *Emerita talpoida* (Say), left first leg, ventrolateral. B, left leg of a crab, *Callinectes sapidus*, showing narrow basipodite ring (*Bspd*) on which the rest of the leg breaks off. C, *Emerita talpoida*, left second leg, posterior. D, same, left third leg, posterior. E, same, left fourth leg, lateral. F, same, left fifth leg of female, dorsal. G, same, anterior surface of distal segments of left second leg, showing process of propodite against anterior surface of dactylopodite. H, same, mesal surface of distal segments of fourth leg of male. I, *Emerita analoga* (Stimpson), mesal surface of distal segments of fourth leg of male. J, *Emerita talpoida*, posterior end of thorax of male, showing fourth and fifth legs. K, same, right fifth leg of male, posterior. L, same, left uropod and muscles from telson, in natural inverted position.

dactylopodite of the fourth leg in the female of *analoga* is the same as that of *talpoida* (E), but in the male (I) the dactylopodite is broad and hook-shaped as in the preceding legs; on its mesal surface is a large oval depression, which is fully exposed when the dactylopodite is extended, but it is overhung by a large brush of stiff hairs from the propodite, and from its upper margin a brush of long hairs projects beyond the tip of the dactylopodite, while a few delicate hairs arise from its lower margin. Otherwise also the setal arrangement on both the propodite and the dactylopodite is entirely unlike that of *talpoida* (H). It seems clear, therefore, that the fourth legs of the male in *analoga* are made for some special purpose, to which the corresponding legs of *talpoida* evidently are not adapted, but it is difficult to understand from the structure of the dactyls in *analoga* how this special function can be adhesion. The means by which the male of *analoga* holds the female with one or both of his fourth legs, therefore, needs closer observation on the living animals.

The fifth legs are small, slender, 7-segmented appendages (fig. 7 F) that can be seen on an intact specimen only by depressing the telson and straightening the abdomen. The coxopodites (J, *5L*) arise close behind the bases of the fourth legs (*4L*); the telopodites turn dorsally and forward and are usually looped in the branchial or subbranchial chambers (*brC*). These legs have diminutive apical chelae, the dactylopodite being a small hook opposed by a short process from the propodite. The distal segments are armed with long hairs, some of which are directed proximally (F), forming brushes, suggestive that the small fifth legs are used for cleaning the branchial chambers, or for preventing the entrance of sand into their open posterior ends. In the male (J, K) the coxopodites are particularly large and are produced distally into thick, soft papillae (*Pen*) on which open the genital exit ducts.

V. THE RESPIRATORY SYSTEM

The respiratory organs of Crustacea are primarily the gills, or branchiae. When the gills are enclosed in branchial chambers, however, various accessories become necessary for efficient respiration: there must be entrances into the chambers containing the gills, an apparatus for maintaining currents of water through the chambers, and an exit for the discharge of the respired water. In the decapods all these parts together constitute the external respiratory system.

In *Emerita* the gills (fig. 1 E, *Brn*) are very closely shut within the branchial chambers both laterally and ventrally by the branchiostegites (*Bstg*), and the posterior ends of the chambers are effectively closed by the deflexed abdomen. The broad, descending lateral folds of the branchiostegites (*bf*) enclose on each side a subbranchial canal (*x*) between the inner fold of the branchiostegite and the legs. Inasmuch as the inner folds taper in width posteriorly (F, *Bstg*), the subbranchial canals and the branchial chambers become confluent in the posterior part of the thorax. Anteriorly the soft inner folds of the branchiostegites are continuous with the sclerotic pterygostomial plates (F, *Ptst*), which are fully exposed on the sides of the body (fig. 1 B, *Ptst*), except as they are partly overlapped by the first legs. The lower margins of the pterygostomial plates lie close against the bases of the first legs, so that in *Emerita* there are here no apparent openings directly into the branchial chambers, as there are in some crabs. At their posterior ends, however, the pterygostomial plates go mesad of the lateral folds of the branchiostegites, where they become continuous with the inner folds of the latter, and thus create openings (fig. 1 B, *n*) that lead directly into the subbranchial canals. The pterygostomial apertures, therefore, would appear to offer a possible way for the intake of respiratory water, which would have easy access to the branchial chambers from the posterior ends of the subbranchial canals, or, in the case of a reversal of the currents, the same openings would serve as exits. This suggestion has only an anatomical basis, and needs the support of experimental evidence.

Each branchial chamber (fig. 8 A, *brC*) opens anteriorly into a pump chamber (*PC*) of the respiratory system, in which is lodged the scaphognathite (*Scpg*) of the corresponding second maxilla. The pump chambers are closed laterally by the pterygostomial plates. The two scaphognathites converge anteriorly past the sides of the labrum (fig. 6 C, *Lm*) into the triangular space below the bases of the antennules (*1Ant*), which finally runs out into the median respiratory tube formed by the close apposition of the four antennular flagella. If water enters through the antennular tube, it will be split into two streams by the apex of the labrum and thus drawn into the two pump chambers; or, if the current is reversed, the outgoing streams from the pumps will unite at the bases of the antennules to be discharged through the flagellar tube.

The vibratory movement of the scaphognathites is the force that drives the water through the respiratory passages. In the decapods generally the currents usually go from behind forward, but it has been observed in some burrowing crabs and also in certain other species that the currents can be reversed, presumably by a reversal in the action of the scaphognathites, and the same is probably true of *Emerita*. According to Smith (1877), when *E. talpoida* is buried, the excurrent forms a small opening and a slightly boiling motion in the sand. Mead (1917) says that by dropping small quantities of ink into the water over a buried individual of *E. analoga* the current was always found passing from posterior to anterior. On the other hand, Weymouth and Richardson (1912), by the same experiment on *E. analoga,* observed that the water is usually drawn into the antennular tube when the animal is buried, though occasionally it goes in the opposite direction, but that when the crabs are resting on the surface of the sand beneath the water or are swimming, the water is drawn in at the sides and expelled through the antennular tube. Evidently, therefore, *Emerita* when buried adjusts the direction of its respiratory currents according to conditions imposed by the sand.

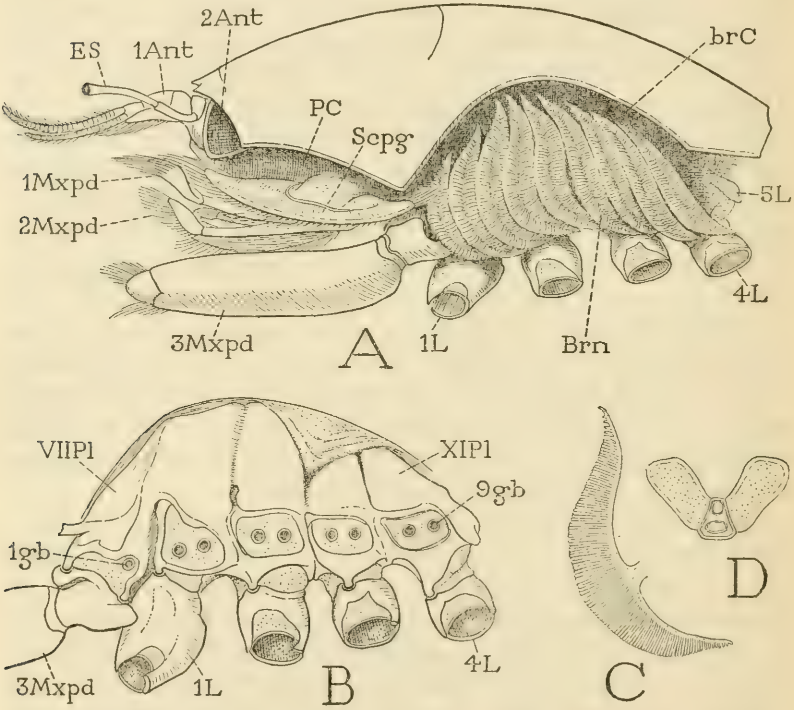


Fig. 8.—*Emerita talpoida* (Say), respiratory organs and thoracic pleuron.

A, lateral view of thorax with pterygostomial plate removed and fold of carapace cut away in the gill region, exposing anteriorly the pump chamber of the respiratory system, with the scaphognathite in place, and posteriorly the nine gills of the branchial chamber. B, left pleuron and leg bases of the gill-bearing segments, gills removed but their positions shown. C, a single gill, posterior. D, section of a gill, with paired lamellae on the axial shaft.

There are nine gills in each gill chamber of *Emerita talpoida* (fig. 8 A, *Brn*). The first gill pertains to the segment of the third maxillipeds (B, *1gb*), the others occur in pairs on the first four leg segments. The gills all arise from large membranous areas above the bases of the appendages. In the leg segments these areas lie within the pleura, since they are closed below by marginal pleural bars bearing the coxal articulations, so that the gills of the leg segments have the position of pleurobranchiae. The membranous area containing the gill base on the maxilliped segment (*1gb*), however, is not separated from the articular membrane of the coxa, which fact gives this gill the status of an arthrobranchia, though in position it falls in line with the other gills, and evidently is serially homologous with them. The coxa of the maxilliped is doubly articulated on the pleuron.

The gills themselves are crescent-shaped (fig. 8 C), and are closely massed in the gill chambers (A, *Brn*) with their upper ends converging to a peak where the pleural wall is highest (B). Each gill consists of two lateral rows of thin, closely set lamellae (D) arising from an axial shaft on the concave inner margin. Below its middle the shaft is connected with the pleuron by a short stalk.

VI. THE ABDOMEN, OR PLEON, AND ITS APPENDAGES

The abdomen of *Emerita* (fig. 1 C) consists of the usual six segments (*1-6*) and the telson (*Tel*) of the decapod abdomen. Dorsally the tergum of the first segment (*1*) appears only as a narrow transverse sclerite wedged between the thoracic carapace and the large tergum of the second abdominal segment, but from its anterior margin there is extended forward a large apodemal plate (D) inflected close beneath the carapace, which gives attachment to numerous muscles. The tergum of the second segment is as wide anteriorly as the carapace, but the next three terga are successively narrower, so that the margins of these four terga complete posteriorly the oval symmetry of the body (A). The sixth tergum (C, *6*) is a larger plate normally having a ventral position (B, *6*) when it is turned forward from the fifth. The sixth segment carries the uropods (*Urpd*) and the telson (*Tel*).

The abdominal appendages of the Crustacea are appropriately called *pleopods,* because the abdomen is known also as the pleon. Some writers limit the term "pleopod" to the appendages of the first five segments, and thus distinguish them from the uropods of the sixth segment, but if the abdomen is the pleon, it is consistent that all its appendages should be pleopods. The pleopods, however, are not necessarily "swimming legs" as the name might seem to imply from its derivation (Gr. *pleo,* sail, or swim), for some of them in the male are usually genital accessories, and in the female egg-carrying organs, the uropods alone being more consistently organs of aquatic locomotion.

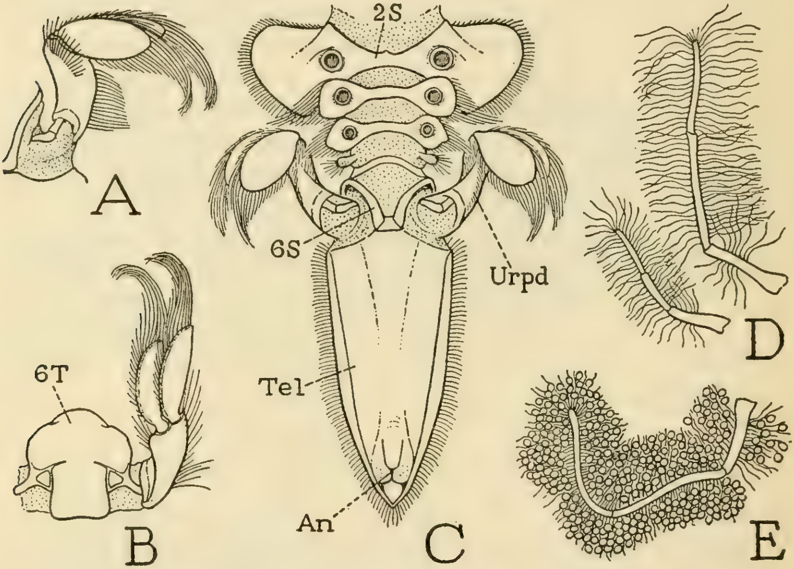


FIG. 9.—*Emerita talpoida* (Say), abdomen and pleopods.

A, left uropod, ventral. B, sixth abdominal tergum and right uropod, dorsal. C, ventral surface of female abdomen and telson, with uropods in place, pleopods of second, third, and fourth segments removed. D, second and third pleopods. E, first pleopod with eggs.

In *Emerita* the adult female has three pairs of slender pleopods pertaining to the second, third, and fourth abdominal segments (the position of their bases is shown at C of figure 9). These pleopods of the female are slender, 3-segmented appendages fringed with long simple hairs (fig. 9 D), and are used as egg-carrying organs (E). The first two pairs are much longer than the third. Corresponding pleopods are absent in the male.

The uropods are present alike in both the female and the male. They are relatively large appendages projecting from the sides of the sixth abdominal segment (fig. 9 C, *Urpd*). Each consists of a long, thick basal segment and of two flat, oval, closely appressed distal lobes with apical brushes of long hairs. The uropods are freely movable appendages, since they have large, membranous basal supports on the body, and are articulated only on pivotlike processes from the sides of the tergum of the sixth segment (B). On the ventral side (A) a rigid leverlike process projects from the base of the uropod into the articular membrane and gives attachment to two small muscles from the sixth tergum, which evidently serve to turn the uropod outward on the tergal pivot. The principal muscles of the uropods, however, arise in the telson. A long outer muscle (fig. 7 L, *mcl*) runs the full length of the telson to be attached on the posterior side of the base of the uropod; a much smaller muscle is attached anteriorly. The long muscles evidently give a strong posterior stroke to the uropods, but when the abdomen is flexed ventrally and the telson turned anteriorly, the direction of the stroke will be forward. *Emerita* is said to swim always backward, and in burrowing the uropods push forward.

VII. COMPARISON OF EMERITA WITH OTHER MEMBERS OF THE HIPPIDAE AND WITH THE ALBUNEIDAE

Inasmuch as *Emerita* appears to stand alone as an antennal feeder, it would be interesting to know the evolutionary steps by which it became structurally adapted to its mode of gathering food, because no halfway stage would seem to be practical. None of its relatives, however, gives any helpful suggestion, since the other hippids have gone their own way in the matter of feeding.

The genus *Hippa* in most respects is very similar to *Emerita*. Its second antennae (fig. 10 B, *2Ant*), however, do not appear to be in any way adapted for food collecting; though the large basal segments are comparable with those of *Emerita*, the flagella are short, and the whole appendages are brushlike by reason of their fringes of long hairs, and are ordinarily folded beneath the bases of the antennules, evidently to protect the respiratory passage between the latter. The third maxillipeds of *Hippa* have broad meropodites similar in shape to those of *Emerita*, but they are relatively smaller and only partly cover the mouth parts. In both *Hippa* and *Mastigocheirus* the mandibles (B, *Md*) are even more reduced than in *Emerita*, but in these two hippid genera substitute jaws have been developed from the mesal lobes of the first maxillae. The first maxilla of *Hippa cubensis* (fig. 10 E) has essentially the same structure as that of *Emerita* (fig. 6 A), but the proximal median lobe is a thick, strongly toothed jaw, those of the two appendages closing together beneath the mouth. Each jaw lobe is articulated on a basal rod of the appendage and has a second articulation on the ventral skeleton by means of an articular arm of its base. From the mesal surface (fig. 10 C) projects a strong process on which is attached the tendon of a large adductor muscle (E, *admcl*). Smith (1877) has described and figured the maxillula of *Hippa* (*Remipes*) *pacificus,* which appears to be the same as that of *H. cubensis.* For some reason, hard to guess, the hippids have all given up their mandibles as feeding organs. *Emerita* has adopted plankton feeding; the food and feeding habits of *Hippa* and *Mastigocheirus* appear to be unknown, but evidently their food is of such a nature that a pair of jawlike organs was found necessary for its proper ingestion.

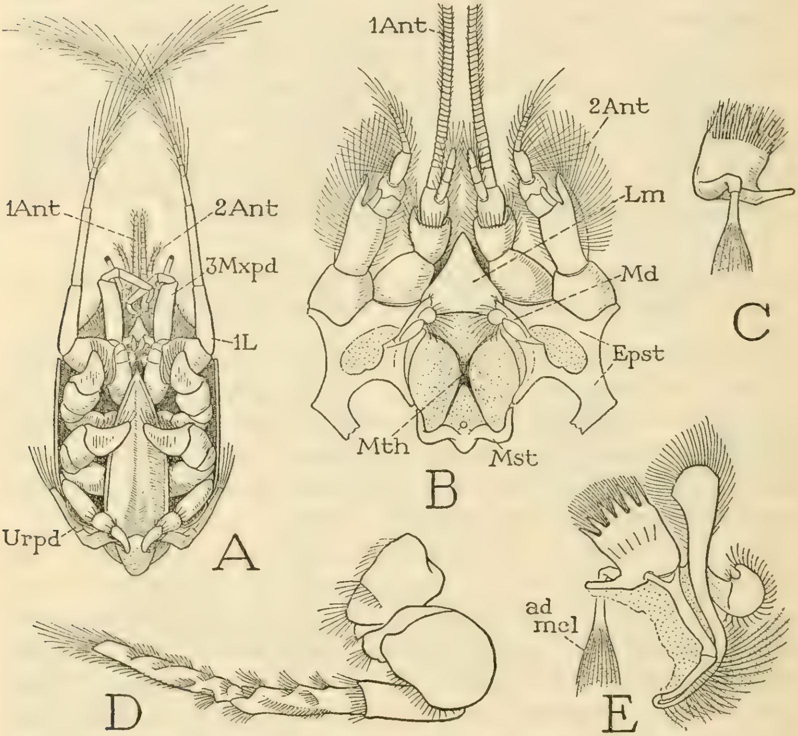


Fig. 10.—*Mastigocheirus* and *Hippa* (Hippidae).

A, *Mastigocheirus gracilis* (Stimpson), ventral surface. B, *Hippa cubensis* Saussure, head and mouth region, ventral. C, same, jaw lobe of first maxilla, mesal. D, same, right first leg, ventral. E, same, left first maxilla, ventral.

The second antennae of *Mastigocheirus* (fig. 10 A, *2Ant*) are relatively smaller than those of *Hippa* (B), but the first legs (A, *1L*) have an extraordinary length, and the long, multiarticulate, brushlike dactylopodites must have some special function when extended into the water over a buried individual; but if the function is food gathering, it is not evident from the structure of these legs that the dactylopodites could be brought back to the mouth. The corresponding legs of *Hippa* (D) are large, but they reach only a little beyond the tips of the antennules.

The antennules of the hippids are not so elaborately fringed as to make a respiratory tube so well enclosed as that of the albuneids (fig. 11 A). In *Emerita* the four antennular rami are of about equal length (fig. 2 A, D), in *Hippa* (fig. 10 B) the ventral rami are short, in *Mastigocheirus* they are minute. The longer rami have fringes of short hairs on their outer margins (fig. 10 B, *1Ant*) and a few very small setae on their mesal margins. The space below and between the antennular bases, however, is completely covered below by the large, flat, brushlike apical segments of the exopodites of the first maxillipeds, which are closely applied against the sides of the labrum, and in turn are shut in below by the infolded second antennae. There is thus formed at the base of the antennules a respiratory chamber which is continuous distally with the interantennular tube, and divides proximally into well-defined passages leading to (or from) the pump chambers.

The members of the family Albuneidae, though clearly related to the Hippidae, differ from the latter in various respects. The antennules have each only a single flagellum, but the two flagella are held securely together by fringes of interdigitating hairs along their dorsal and ventral margins, forming thus an efficient respiratory tube, which in *Albunea* (fig. 11 A) and *Lepidopa* is longer than the body. The second antennae of these two genera are relatively short, but in *Blepharipoda* they are long and the flagella are plumose, resembling those of *Emerita*. A distinctive feature of the albuneids, in contrast to the hippids, however, is the presence of strongly developed mandibles of the typical crab type of structure. The albuneids thus retain their ancestral feeding organs. Benedict (1886) reports that the stomach of a specimen of *Lepidopa* was found to contain setae of annelids, the skin of a very small holothurian, and parts of the flagella of some small crustacean.

The mandibles of *Blepharipoda occidentalis* converge anteriorly and mesally behind the epistome, so that when closed the gnathal lobes come together beneath the mouth. Each mandible (fig. 11 B) has an elongate basal part expanded mesally, where it bears a broad, flat gnathal lobe (*gnL*) and a 3-segmented palpus (*Plp*). The narrowed lateral end is bent posteriorly, and from the point of angulation a strong apodemal arm (*Ap*) projects laterally. The mandible is hinged on the edge of the epistome, but has a specific mesal articulation in front of the palpus, and a lateral articulation (*a*) with the ventral skeleton at its recurved posterior end. The axis of rotation (*a-c*), therefore, is oblique through the body of the jaw, and the apodeme (*Ap*) stands almost at right angles to the axis. The apodeme supports a large plate (*mp*) on which are attached antagonistic masses of muscle fibers, and is thus an effective lever for abduction and adduction of the gnathal lobe.

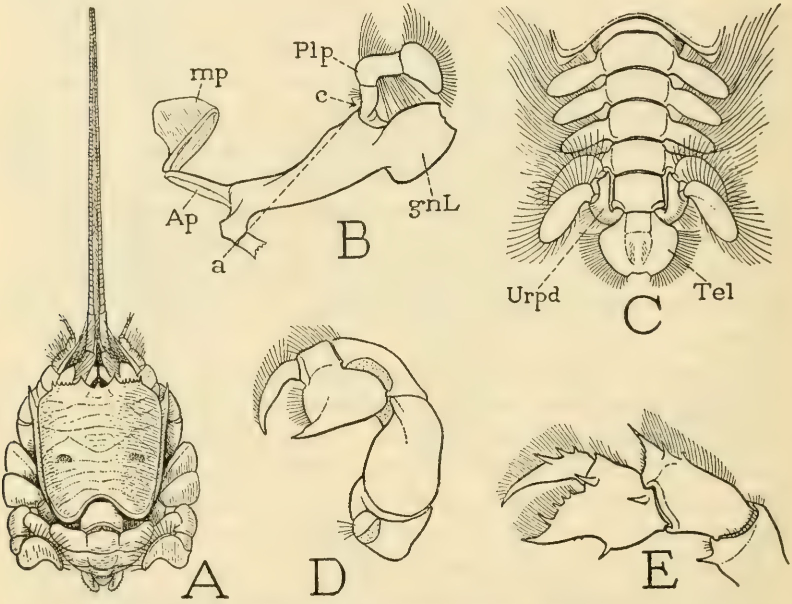


FIG. 11.—*Albunea* and *Blepharipoda* (Albuneidae).

A, *Albunea oxyophthalma* Leach, dorsal. B, *Blepharipoda occidentalis* Randall, right mandible, ventral. C, same, abdomen extended, dorsal. D, *Albunea oxyophthalma,* left first leg, ventral. E, *Blepharipoda occidentalis,* distal segments of left first leg, lateral.

The third maxillipeds of the albuneids have exopodite branches, and the meropodites are not widened. The first legs are strongly chelate (fig. 11 D, E). The pterygostomial plates are continuous posteriorly with the wide, soft branchiostegites, the two together forming on each side of the thorax a broad fold flexibly attached on the edge of the carapace, much the same as in *Galathea* (fig. 1 G). There are no outer folds of the branchiostegites such as are characteristic of the Hippidae. The albuneid telson is a short apical lobe of the abdomen (fig. 11 C, *Tel*), which, when the abdomen is flexed ventrally, covers the bases of only the fourth and fifth legs.

EXPLANATION OF LETTERING ON THE FIGURES

a, pleural articulation of coxopodite (lateral articulation of mandible).
admd, adductor muscle.
An, anus.
1Ant, first antenna, antennule.
2Ant, second antenna, antenna.
b, sternal articulation of coxopodite.
BC, body cavity, haemocoele.
bf, fold of branchiostegite.
BIscpd, basi-ischiopodite.
brC, branchial chamber.
Brn, branchia, gill.
Bspd, basipodite.
Bstg, branchiostegite, gill cover.
c, epistomal articulation of mandible.
Cp, carapace.
Crppd, carpopodite.
Cxpd, coxopodite.
D, dorsum.
Dactpd, dactylopodite.
Dbl, doublure of carapace.
d-e, axis of ventral flexion of antennal flagellum.
e, ocular plate of head.
Epst, epistome.
ES, eyestalk.
gb, gill base.
gnL, gnathal lobe of mandible.
ipB, interpedal brachium.
Iscpd, ischiopodite.
k, postantennal extension of epistome.
L, leg.
Lm, labrum.
m, postocular area of head.
mcl, muscle.
Md, mandible.
Mrpd, meropodite.
Mth, mouth.
1Mx, first maxilla, maxillula.
2Mx, second maxilla, maxilla.
mxB, pleural bridge of maxillary segment.
1Mxpd, first maxilliped.
2Mxpd, second maxilliped.
3Mxpd, third maxilliped.
n, aperture into subbranchial canal.
PC, pump chamber of respiratory system.
Pen, penis.
Pgn, paragnath.
Pl, pleuron.
Plp, palpus.
Propd, propodite.
Ptst, pterygostomial plate.
S, sternum.
Scpg, scaphognathite.
T, tergum.
Tel, telson.
tf, tergal fold.
Urpd, uropod.
V, venter.
W, wing.
x, subbranchial canal.

REFERENCES

BENEDICT, J. E.

1886. Revision of the Crustacea of the genus *Lepidopa.* Proc. U. S. Nat. Mus., vol. 26, pp. 890-895, 8 figs.

HENRY, LAURA M.

1948. The nervous system and the segmentation of the head in the Annulata. Microentomology, vol. 13, pt. 1, pp. 1-26, figs. 1-9.

MACGINITIE, G. E.

1938. Movements and mating habits of the sand crab, *Emerita analoga.* Amer. Midl. Nat., vol. 19, pp. 471-481, 9 figs.

MEAD, H. F.

1917. Notes on the natural history and behavior of *Emerita analoga* (Stimpson). Univ. California Publ. Zool., vol. 16, No. 23, pp. 431-438, 1 fig.

SCHMIDT, W.
1915. Die Muskulatur von *Astacus fluviatilis* (*Potamobius astacus* L.). Zeitschr. wiss. Zool., vol. 113, pp. 165-251, 26 figs.

SMITH, S. J.
1877. The early stages of *Hippa talpoida,* with a note on the structure of the mandibles and maxillae in *Hippa* and *Remipes.* Trans. Connecticut Acad. Arts Sci., vol. 3, pp. 311-342, 4 pls.

SNODGRASS, R. E.
1951. Comparative studies on the head of mandibulate arthropods. 118 pp., 37 figs. Ithaca, N. Y.

TIEGS, O. W.
1940. The embryology and affinities of the Symphyla, based on a study of *Hanseniella agilis.* Quart. Journ. Micr. Sci., vol. 82, pt. 1, 225 pp., 41 figs., 9 pls.

WEYMOUTH, F. W., and RICHARDSON, C. H.
1912. Observations on the habits of the crustacean *Emerita analoga.* Smithsonian Misc. Coll., vol. 59, No. 7, 13 pp., 1 pl.

WHARTON, G. W.
1942. A typical sand beach animal, the mole crab, *Emerita talpoida* (Say). *In* Pearse, A. S., Humm, H. J., and Wharton, G. W., "Ecology of Sand Beaches at Beaufort, North Carolina." Ecol. Monogr., vol. 12, pp. 135-190, 24 figs.

ZOBELL, C. E., and FELTHAM, CATHARINE B.
1937-38. Bacteria as food for certain marine invertebrates. Journ. Marine Res., vol. 1, pp. 312-327.

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 117, NUMBER 9

Roebling Fund

PRECIPITATION AND TEMPERATURE IN WASHINGTON, D. C., FOR 1951 AND 1952

BY
C. G. ABBOT
Research Associate, Smithsonian Institution

(Publication 4087)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
MARCH 18, 1952

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

Roebling Fund

PRECIPITATION AND TEMPERATURE IN WASHINGTON, D. C., FOR 1951 AND 1952

By C. G. ABBOT

Research Associate, Smithsonian Institution

A. PRECIPITATION AT WASHINGTON

Based on a cycle of 27.0074 days, I have predicted about 175 dates each year when precipitation in Washington, expressed as the average value per day, should exceed that quantity for all other dates.[1] The ratio of precipitation, $\frac{\text{preferred dates}}{\text{all other dates}}$, has exceeded unity each year for 18 consecutive years. The value of this ratio for the year 1951 is 134 percent. The expected value is 142 percent, and the average of it, for 18 years, is 146 percent. Details for the year 1951 are given in table 1.

Table 1.—*Statistics of Washington precipitation, 1951*

(Values in inches)

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
Average per day: Pfd.	0.053	0.152	0.169	0.154	0.183	0.277	0.028	0.088	0.089	0.036	0.197	0.174	0.134
Average per day: All other	0.085	0.040	0.040	0.111	0.031	0.337	0.129	0.018	0.089	0.066	0.117	0.133	0.100
Ratio $\frac{\text{Pfd.}}{\text{All other}}$	0.62	3.80	4.22	1.39	5.98	0.82	0.22	4.89	1.00	0.55	1.68	1.31	1.34
Total ppt.	2.18	2.57	3.17	3.93	3.23	9.28	2.50	1.75	2.67	1.66	4.79	4.77	42.50
Normal ppt.	3.55	3.27	3.75	3.27	3.70	4.13	4.71	4.01	3.24	2.84	2.37	3.32	42.16
Percent of normal	0.61	0.79	0.85	1.20	0.87	2.25	0.53	0.44	0.83	0.58	2.02	1.44	1.01

Preferred days of 1951 had a higher average precipitation than all

---

[1] See Smithsonian Misc. Coll., vol. 104, Nos. 3 and 5, 1944; vol. 111, No. 17, 1950; vol. 116, No. 4, 1951.

SMITHSONIAN MISCELLANEOUS COLLECTIONS, VOL. 117, NO. 9

other days in all months but January, June, July, September, and October. In September the ratio was 1.00. In June 5.08 inches of rain fell within 12 hours of preferred dates, so that the prediction on these dates was but a half day amiss.

Table 2.—*Predicted dates when average daily precipitation should exceed average daily precipitation for all other dates for the year 1952 in Washington, D. C.*

"Preferred" cycle places	Jan.	Feb.	Mar.	Apr.	May	June
I	10	6	4, 31	27	24	20
II	11	7	5	28, 1	25	21
III	12	8	6	29, 2	26	22
IV	13	9	7	30, 3	27	23
V	14	10	8	4	28, 1	24
XII	21	17	15	11	8	4
XIII	22	18	16	12	9	5
XV	24	20	18	14	11	7
XVII	26	22	20	16	13	9
XVIII	27	23	21	17	14	10
XXII	31, 4	27	25	21	18	14
XXVI	..	..	29, 2	25	22	18
XXVII	..	..	30, 3	26	23	19

"Preferred" cycle places	July	Aug.	Sept.	Oct.	Nov.	Dec.
I	17	13	9	6	2, 29	26
II	18	14	10	7	3, 30	27
III	19	15	11	8	4	28, 1
IV	20	16	12	9	5	29, 2
V	21	17	13	10	6	30, 3
XII	28, 1	24	20	17	13	10
XIII	29, 2	25	21	18	14	11
XV	31, 4	27	23	20	16	13
XVII	6	29, 2	25	22	18	15
XVIII	7	30, 3	26	23	19	16
XXII	11	7	30, 3	27	23	20
XXVI	15	11	7	31, 4	27	24
XXVII	16	12	8	5	28, 1	25

Table 2 gives the dates in 1952 when the average daily precipitation in Washington is expected to exceed the average daily precipitation in this city for all other dates. Readers should neglect the first column of the table, to avoid being confused. It merely gives, in Roman numerals, the "preferred days" in the standard 27-day period. The other columns show when these dates occur in all the months.

While it is expected that the dates given in table 2 for the months of 1952 will yield a higher average of daily precipitation than this average for all other dates of 1952 in Washington, the probability that any individual date of the table will have any precipitation at all is not greatly above 50-50.

The basic tabulation, on which table 2 rests, began with January 1924 and ended with December 1941. The length deduced for the precipitation cycle is 27.0074 days. In 379 cycles of this length there are 10,235.8046 days. From January 1, 1924, to December 31, 1951, there are 10,227 days. Hence the 379th cycle begins on January 10, 1952, as given in table 2.

This paper was prepared on January 14, 1952, but could not be circulated in printed form until March 1952. Readers who may wish to extend table 2 to cover the first three months of 1953 should note that January dates are four days earlier than December dates, February four days earlier than January and March and one day earlier than February in 1953.

B. TEMPERATURE AT WASHINGTON

In previous papers [2] I have noted a period of 6.6485 days in the temperatures of Washington and New York, which has subsisted, on the average, unaltered since 1910, though individual recurrences of it are apt to depart one, two, and sometimes three days from regularity.

In table 3 I give the dates predicted for minima in 1951, the dates when minima occurred, and the dates predicted for minima in 1952. The predicted dates tabulated are those within a half day of those accurately computed for minima, based on a cycle of 6.6485 days, with zero date January 17.0000, 1946.

Figure 1 shows the relative frequency of departures of zero and ±1, 2, 3 days from the computed dates of minima of temperatures.

As another graphical example of the close accordance between computed and observed minima of temperature in Washington I submit figure 2. This gives the departures from normal temperatures in Washington from March 21 to May 10, 1951. At the exact places of minima, as computed with the cycle of 6.6485 days, from January 17.0000, 1946, heavy solid lines are drawn. As shown in the paper just cited (Smithsonian Misc. Coll., vol. 111, No. 13, p. 6), a subsidiary cycle of $\frac{6.6485}{2}$ days was discovered. Dotted heavy lines represent the places of minima of temperature at Washington for this subsidiary cycle. It will be apparent that all the minima of the curve of temperatures in figure 2 fall within one day of these heavy lines, indicating places of computed minima.

---

[2] Smithsonian Misc. Coll., vol. 107, No. 4, 1947; vol. 111, No. 6, 1949; vol. 111, No. 13, 1949; vol. 116, No. 4, 1951.

TABLE 3.—*Dates in 1951 when minima in Washington temperatures were predicted and observed, and dates predicted in 1952*

	January	February	March
1951 predicted	6 13 19 26	2 8 15 22 28	7 14 20 27
1951 observed	8 13 22 26 31	3 8 15 24	3 10 22 26
1952 predicted	6 12 19 26	1 8 15 21 28	6 12 19 25

	April	May	June
1951 predicted	3 10 17 23 30	7 13 20 27	2 9 16 22 29
1951 observed	3 10 17 23 28	5 12 19 29	5 10 13 19 29
1952 predicted	1 8 14 27 28	4 11 18 24 31	7 13 20 27

	July	August	September
1951 predicted	6 12 19 25	1 8 14 21 28	3 10 17 22 29
1951 observed	6 13 20 24	2 6 13 24 28	8 18 24 29
1952 predicted	3 10 16 23 30	5 12 19 25	1 8 14 21 28

	October	November	December
1951 predicted	6 12 19 26	1 8 15 21 28	4 11 18 24 31
1951 observed	10 20 29	3 8 .. 19 28	10 16 22 27
1952 predicted	4 11 18 24 31	7 13 20 26	3 10 16 23 30

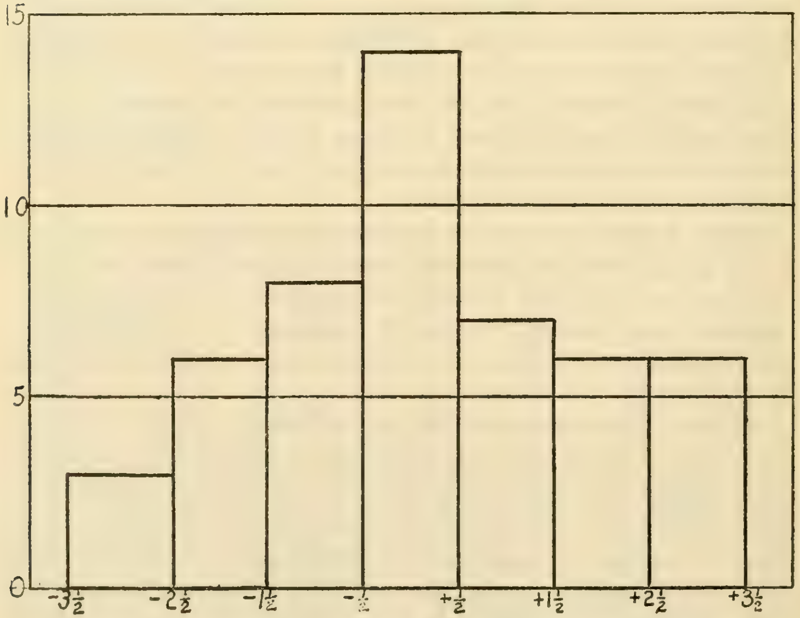


FIG. 1.—Relative frequency of minima of temperature at Washington 0 to ± 3 days from dates predicted.

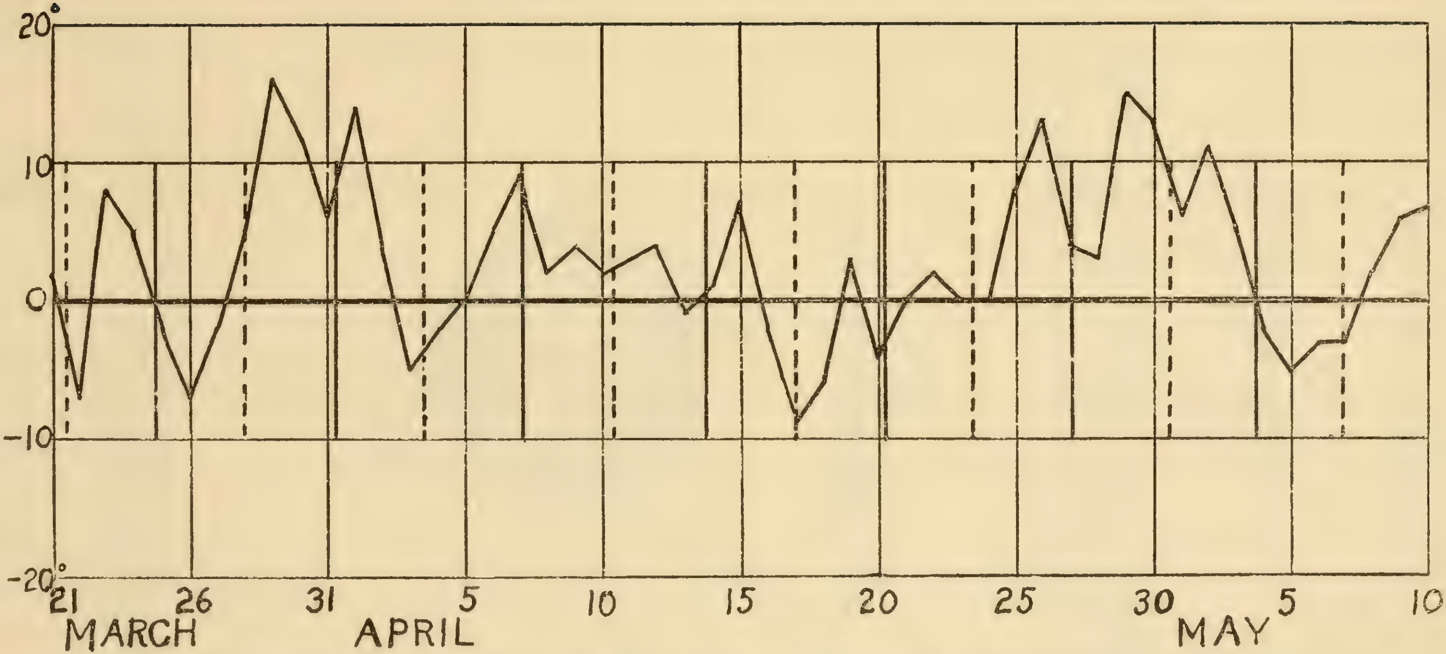


Fig. 2.—Departures from mean temperatures at Washington March 21 to May 10, 1951. Heavy solid lines are dates computed from January 17, 1946, by cycle of 6.6485 days. Heavy dotted lines are similarly for cycle of $\frac{6.6485}{2}$ days.

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 117, NUMBER 10

Roebling Fund

PERIODICITIES IN THE SOLAR-CONSTANT MEASURES

BY
C. G. ABBOT
Research Associate, Smithsonian Institution

(Publication 4088)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
MAY 28, 1952

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

Roebling Fund

PERIODICITIES IN THE SOLAR-CONSTANT MEASURES

By C. G. ABBOT[1]
Research Associate, Smithsonian Institution

INTRODUCTION

This paper, based on over 40 years of observations of solar radiation, ties together the following conclusions:

1. The sun's output of radiation varies.
2. It varies in at least 23 regular periodicities, all proceeding simultaneously.
3. The periods of solar variation are integral submultiples of 22$\frac{3}{4}$ years.
4. Synthesis of curves representing the 23 periodicities reproduces the original observations of the "solar constant" to within about 0.1 percent.
5. Synthesis of these curves for 12 years as a prediction, prior to the observations on which they depend, shows rough agreement with Mount Wilson observations of the solar constant, in the years 1908 to 1920.
6. A much more satisfactory agreement is found between this predicted synthetic solar-constant curve and the Mount Wilson determinations of the march of contrast along the east-west diameter of the sun, of 1913 to 1920.
7. Higher contrast attends higher solar-constant values.

In several former publications[2] I have discussed the periodic changes in observed values of the solar constant of radiation.

For several years I have been investigating the effect on terrestrial weather of these periodic changes in the sun's emission. I had become convinced by the earlier solar-constant studies, just cited, that the sun's radiation varies simultaneously in many regular periods, all

---

[1] I wish to express my sincere acknowledgments to L. B. Aldrich, Director of the Astrophysical Observatory, who made the data available for this paper and gave highly valuable criticisms; to Frederick E. Fowle, deceased, whose careful measurements of solar contrast appear in table 6; to Mrs. A. M. Bond, deceased, whose critical judgment and accurate computations aided in the preparation of the data; to the many observers on high mountains in distant lands who sacrificially kept up this long campaign of measurement; to Mrs. I. W. Windom, who assisted in preparing this text; and to Miss M. A. Neill, who continuously over many years greatly assisted me in keeping the observing stations in operation.

[2] Annals Astrophys. Obs., Smithsonian Inst., vol. 5, p. 250 et seq., 1932; vol. 6, p. 178 et seq., 1942. Smithsonian Misc. Coll., vol. 111, No. 7, 1949.

aliquot parts of 22¾ years. I hoped, by using a long interval of scores of years of an unbroken series of monthly weather records, that I could discover from them all the submultiples of 22¾ years which yield effective periodic variations of the solar radiation.

But I found that the variations of the atmospheric conditions from time to time, some associated with the seasons and some with the sunspot cycle, so badly confuse the phases of responses to solar variation that I could not be certain that all the suspected solar periodicities, inferred from weather records, are real. Hence I felt constrained to reinvestigate the observed fluctuations of the solar constant, to determine directly which of the submultiples of 22¾ years are truly periods in solar variation.

In former papers I have used 273 months as the master period, of which the others are integral submultiples. My present work leads me to prefer 272 months. All the periods which I have found lie within less than 1 percent of being integral fractions of 272 months.

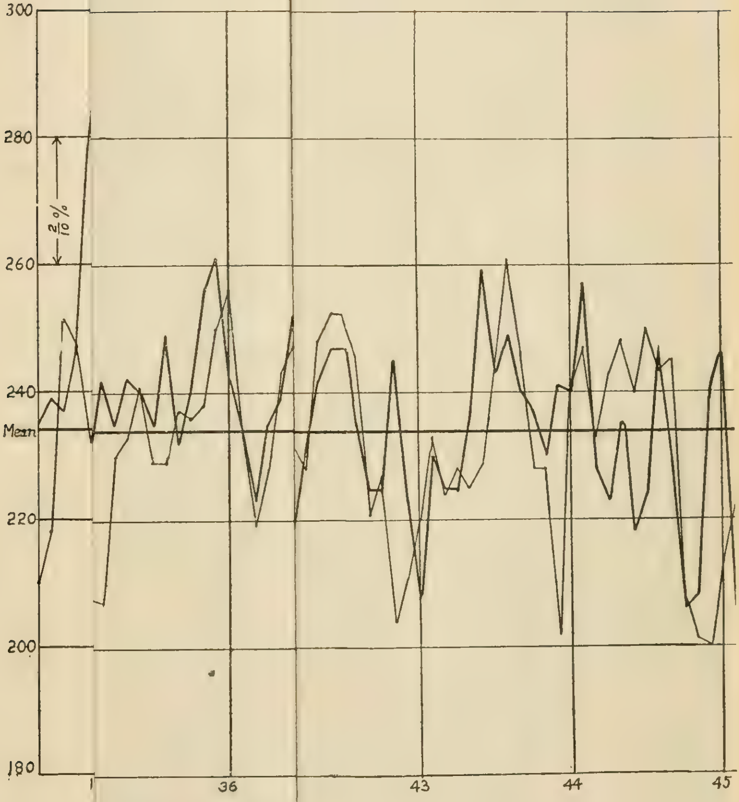
ADVANTAGES OF METHOD

Some investigators would prefer to submit the available solar-constant data to a Fourier analysis based on 272 months. I prefer to tabulate the data according to each suspected possible period. There are several advantages in this method. In so doing, I divide the total interval covered by the data into several parts, if periods are short enough to furnish a large number of repetitions. In this way the phases of features may be compared in the several independent tabulations of one period. Graphs showing this procedure are given in figure 1. Slight shifts,[3] from one to another of the successive tabulations, indicate small corrections to the assumed period. The form of the curve of fluctuation is determined by the tabulations. Also the amplitude of the periodic variation is found. If it is too small to be certainly exceeding the probable error, then the periodicity is to be rejected altogether. Proceeding in this way, I found 23 periodicities in solar-constant results which meet the tests of veridity just indicated. Fifteen other periods were tabulated, but rejected. Each search involved tabulating more than a thousand decade mean values of the solar constant. The results appear in table 1.[4]

---

[3] See the curves, 6 1/30, of figure 1, in comparison with table 1C, below.

[4] In tabulating any one periodicity, all the others exercise confusing influences, which are not wholly eliminated, because of the small numbers of repetitive columns going to make up the tables. Hence, irregularities in the curves of figure 1 are caused by conflicting periodicities, in addition to the effects of accidental errors of observation.



npared to a synthesis

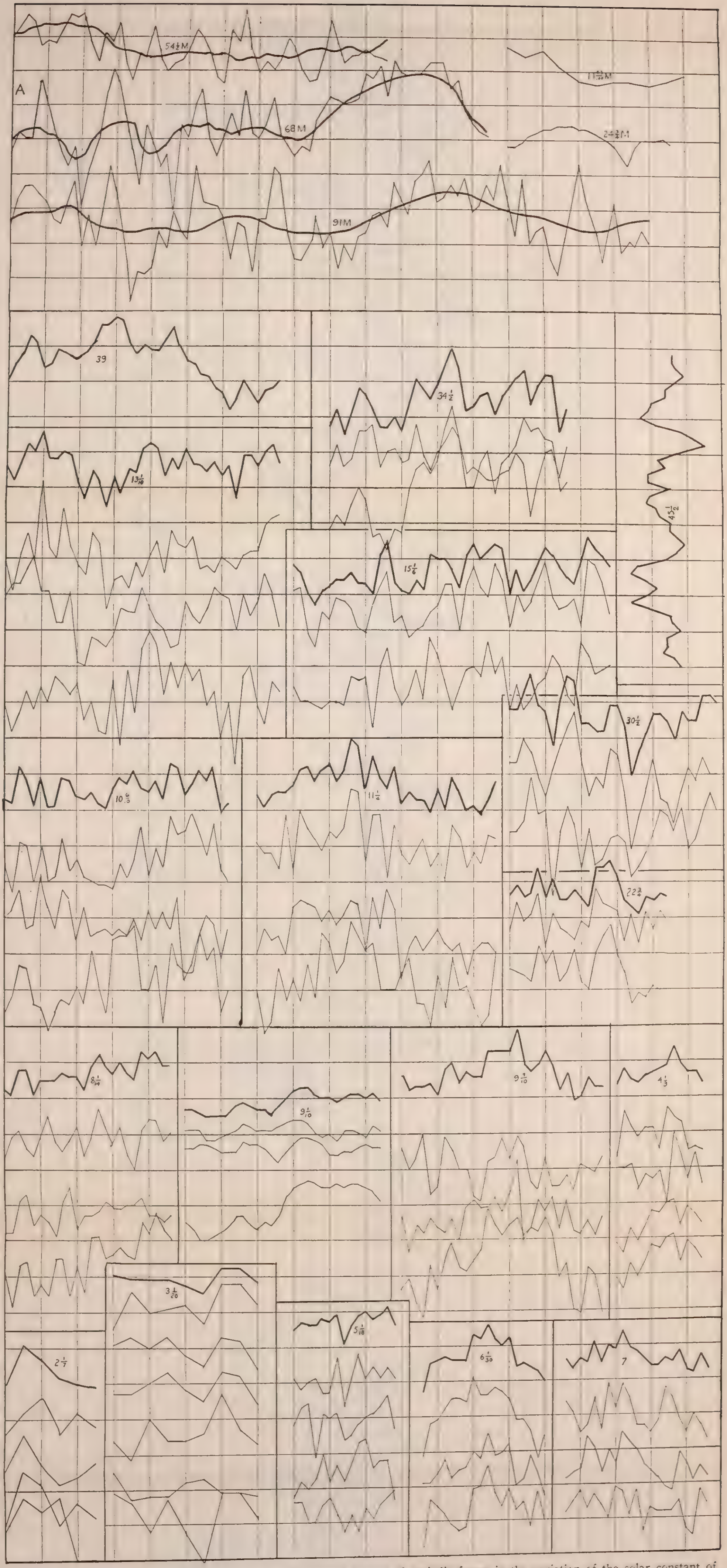
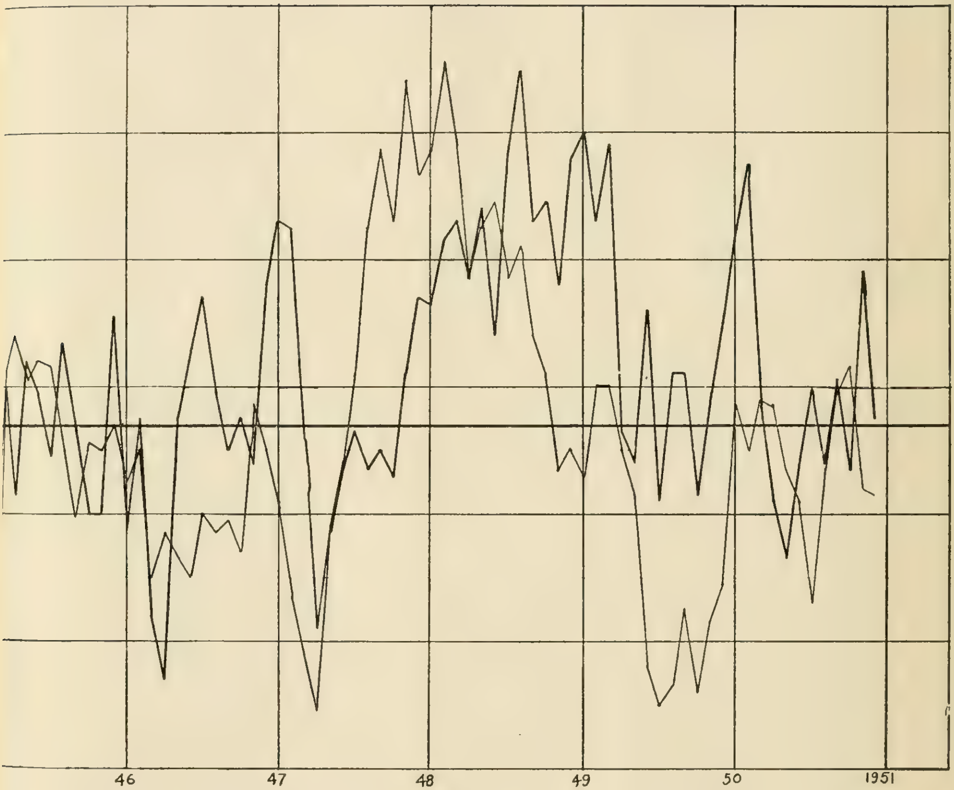


FIG. 1.—Consecutive partial determinations and general means of periodic forms in the variation of the solar constant of radiation as observed 1920 to 1950. Periods are indicated in months. Spaces in ordinates represent 1/10 percent variation in solar radiation.


46
47
48
49
50
1951

It may aid to fix ideas on the method of tabulation to give an example. Table 1C is a facsimile of the computation for the period 6 1/30 months. I select it as indicating how fractional parts of months and of 10-day means are treated, so as to preserve the exact average period. I had at first assumed that 6 1/15 months was the proper length of period. The data were separated into three groups. The assumed period corresponds with 18 1/5 10-day intervals. When the mean values for the three groups were computed, they were plotted, superposed. It was then apparent that the maximum ordinates shifted progressively toward earlier dates, as time went on. This indicated that the assumed period is too long by 4/700 of itself. Making this correction, the true period is 6 1/30 months.

PREPARATION OF DATA

L. B. Aldrich, Director of the Astrophysical Observatory, and his associates had painstakingly considered every circumstance affecting every daily solar-constant observation, at all the Smithsonian mountain stations in various lands. By consensus of three individual opinions, they had assigned to every observed day its most probable solar-constant value, as indicated by the checked results of all stations. Many days were not observed at all. However, there was no decade of any month, from 1920 to 1950, which did not have at least more than one observation.

Mr. Aldrich having been good enough to place these daily solar-constant results in my hands, I computed 10-day and monthly mean values from them for the 31 years 1920 to 1950. To have them in most convenient form for my use, I took their departures from the value 1.900 calories per square centimeter per minute and divided these departures by 1.940. Thus the results became expressed in percentage departures of the solar constant from 1.900 calories. In that form any well-evidenced periodic change resulting from a tabulation shows at once its amplitude in percentage of the solar constant. All values are positive as thus treated, which is convenient in tabulation. These data are given in table 4, appendix I.

PERIODS FOUND AND NOT FOUND

With these clarifying remarks, I now introduce the results. The following periodic changes in the solar constant were found well evidenced. Their approximate relation to 272 months and their amplitudes in percentage of the solar constant are given in table 1A.

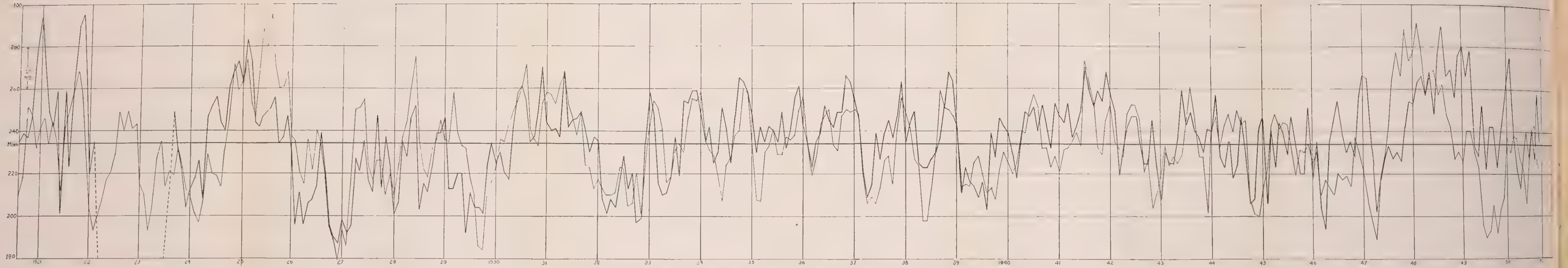


FIG. 4—The march of solar variation, 1920 to 1950 (heavy lines) compared to a synthesis of the 23 regular periodicities given in table 2, shown here in light lines.

The following periodic changes, given in table 1B, if real, are too small in percentage to be verified.

TABLES 1A, 1B.—*Periodicities in solar-constant observations*

A. Periodicities confirmed *

Period Months	Amplitude Percent	Period Fraction of 272
2 1/7	0.05	1/127
3 1/20	0.05	1/90
4 1/3	0.06	1/63
5 1/18	0.05	1/54
6 1/30	0.12	1/45
7	0.08	1/39
8 1/14	0.06	1/34
9 1/10	0.08	1/30
9 7/10	0.10	1/28
10 6/10	0.06	1/26
11 1/5	0.17	1/24
11.43	0.11	1/24
12.0	0.20	....
13 1/10	0.11	1/21
15 1/6	0.09	1/18
22 3/4	0.07	1/12
24 3/4	0.12	1/11
30 1/3	0.13	1/9
34 1/2	0.15	1/8
39	0.20	1/7
45 1/2	0.13	1/6
54 1/2 †	0.13	1/5
68	0.25	1/4
91	0.12	1/3
272	...	1

B. Periodicities sought but not found

Period Months	Period Fraction of 272
4 1/2	1/60
5 1/2	1/50
6 1/2	1/42
7 5/6	1/35
8 1/2	1/32
10 1/9	1/27
10 9/10	1/25
13 6/10 †	1/20
14 4/10	1/19
17	1/16
18 1/5	1/15
19 1/2	1/14
21	1/13
24 8/10	1/11
136	1/2

* The periodicities of 11.43, 12.0 (the periodicity of 12 months is not used in preparing figure 4; if it were, that figure would present closer accord between the curves), and 24¾ months were added to the list after search among the departures of the synthetic values, found by summing 21 periodicities, from the observed solar-constant values. It is indeed curious to find *two* periodicities both within 1 percent of 1/24 of 272 months. Both of them are excellently evidenced and of good amplitude. The 12-month period is of terrestrial, not solar, causation. When one reflects that the pyrheliometer observes only about 70 percent of the solar constant, the remaining 30 percent being supplied by our estimates of atmospheric transmission, it is perhaps not surprising that the yearly (terrestrial) periodic error in the solar-constant values is as large as 0.2 percent in amplitude. The periodicity of 24¾ months was the only other one which could be discerned in a residual plot of differences, smoothed by 7-month running means.

† After this work was done, I computed a table of the periodicity 54 8/10 months in the precipitation of Peoria, Ill., 1856 to 1939. It showed *no* periodicity of 54 8/10 months, but *four* strong, well-shaped periodicities of 54 8/10 ÷ 4 = 13 7/10 months. Hence I think the sun's radiation has a periodic variation of one-twentieth of 22⅔ years, though it did not impress me as real in the tabulation of the solar constant.

All periods of these two lists were separately sought for by tabulating over 1,000 solar-constant 10-day means for each suspected periodicity. The investigation does not cover entirely the years 1922 and

1923. I have elsewhere discussed the large solar change observed in those years.[5] I still think it was a real one. But it may be either a very unusual sporadic solar change, or it may be a periodic change related to a longer period than 272 months.

CONCERNING DOUBTS OF SOLAR VARIATION

For those who do not have intimate association with the Smithsonian observations of the solar constant of radiation, it seems difficult to accept the results as having the high degree of accuracy claimed for them. Observers, familiar with the clouds, dust, and water-vapor load which the lower atmosphere bears to make it milky, do not readily visualize a sky so clear that, if one holds his little finger at arm's length before the sun, the sky seems deep blue right down to the sun's edge. But even if the superior excellence of stations like Montezuma, Table Mountain, and St. Katherine be granted, it still seems incredible to many that the fraction, amounting to about 30 percent of the solar constant, cut off by the atmosphere, can be so correctly estimated that variations of the order of 1/10 percent of the solar constant can be evaluated.

Still more doubtful does it appear to many that, lacking any theoretical support, it can be proved from the observations that the solar variation consists of 23 simultaneously operating regular periodicities, all aliquot parts of 22$\frac{3}{4}$ years. Yet it seems to me this cannot longer be doubted. I have tried to demonstrate by a couple of examples that it is necessary to use integral fractions of 22$\frac{3}{4}$ years, rather than any other intervals, to represent the the sun's periodic variation. The two periods I have chosen to experiment upon are those which are 1/7 and 1/45 of 22$\frac{3}{4}$ months. In figure 1 the longer period is plotted as 39 months.

I made a new tabulation in four parts for a period lying between 1/45 and 1/44 of 22$\frac{3}{4}$ years. It was assumed to be 6$\frac{1}{6}$ months, or 19 10-day intervals. In each of the four groups tabulated there are 14 columns. Taking the mean values, they are as plotted in figure 2,A. Evidently, if the four mean results were combined directly, they would so contradict each other that the general mean would show no periodicity at all. But the principal feature, marked A at its right-hand edge in each plot, is equally displaced from curve to curve toward the left by about 6 10-day intervals. The displacement is 19

---

[5] Monthly Weather Rev., U. S. Weather Bureau, February 1923. Proc. Nat. Acad. Sci., vol. 9, No. 6, pp. 194-198, 1923. Smithsonian Misc. Coll. vol. 77, No. 5, 1925 (see fig. 11); vol. 80, No. 2, 1927.

10-day intervals, in all, from curve I to curve IV. Between these curves I and IV lies a stretch of time of about 800 10-day intervals. Hence the period should have been taken less than $6\frac{1}{6}$ months by $19/800 \times 6\frac{1}{6} = 0.146$. Subtracting from 6.163, this yields a corrected period of 6.017 months. Within the error of determination, this checks with 6.003, which is the period given in table 1C. Having displaced curves II, III, and IV by 6, 12, and 19 10-day intervals respectively, and having taken the general mean of the four and plotted it, the result appears in figure 2,B. It is to be compared with the curve of 6.033 months above it, representing the mean value as given in table 1C. It must be admitted that the agreement is striking.

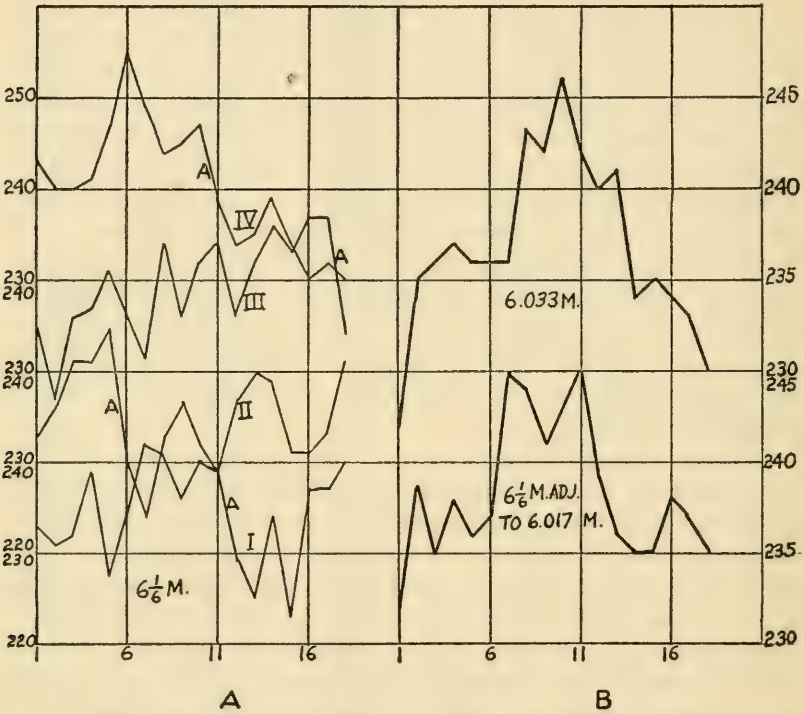


FIG. 2.—The periodicity 6.033 months, confirmed by the displacement of the feature A gradually from I to IV, when the period is assumed to be $6\frac{1}{6}$ months, as shown in figure A. In figure B this displacement is adjusted to a period of 6.017 months, which nearly agrees with the true period, 6.033 months.

Proceeding similarly, I computed two curves [6] for the seventh of

---

[6] There being but four columns in these part computations for 39 and 37 months, the plots of the results are very ragged, owing to the disturbing influences of 22 other periodic factors superposed.

																			Σ	÷ 18	Adjusted places		Mean	Δ
1	254	237	211	206	201	232	288	273	180	252	154	237	237	201	242	191	211	227	3998	222	231	229	227	—10
2	239	288	263	211	232	211	299	263	211	216	216	258	247	237	191	211	216	232	4241	236	231	238	235	— 2
3	265	278	196	252	252	232	263	263	232	216	216	247	221	196	206	211	221	227	4205	234	234	239	236	— 1
4	263	299	227	252	211	278	258	242	191	227	247	221	216	227	191	216	206	232	4178	232	238	242	237	0
5	227	206	263	242	216	252	263	232	170	201	232	206	227	232	242	175	227	247	4115	229	233	245	236	— 1
6	227	242	268	237	196	268	252	237	201	206	201	211	242	211	227	206	232	242	4080	227	235	245	236	— 1
7	227	242	268	221	206	263	216	232	216	180	206	232	227	227	216	227	252	242	4105	228	236	244	236	— 1
8	278	242	294	237	221	263	221	216	201	185	242	232	263	252	216	237	242	263	4305	239	240	251	243	+ 6
9	206	242	309	221	237	268	258	252	206	185	216	247	247	237	227	237	242	268	4321	240	238	246	242	+ 5
10	278	267	294	227	252	273	247	242	211	201	253	242	247	237	206	237	273	278	4434	246	245	246	246	+ 9
11	258	247	283	211	252	283	237	247	196	170	221	227	278	227	175	227	258	263	4241	238	239	248	242	+ 5
12	201	263	309	221	297	263	247	237	216	201	227	201	232	252	196	211	232	216	4212	234	240	247	240	+ 3
13	294	185	273	216	247	273	258	258	211	191	232	221	232	242	206	232	278	247	4311	239	242	245	242	+ 5
14	263	206	247	175	263	242	263	237	221	206	216	196	221	258	211	232	273	268	4188	233	230	239	234	— 3
15	278	211	268	216	247	263	278	258	211	196	232	216	216	237	216	211	242	247	4238	235	232	239	235	— 2
16	299	258	165	211	268	283	206	196	211	191	211	237	191	232	201	232	268	258	4102	228	239	236	234	— 3
17	304	268	247	211	252	278	258	201	232	175	221	211	227	211	206	247	252	216	4284	238	234	228	233	— 4
18	278	252	247	221	278	283	221	206	232	242	232	201	227	196	206	232	247	227	4146	230	227	234	230	— 7
19					221					160					211									

Mean 237

																				÷ 18
1	237	232	206	237	206	263	258	263	237	237	232	252	211	227	206	247	227	227	4205	234
2	258	263	191	211	211	263	232	268	242	242	237	252	216	242	237	263	201	258	4289	238
3	237	263	221	180	227	237	221	263	227	242	237	242	180	247	237	268	211	258	4198	233
4	237	221	211	201	191	263	221	268	247	247	237	268	227	247	227	268	221	221	4223	235
5	237	237	232	211	196	242	227	263	232	268	232	273	237	247	206	268	211	227	4246	236
6	288	221	227	185	206	263	242	258	247	252	247	258	237	258	211	258	211	258	4327	240
7	258	232	154	201	232	273	221	268	237	247	258	278	237	252	227	273	196	242	4286	238
8	258	237	206	258	206	268	242	258	237	263	252	263	242	278	232	258	221	237	4416	245
9	247	221	221	237	216	252	258	247	247	273	247	247	221	232	227	242	221	242	4298	239
10	247	247	221	211	232	258	252	242	247	237	252	247	227	268	232	237	227	237	4321	240
11	232	242	263	258	247	258	258	268	227	263	242	273	232	206	221	242	201	227	4360	242
12	232	242	206	247	242	237	232	232	232	227	242	242	242	221	227	216	201	227	4147	230
13	252	242	216	268	221	247	232	237	247	242	232	247	232	237	232	185	180	232	4181	232
14	247	221	196	258	221	263	211	237	263	263	252	237	242	273	232	232	227	232	4307	239
15	247	227	227	242	221	216	237	216	237	196	242	252	252	268	237	221	252	211	4201	234
16	258	232	216	242	216	227	227	221	232	201	232	211	247	237	232	216	232	211	4090	227
17	232	165	191	237	252	247	232	242	237	237	252	221	237	242	242	232	232	227	4157	231
18	252	175	232	206	247	221	247	263	227	232	262	227	242	232	247	221	221	211	4165	231
19		221					263					201					237			

Adjusting period

$\frac{4}{700}\times 6 = 0.034$

6.067 — 0.034

is 6.033

or 6 1/30

																					Σ	÷ 20
1	268	252	221	247	227	237	242	237	242	237	237	242	252	237	216	247	263	283	242	263	4892	245
2	242	252	247	268	242	242	232	247	237	232	242	252	227	232	211	258	283	278	232	242	4898	245
3	237	227	216	247	257	257	237	206	227	237	232	221	258	304	247	237	273	283	191	288	4882	244
4	268	216	263	247	257	232	252	232	237	268	227	216	247	273	242	263	273	278	242	288	5021	251
5	247	242	263	263	237	211	263	227	221	232	227	216	258	221	237	278	299	278	237	268	4925	246
6	252	258	216	258	247	227	263	263	227	201	258	221	237	278	232	247	288	247	242	268	4930	246
7	242	258	268	283	252	206	252	252	237	211	242	227	258	258	211	263	283	273	247	227	4950	248
8	258	232	258	288	257	206	221	242	227	206	242	258	221	258	216	273	283	309	242	237	4934	247
9	252	268	268	237	232	211	257	227	237	242	247	211	221	216	221	268	278	294	263	247	4897	245
10	242	242	283	247	232	216	247	257	263	247	232	201	216	237	252	258	237	232	221	227	4789	239
11	242	216	283	247	237	242	242	263	216	232	221	201	252	242	221	278	252	242	227	227	4783	239
12	237	247	252	252	237	232	257	252	206	232	232	191	252	185	237	247	278	252	237	211	4726	236
13	242	273	242	247	247	247	206	216	206	232	216	185	232	206	221	247	278	206	206	221	4561	228
14	263	258	278	221	196	247	247	242	221	206	211	206	221	216	227	293	258	221	232	211	4675	234
15	252	232	263	221	232	221	242	227	191	232	232	252	216	191	237	252	258	206	221	206	4584	229
16	242	268	216	216	232	211	232	216	232	253	221	242	232	227	263	258	253	258	263	232	4767	238
17	247	247	273	227	227	227	247	227	206	247	206	211	237	232	273	258	278	242	268	206	4786	239
18	227	242	258	237	216	237	232	227	185	237	258	252	247	232	242	252	268	273	247	247	4816	242
19				232					247					232				7	237			

Mean values when plotted show progressive displacement.

Total displacement, 4 places on 700 places.

$22\frac{3}{4}$ years, assumed as 39 months. In this new tabulation I used monthly mean values, instead of 10-day means, as had been done in computing for the curve shown in figure 1. I also computed two curves for a period of 37 months. They show opposition rather than similarity. It now appeared that in both the 39-month and the 37-month computations, the principal features were displaced toward the right in the second half of the 31-year interval. The corrected interval from the 39-month tabulation is $39\frac{1}{2}$ months. Plots of the 37-month tabulation shown in figure 3,A indicated a displacement toward the right of 8 months in an interval of 180 months of time. This gives a positive correction of $\frac{8}{180} \times 37 = 1.6$ months. Thus combined, the contrary curves of figure 3,A yield the lower curve of figure 3,B. Thus the 37-month tabulation yields an adjusted period of 39.6 months, closely agreeing with that yielded by the adjusted 39-month tabulation which was 39.5 months. This later period agrees within slightly more than 1 percent of being $\frac{273}{7}$, or 39.0 months. (See figure 3,B.)

If critics feel that still more evidence is needed to prove that only integral fractions of $22\frac{3}{4}$ years are to be found in the solar variation, I will remind them that many of the periodicities plotted in figure 1 show integral fractions of the periods in question superposed upon them. Conspicuous examples in figure 1 are periodicities of $15\frac{1}{6}$, $34\frac{1}{2}$, 39, $45\frac{1}{2}$, and $54\frac{1}{2}$ months.

ACCURACY OF DATA

As shown in Annals of the Astrophysical Observatory of the Smithsonian Institution (vol. 6, p. 163), the comparison of daily solar-constant values, independently measured at stations thousands of miles apart, in opposite hemispheres of the earth, extending over many years, yields a probable error for a well-observed solar-constant value, resulting from work of two stations on a single day, of $\frac{0.164}{\sqrt{2}}$ percent or $\frac{1}{8}$ percent. Using the familiar relation (the probable error of a mean is that of the individual divided by the square root of the number of values), this indicates that a 10-day mean of good quality should be assigned a probable error of 1/25 percent. Then if nine such 10-day means are tabulated in searching for a solar periodicity, the probable error of their mean becomes only 1/75 percent. These considerations indicate not only that real solar variations of 1/10 percent of the solar constant might be detected, but that the features of the march of a periodic variation of this small amplitude would appear well delineated from a tabulation.

To be sure, these optimum conditions do not always prevail. Not infrequently no more than three or five days of a decade yielded solar-constant observations. Often no more than one station reported. During parts of the year less favorable conditions prevailed at one or other of the stations. Such is the case at Table Mountain from March through June, and at Montezuma from November through January. (See figs. 7, 8, pp. 70, 71, Annals, vol. 5.)

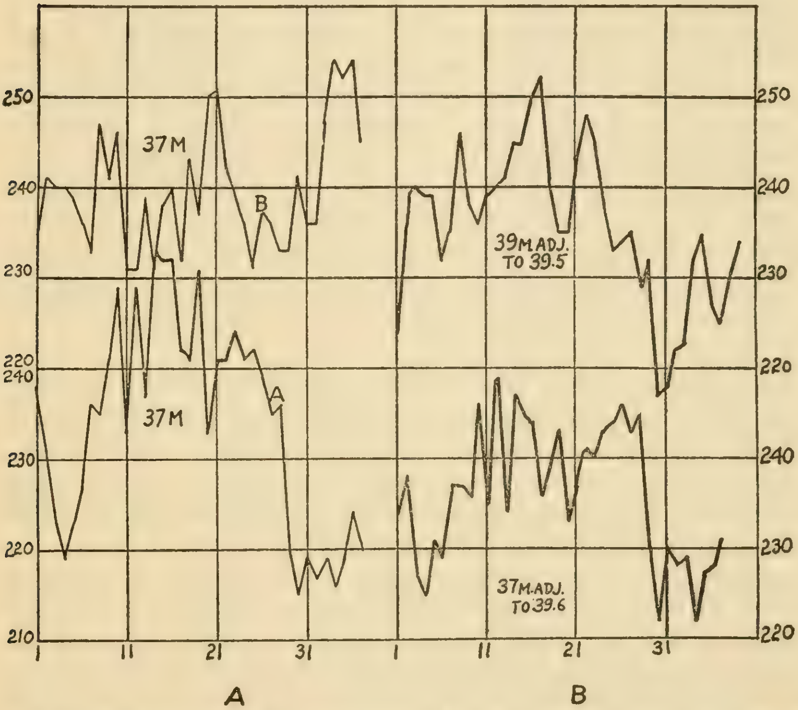


Fig. 3.—The periodicity of approximately $\frac{1}{7} \times 272$ months, tested just as the periodicity of approximately $1/45 \times 272$ months was tested in figure 2.

On these accounts it need not surprise us that, as shown below, while the sum of periodic variations represents the variation of monthly mean solar-constant results to within an average deviation of 1/10 percent, much larger departures sometimes occur. However, divergences depend not only on accidental errors of the observations, but, in part also on imperfect determination of the form, amplitude, and period of the periodicities, for reasons explained above.

SUPPORTING EVIDENCES OF VERIDITY OF PERIODICITIES

There are several indications, not flowing from a consideration of probable errors, that strongly support the veridity of periodicities here disclosed:

1. In tabulating periodicities, the data have been treated independently in several parts. That is to say, there being nearly 1,100 consecutive 10-day means covering an interval of 30 years, it is possible to tabulate in three or more groups, each with numerous columns, all periodicities of less than 20 months in length. For periodicities of between 20 and 40 months I use two tables, covering consecutive intervals of time. (See fig. 1.) Unless these independent part-tabulations agree within their measure of accuracy to indicate continuance of the same form of periodic variations, and with maxima in the same phase throughout the whole time, then such a supposed period is thrown out as nonexisting. For periods exceeding 40 months, the data were not numerous enough to be thus separated into several groups.

2. There is an integral relationship between the periods disclosed. All the periods, which the first criterion certifies as veridical, are, to within a deviation of 1 percent, integral submultiples of 272 months. For example, those approximately 91, 68, 54, 45, 39, 34, 30, and a dozen others of shorter period, are all integral fractions, to within 1 percent, of 272 months. We know that a period of about 272 months is related to the average sunspot period of 11⅓ years, and it was found by G. E. Hale in the behavior of sunspots and magnetism. It is also approximately the period discovered by meteorologists in many climatic phenomena, as well as by Douglass in the growth of trees.

I cannot but think that the fact of the integral relationship, each to each, of the solar-radiation periodicities here disclosed, and the relationship of all of them to a master period of 272 months, well known in other solar and terrestrial phenomena, strengthens the case for validity of these periodicities. If that be granted, surely the existence of these integral solar-radiation relationships, so reminiscent of the overtones of the vibrations of musical instruments, is a phenomenon well worth investigating by astronomers and by students of hydrodynamics.

I have just stated three arguments for the reality of numerous regularly periodic variations of the output of radiation from the sun as follows: A. Measurements whose small probable error is consistent with the amplitudes of the apparent periodicities display them. B. Tabulations of a chosen periodicity, with the data separated into independent groups, covering successive time intervals, show separately the periodicity in similar amplitudes, forms, and phases. C. The periods are integrally related, each to each, and all are approximately exact integral submultiples of 272 months, itself a well-known period in other solar and terrestrial phenomena. A fourth supporting evidence is to be referred to later.

The argument B is undoubtedly the most telling. In order to display its full weight, I give, in figure 1, a résumé of all the periodicities which I consider real. It is my firm expectation that scientists who examine without bias the arguments A, B, and C and carefully scan figure 1 and table 1C, will yield to the conviction that the sun's contribution of radiation that warms the earth varies in a complex way. In short, they will admit that, like the overtones of a musical note, the radiation of the sun varies simultaneously in a period of approximately 272 months, and in periods, exceeding 20 in number, which are integral submultiples of approximately 272 months. If scientists go thus far, I cannot but think they will go farther and investigate theoretically the hydrodynamics of the phenomenon.

PERIODICITIES OF 22¾ AND 11⅜ YEARS

I have not tabulated the data so as to display the periodicity of 272 months, because the values are insufficient. There would be too few repetitions to fairly fix the form of this curve. As for the periodicity of $\frac{272}{2} = 136$ months, though it is the well-known 11⅓-year sunspot period, it is inconspicuous in the variation of the solar constant. I have twice sought for it. First, I tabulated the original data in columns of 136 months and smoothed their mean values. Second, I smoothed by 7-month running means the residual departures, which separate the original data from the synthetic reproduction of them in figure 4 by 23 periodic terms. Neither treatment gave conclusively a periodicity of 136 months. Its well-evidenced weather influence, I think, is attributable to fluctuation of the intensity of the bombardment of the atmosphere by electric ions, acting as centers of condensation of water vapor and dust, as sunspot numbers wax and wane.

GRAPHS OF RESULTS

Figure 1 is introduced to emphasize the force of the argument B by a graphical appeal to the eye. The figure shows the mean result of every partial tabulation of the values used to compute table 1A, and also the general mean of these partial tabulations for almost all periodicities included in table 1A. Curves for periodicities of 2 1/7 and 3 1/20 months are given on a scale of abscissae $2\frac{1}{2}$ times as great as the other curves. Horizontal lines in figure 1 are separated by 1/10 percent of the solar constant. The curves for periodicity 2 1/7 months are given on a scale of ordinates twice as great as that used for all others. Up to a periodic length of $22\frac{3}{4}$ months, all the curves are plotted at 10-day intervals. Periodicities of $22\frac{3}{4}$ months and longer are plotted in monthly intervals. Of periodicities less than $22\frac{3}{4}$ months in length, one, that of 9 1/10-months period, is shown smoothed throughout by 5-decade running means. It has a small amplitude and would perhaps have seemed doubtful to many had not running means of 5-decade values been shown, instead of the separate 10-day mean values. This smoothing brings out plainly the similarity of the partial tabulations.

The amplitudes of the 23 periodicities plotted in figure 1 may seem to some critics too small to be of any significance. Not so. For it is shown in figure 4 that the synthesis of these 23 periodic fluctuations produces a curve closely matching, and of the same amplitude of variation as, the curve of original observation. A 12-month period of terrestrial origin with amplitude of 0.2 percent is not introduced into figure 4. Its inclusion would improve the agreement there. No additional regular periodicities were discernible. The analysis appears to be exhaustive.

As the periods grow longer, they are apt to display integral submultiples riding upon the period under examination. This is strongly marked with the period of $15\frac{1}{6}$ months. It shows seven subperiods of 2 1/7 months very plainly. Similarly the $30\frac{1}{2}$-month curve shows also the 6 1/30-month influence. The $34\frac{1}{2}$-month curve shows influence of the $11\frac{1}{4}$-month period. Other examples are obvious. Note the curves for periodicities of $54\frac{1}{2}$, 68, and 91 months shown in figure 1. Owing to superposed periods of less length, these long periodicities had to be smoothed by 5- or 7-month running means.

In addition to the direct mean results for each period, I give in a few cases also the smoothed mean, resulting from taking 5-value or 7-value running means for the entire length of the periodicity under consideration. These smooth curves give a more convincing and truer idea of the periodicities, thought to be real, than do the rougher direct means, affected by accidental errors of observation and influences of extraneous periods. Readers should bear in mind that the knicks in the broken lines, which look so large, really average less than 1/10 percent of the solar constant. This bears witness to the high accuracy of the Smithsonian solar-constant observing. Its probable error has been discussed above.

INTEGRAL RELATIONSHIPS

I had long been of the opinion that the regular periodicities of solar variation are all integrally related to approximately 272 months. This impression is supported by the fact, so obvious in figure 1, that the longer periods shown, themselves being integrally related to 272 months, have in several instances shorter periodicities riding on their backs, which are integral submultiples of them. Further proof of the integral relationships is shown in figures 2 and 3, already described.

Assuming that this integral relationship to 272 months is a condition necessary to the real existence of a regular period in solar variation, the number of such periods that are of considerable amplitudes seems not to exceed 23. At least a rather extensive search has not yielded others strong enough to be certainly real. If these be all, and their forms and amplitudes are as shown in figure 1, then a synthesis of them ought to represent the march of solar variation from 1920 to 1950, except for the interval of 1922 and 1923, when exceptionally large solar variations were observed and which is excluded from this analysis. I have made such a synthesis, and compare it with the march of the solar variation in figure 4.

SYNTHESIS OF PERIODICITIES

To determine the quantities plotted in figure 4, I have computed the departures, plus and minus, from the mean ordinate for each smoothed periodicity, as expressed monthly, which together fix the form of its curve. This gives, in each case, a short series of small monthly departures suitable to the form of each periodicity. All the tabulations begin with August 1920 as zero time. In table 2 they are all tabulated in the smoothed form actually used in preparing the synthetic curve shown in figure 4. In computing the mean periodic forms, and afterward in using them for synthesizing the solar-constant values, I allow for fractions of a decade, or of a month, by adding or withdrawing a value from certain columns, or at appropriate intervals in synthesizing, so as to preserve the correct period.

I tabulate these series, end to end, over the whole interval of more than 30 years. Thus I make a great table of 23 columns and 367 lines. Adding algebraically the plus and minus values of the lines across the table, I find the total synthesized monthly departures, in ten-thousandths of the solar constant, from the mean solar constant 1.94 calories. The results, covering 367 months, are compared in figure 4 with the monthly observational values recorded in table 4.

CLOSE AGREEMENT BETWEEN SYNTHESIS AND OBSERVATION

Table 3, below, shows the high degree of accuracy with which the synthesis of the original 21 periodicities (before those of 11.43 and $24\frac{3}{4}$ months were found) corresponded to the observations.

These results came from the comparison of observation with the synthesis of 21 periodicities. The average departures are reduced below these figures when periodicities of 11.43, 12.0,[7] and $24\frac{3}{4}$ months are introduced. The value for the best 233 months then becomes 1.00-tenths percent. The larger average departures prior to July 1926 are attributable to the then imperfect development of the "short method" of solar-constant work. The larger departures after 1945 are thought by Mr. Aldrich to be caused by temporary errors in the scales of pyrheliometers used in the field. He hopes to correct this discrepancy.

Some minds may still prefer to think that the solar-constant observations do not prove the variability of solar radiation. They may point out that the average deviation of the observations from their mean is 0.15 percent, and the average deviation of the synthetic curve from that of observation is still 0.10 percent. They may urge that this amount of improvement is not sufficient to warrant belief in the thesis that the sun's radiation varies in the discovered 23 regular periods, all integral submultiples of 272 months.

Such critics may be reminded that the "weight" of any measurement, that is, its claim to respectful recognition, is proportional to the number of observations that enter into the result; but the probable error (proportional to the average deviation from the mean) is proportional to the square root of the number of observations. It follows that the "weight," or credibility of a solution, is proportional to the square of the average deviation of its components. Hence the weight of the solution here advocated is $\left(\frac{15}{10}\right)^2 = 2.25$ times the weight of the conclusion of an invariable sun.

But it must also be considered that a certain irreducible minimum of accidental error, comparable in a graph to the teeth of a saw, adheres to the solar-constant observations. Whatever excursions from the mean value may be produced by real solar variations, these acci-

---

[7] The 12-month period is not used in preparing figure 4; its use would improve the agreement of the curves.

TABLE 2.—*Twenty-three solar periodicities in ten-thousandths of the solar constant, based on August 1920. Also the 12-month terrestrial period, same unit*

2 1/7 M: +2 −2. 3 1/20 M: 0 −2 +2. 4 1/3 M: −1 −2 +3 ±0.

5 1/18 M: −1 ±0 −2 +2 +2. 6 1/30 M: −4 −1 +3 +6 ±0 −5.

7 M: −1 +1 +5 +2 −1 −1 −2. 8 1/14 M: −2 −2 −1 −1 +1 +1 +3 +2.

9 1/10 M: −2 −4 −3 −1 ±0 +2 +3 +1. ±0.

9 7/10 M: −4 −3 −1 +1 +5 +5 +2 −1 −4 −3.

10 6/10 M: −1 −1 −1 −1 −3 +1 +1 +2 +3 +1 −1.

11 1/5 M: −4 −2 ±0 +3 +1 +9 +3 −1 +4 −2 −8.

11.43 M: +7 +4 +6 +1 −3 −4 −3 −3 −4 −3 −1.

13 1/10 M: +1 +4 +3 −2 −6 −4 +2 +2 +1 ±0 −2 +1 +3.

15 1/6 M: −3 −6 −6 −1 ±0 +2 +1 +2 +3 +2 ±0 ±0 +2 +1 +1.

22 3/4 M: −1 +1 ±0 +1 +1 +1 +1 +1 ±0 ±0 +1 +2 +3 +3 +2 +2 +1 −1 −2 −3 −3 −2 −1.

24 3/4 M: −2 −2 −1 +1 +2 +3 +3 +4 +4 +4 +3 +3 +2 +1 ±0 −2 −5 −7 −2 ±0 ±0 ±0 ±0 −1 −1.

30 1/3 M: +6 +5 +4 +3 +3 +4 +3 +1 +1 ±0 ±0 ±0 −1 −3 −5 −6 −6 −5 −5 −6 −6 −4 −3 −2 −1 −1 ±0 +3 +3 +4.

34 1/2 M: −5 −6 −4 −3 −3 −2 −3 −5 −7 −6 −3 −1 −1 +2 +5 +6 +8 +7 +6 +4 +1 −1 ±0 +1 +2 +3 +3 +4 +5 +5 +2 +1 −1 −3.

39 M: −4 +1 +2 +2 +2 +2 +1 +1 +1 +2 +2 +4 +6 +8 +10 +10 +8 +7 +5 +3 +4 +5 +5 +4 +3 +3 +1 −1 −4 −6 −8 −10 −10 −10 −9 −9 −9 −8 −6.

45 1/2 M: −3 −4 −3 −3 −2 −1 ±0 +1 +1 +3 +4 +6 +6 +3 +2 +1 ±0 −2 −3 −1 −1 +1 +1 +2 +3 +2 +2 ±0 −1 −3 −4 −5 −4 −3 −2 ±0 +1 +1 ±0 −2 −3 −4 −2 −2 −1.

54 1/2 M: +4 +4 +5 +6 +6 +7 +7 +7 +7 +6 +6 +6 +5 +3 ±0 −1 −1 −1 −2 −4 −4 −3 −3 −2 −2 −2 −2 −3 −2 −3 −2 −4 −5 −4 −3 −4 −2 −3 −3 −4 −3 −2 −1 −1 −1 −2 −1 ±0 ±0 −2 −2 −1 +1 +2.

68 M: −7 −5 −4 −4 −4 −6 −6 −8 −12 −13 −12 −9 −5 −4 −2 −3 −2 −2 −8 −11 −11 −10 −6 −6 −4 −3 −4 −4 −3 −5 −5 −6 −5 −4 −4 −4 −4 −6 −7 −8 −7 −8 −6 −4 −2 ±0 +2 +4 +5 +6 +7 +8 +9 +10 +10 +11 +11 +12 +12 +11 +11 +10 +8 +5 +2 −2 −3 −7.

91 M: ±0 +1 +2 +2 +2 +2 +2 +3 +4 +2 +1 −1 −2 −3 −3 −3 −4 −4 −4 −3 −3 −3 −3 −4 −4 −4 −4 −3 −2 −1 ±0 ±0 ±0 ±0 ±0 −1 −2 −3 −3 −4 −4 −4 −4 −4 −4 −4 −4 −4 −3 −2 −1 ±0 +1 +2 +2 +3 +4 +5 +6 +6 +7 +7 +7 +7 +7 +6 +5 +4 +3 +2 +2 +1 +1 +1 ±0 ±0 −1 −2 −2 −3 −4 −4 −4 −4 −3 −2 −1 −1 ±0 ±0 ±0.

The 12-month period of terrestrial causation

Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
+0.1	+0.6	−2.1	−6.7	−0.9	+1.7	+1.4	+2.1	+4.3	+6.2	+13.2	+13.5

dental errors of observation will still load the curve with their sawtoothlike vibrations about its true course. No system of periodicities, which may truly represent the true courses of the solar variation, can possibly follow these small accidental errors of observation. It is therefore unreasonable to demand that such a system of periodicities, even though the true one, can be expected to reduce the average deviation of its curve from the curve of observation below the one-tenth of a percent found. For though, as stated, the probable error of *first-rate* 10-day means, as found by comparing the simultaneous observations of two solar-constant observations, is 1/25 percent, very many 10-day means are not first rate, as explained above. Moreover the "average deviation" is 5/4 of the "probable error," as is well known, raising the figure to 1/19 percent for the average deviation of first-rate 10-day means.

TABLE 3.—*Average departures of synthetic from observational curve*

Aug. 1920—Mar. 1922,	20 months,	2.01	tenths	percent.
Aug. 1923—July 1926,	36 months,	1.82	"	"
Aug. 1926—Dec. 1945,	233 months,	1.10	"	"
Jan. 1945—Dec. 1950,	60 months,	2.38	"	"
Aug. 1920—Dec. 1950,	349 months,	1.45	"	"

The real crux of the question, as between the hypothesis of constant solar radiation, and solar radiation varying in 23 regular periods, painstakingly determined and tested by several criteria of reality, lies in considering the large excursions of the curve of observation from its mean. Examples of such methodically marching excursions are found from 1924 to 1927, from 1929 to 1933, from 1937 to 1942, and from 1947 to 1949. The hypothesis of a constant solar radiation offers no explanation for them. On the other hand, the synthetic curve follows these large, methodically marching excursions with some fidelity.

Yet notwithstanding this striking harmony in the principal features between the curve of observation and the synthetic curve of regular periodicities, there are limited intervals of substantial disagreement. Among these the major one occurs in 1922 and 1923, regarding which I have already written. The disagreement in 1920 and 1921 may be attributed to the incomplete development of the short method of solar-constant determination in those earliest years. The same perhaps applies to the disagreement in the years 1924 and 1925, for even then the short method was not fully developed, as now used. As for the period 1946 to 1950, Mr. Aldrich inclines to think the scales of pyrheliometry may have varied a little in those years. There is also a possibility that, in carrying the computations so far forward as 1950 from their base in 1920, slight errors in the length of the periods have accumulated so as to mar the results of synthesis.

Brief intervals of unusually large divergence between the synthetic and the observed curves occur in 1927, 1929, 1934-1935, 1938, 1940-1941, and 1944. Nearly all these cases occur at the times of the year when sky conditions for observing are inferior at one or both stations, as indicated by figures 7 and 8, pages 70 and 71, Annals, volume 5, already cited. It is not probable, however, that regular periods of variation include *all* the variations of solar radiation. We know, indeed, that outbursts of sunspots and flares cause changes in the sun's output of radiation. Some of the discrepancies referred to are doubtless due to such causes.

I hope the reader will agree that the synthesis of 23 independently and separately computed periodic terms has represented, to within the error of observation, the march of the solar constant as given by the monthly means of the original observations from 1920 to 1950, excluding the extraordinary values of 1922 and 1923. This close agreement in form and amplitude between the observed and the synthetic curve seems to me a fourth kind of evidence supporting the existence of a complex of over 20 regular periods all approximately integral submultiples of 272 months in the observed variation of the sun's output of radiation.

It will occur to the reader that curves of solar observation should tend to repeat their features after 272 months, or approximately 23 years. There is a slight indication that the curve of 1921 in figure 4 is similar to that of 1944, but the work of 1921, as mentioned elsewhere, is too inaccurate to prove it. In the years 1922 and 1923 occurred a unique large depression of the curve of observation. A real test must begin with the year 1924. Unfortunately, as stated elsewhere, there appears to have been a change of scale of about $\frac{1}{3}$ percent in 1948. To correct for it, I subtract 32 units from all the monthly means, July 1948 to February 1950.

In figure 4A, I superpose the corrected curve 1947 to 1950 (light line) upon the observed curve of observation 1924 to 1927 (heavy line). The similarity is striking. During 48 months there are five large divergencies: 0.55, 0.50, and three of 0.45 percent. The extreme range of the great feature shown in figure 4A is 0.9 percent, and the average deviation between the curves is but 0.19 percent—less than the expected combined probable errors of observing. One regrets that the interval, 276 months, exceeds the expected interval, 272 months. But as solar conditions modify the lengths of the sunspot cycles, they may also slightly modify that of the 272-month cycle from time to time.

FIG. 4A.—Comparison of solar constants 1924-1927 (heavy lines) and 1947-1950 (light lines).

SCALE OF SOLAR CONSTANT NEARLY UNCHANGED IN 30 YEARS

It is very pleasing that the comparison of synthesized and original curves shows the features generally with equal amplitudes in the two curves. The comparison gives no indication that the scale of observation has changed in 30 years, except perhaps for a rise of 3/10 percent from June 1948 to January 1950. This is remarkable in view of many changes of instruments and of procedures that have taken place meanwhile.

APPENDIX 1

SOLAR-CONSTANT MONTHLY AND 10-DAY MEANS, 1920–1950

Doubtless there are those who are engaged in research on cycles in various lines who may wish to know the Smithsonian results on solar variability as nearly as possible up to date. Mr. Aldrich kindly permits me to publish the following table (table 4) giving the percentage excesses of solar-constant values above 1.900 calories from 1920 to 1950. These percentage excesses are in the form of means of 10 days (i.e., decades of months) and means of months. Taking the first trio of values, given here for illustration, the table may be explained as follows. We have:

2, 8, I, 0, 1, 154
2, 8, II, 0, 2, 139, 153[8]
2, 8, III, 0, 3, 165

The above figure 2, with the figure 0, makes 20, meaning the year 1920. The figure 8 means August, the eighth month of 1920. The Roman numerals I, II, III stand for the first, second, and third decades of August. That is: August 1-9, 10-19, 20-31. The values 154, 139, 165 represent decade-means of the daily excesses of the solar constant by which these observations exceeded in ten-thousandth parts of the mean solar constant (taken as 1.94 calories) the value 1.9000 calories. Thus the value 154 signifies that the mean solar constant for the first decade of August 1920 was 1.54 percent of 1.94 or 0.0299 calorie above 1.90 calories. Finally, the value 153 is the mean of the three decade values and signifies that the average solar constant for August 1920 was 1.90+1.53 percent of 1.94 calories, or 1.930 calories.[8] As stated above, the percentages of excess over 1.90 calories was chosen to suit my investigation because, first, all values are positive, and second, results come out in percentages of the solar constant.

APPENDIX 2

PROBABLE SOLAR-CONSTANT VALUES BEFORE 1920

Smithsonian solar-constant observations were made in the summers on Mount Wilson, Calif., in most years from 1905 to 1920. But partly because of experimental crudity, and partly from the variability of sky transparency, and mainly because those measurements were all made by the fundamental "long method," which requires constant sky transparency for hours, the results were wide-ranging, from about

---

[8] This result is far out of line, and indicates experimental error. In drawing figure 4 I have assumed, instead, 235, given in parenthesis in table 4.

TABLE 4.—*Ten-day and monthly means*

2, 8	I, 0	1	154	
	II	2	139(235)	
	III	3	165	153
2, 9	I, 0	4	263	
	II	5	227	
	III	6	227	239
2, 10	I, 0	7	227	
	II	8	278	
	III	9	206	237
2, 11	I, 0	10	278	
	II	11	258	
	III	12	201	246
2, 12	I, 0	13	294	
	II	14	263	
	III	15	278	278
2, 1	I, 1	16	299	
	II	17	304	
	III	18	278	294
2, 2	I, 1	19	237	
	II	20	288	
	III	21	278	268
2, 3	I, 1	22	299	
	II	23	206	
	III	24	242	249
2, 4	I, 1	25	242	
	II	26	242	
	III	27	242	242
2, 5	I, 1	28	267	
	II	29	247	
	III	30	263	259
2, 6	I, 1	31	185	
	II	32	206	
	III	33	211	201
2, 7	I, 1	34	258	
	II	35	268	
	III	36	252	259
2, 8	I, 1	37	211	
	II	38	263	
	III	39	196	223
2, 9	I, 1	40	227	
	II	41	263	
	III	42	268	253
2, 10	I, 1	43	268	
	II	44	294	
	III	45	309	290
2, 11	I, 1	46	294	
	II	47	283	
	III	48	309	295
2, 12	I, 1	49	273	
	II	50	247	
	III	51	268	263
2, 1	I, 2	52	165	
	II	53	247	
	III	54	247	220
2, 2	I, 2	55	206	
	II	56	252	
	III	57	247	235
2, 3	I, 2	58	221	
	II	59	201	
	III	60	154	192
2, 4	I, 2	61	165	
	II	62	165	
	III	63	139	156
2, 5	I, 2	64	139	
	II	65	160	
	III	66	165	156
2, 6	I, 2	67	129	
	II	68	72	
	III	69	72	91
2, 7	I, 2	70	21	
	II	71	88	
	III	72	72	60
2, 8	I, 2	73	98	
	II	74	124	
	III	75	103	108
2, 9	I, 2	76	160	
	II	77	52	
	III	78	88	100
2, 10	I, 2	79	144	
	II	80	129	
	III	81	93	122
2, 11	I, 2	82	134	
	II	83	154	
	III	84	98	129
2, 12	I, 2	85	124	
	II	86	113	
	III	87	118	118
2, 1	I, 3	88	232	
	II	89	185	
	III	90	154	190
2, 2	I, 3	91	160	
	II	92	142	
	III	93	77	126
2, 3	I, 3	94	160	
	II	95	175	
	III	96	160	165
2, 4	I, 3	97	175	
	II	98	134	
	III	99	165	158
2, 5	I, 3	100	175	
	II	101	180	
	III	102	191	182
2, 6	I, 3	103	118	
	II	104	170	
	III	105	165	151
2, 7	I, 3	106	180	
	II	107	144	
	III	108	227	184
2, 8	I, 3	109	216	
	II	110	206	
	III	111	211	211
2, 9	I, 3	112	252	
	II	113	252	
	III	114	242	249
2, 10	I, 3	115	237	
	II	116	221	
	III	117	237	232
2, 11	I, 3	118	221	
	II	119	227	
	III	120	211	220
2, 12	I, 3	121	221	
	II	122	216	
	III	123	175	204
2, 1	I, 4	124	216	
	II	125	211	
	III	126	211	213
2, 2	I, 4	127	221	
	II	128	201	
	III	129	232	218
2, 3	I, 4	130	252	
	II	131	211	
	III	132	216	226
2, 4	I, 4	133	196	
	II	134	206	
	III	135	221	208
2, 5	I, 4	136	237	
	II	137	252	
	III	138	252	247
2, 6	I, 4	139	247	
	II	140	247	
	III	141	263	252
2, 7	I, 4	142	247	
	II	143	268	
	III	144	252	256
2, 8	I, 4	145	278	
	II	146	221	
	III	147	232	244
2, 9	I, 4	148	211	
	II	149	232	
	III	150	278	240
2, 10	I, 4	151	252	
	II	152	268	
	III	153	263	261
2, 11	I, 4	154	263	
	II	155	268	
	III	156	273	268
2, 12	I, 4	157	283	
	II	158	263	
	III	159	273	273
2, 1	I, 5	160	242	
	II	161	263	
	III	162	283	263
2, 2	I, 5	163	278	
	II	164	283	
	III	165	288	283
2, 3	I, 5	166	299	
	II	167	263	
	III	168	258	273
2, 4	I, 5	169	263	
	II	170	252	
2, 4	III, 5	171	216	244
2, 5	I, 5	172	221	
	II	173	258	
	III	174	247	242
2, 6	I, 5	175	237	
	II	176	247	
	III	177	258	247
2, 7	I, 5	178	263	
	II	179	278	
	III	180	206	249
2, 8	I, 5	181	258	
	II	182	221	
	III	183	273	251
2, 9	I, 5	184	263	
	II	185	263	
	III	186	242	256
2, 10	I, 5	187	232	
	II	188	237	
	III	189	232	234
2, 11	I, 5	190	216	
	II	191	252	
	III	192	242	237
2, 12	I, 5	193	247	
	II	194	237	
	III	195	258	247
2, 1	I, 6	196	237	
	II	197	258	
	III	198	196	230
2, 2	I, 6	199	201	
	II	200	206	
	III	201	180	196
2, 3	I, 6	202	211	
	II	203	232	
	III	204	191	211
2, 4	I, 6	205	170	
	II	206	201	
	III	207	216	196
2, 5	I, 6	208	201	
	II	209	206	
	III	210	211	206
2, 6	I, 6	211	196	
	II	212	216	
	III	213	211	208
2, 7	I, 6	214	221	
	II	215	211	
	III	216	211	214
2, 8	I, 6	217	232	
	II	218	232	
	III	219	252	239
2, 9	I, 6	220	216	
	II	221	216	
	III	222	227	220
2, 10	I, 6	223	201	
	II	224	206	
	III	225	180	196
2, 11	I, 6	226	185	
	II	227	185	
	III	228	201	190
2, 12	I, 6	229	170	
	II	230	201	
	III	231	191	187
2, 1	I, 7	232	206	
	II	233	196	
	III	234	191	198
2, 2	I, 7	235	175	
	II	236	242	
	III	237	160	192
2, 3	I, 7	238	154	
	II	239	216	
	III	240	216	195
2, 4	I, 7	241	247	
	II	242	232	
	III	243	201	227

TABLE 4.—Continued

2, 5	I, 7	244	206		2, 8	I, 9	325	201		3, 11	I, 1	406	221	
	II	245	242			II	326	206			II	407	232	
	III	246	216	221		III	327	206	204		III	408	237	230
2, 6	I, 7	247	258		2, 9	I, 9	328	211		3, 12	I, 1	409	221	
	II	248	221			II	329	191			II	410	247	
	III	249	227	235		III	330	211	204		III	411	242	237
2, 7	I, 7	250	232		2, 10	I, 9	331	211		3, 1	I, 2	412	242	
	II	251	216			II	332	216			II	413	242	
	III	252	232	227		III	333	175	201		III	414	221	235
2, 8	I, 7	253	211		2, 11	I, 9	334	206		3, 2	I, 2	415	227	
	II	254	221			II	335	227			II	416	232	
	III	255	232	227		III	336	237	223		III	417	165	208
2, 9	I, 7	256	237		2, 12	I, 9	337	237		3, 3	I, 2	418	175	
	II	257	258			II	338	237			II	419	221	
	III	258	247	247		III	339	227	234		III	420	206	201
2, 10	I, 7	259	221		3, 1	I, 0	340	211		3, 4	I, 2	421	191	
	II	260	206			II	341	232			II	422	221	
	III	261	211	213		III	342	232	225		III	423	211	208
2, 11	I, 7	262	232		3, 2	I, 0	343	211		3, 5	I, 2	424	232	
	II	263	232			II	344	232			II	425	227	
	III	264	247	237		III	345	247	230		III	426	154	204
2, 12	I, 7	265	242		3, 3	I, 0	346	232		3, 6	I, 2	427	206	
	II	266	227			II	347	211			II	428	221	
	III	267	201	223		III	348	216	220		III	429	221	216
2, 1	I, 8	268	221		3, 4	I, 0	349	221		3, 7	I, 2	430	263	
	II	269	196			II	350	206			II	431	206	
	III	270	216	211		III	351	227	218		III	432	216	228
2, 2	I, 8	271	237		3, 5	I, 0	352	232		3, 8	I, 2	433	196	
	II	272	211			II	353	252			II	434	227	
	III	273	201	216		III	354	242	242		III	435	216	213
2, 3	I, 8	274	237		3, 6	I, 0	355	242		3, 9	I, 2	436	191	
	II	275	247			II	356	273			II	437	232	
	III	276	221	235		III	357	258	258		III	438	237	220
2, 4	I, 8	277	216		3, 7	I, 0	358	232		3, 10	I, 2	439	211	
	II	278	227			II	359	278			II	440	180	
	III	279	242	228		III	360	273	261		III	441	201	197
2, 5	I, 8	280	227		3, 8	I, 0	361	242		3, 11	I, 2	442	211	
	II	281	263			II	362	268			II	443	185	
	III	282	247	246		III	363	252	254		III	444	201	199
2, 6	I, 8	283	247		3, 9	I, 0	364	247		3, 12	I, 2	445	258	
	II	284	278			II	365	227			II	446	237	
	III	285	232	252		III	365	232	235		III	447	211	235
2, 7	I, 8	286	232		3, 10	I, 0	367	227		3, 1	I, 3	448	258	
	II	287	221			II	368	237			II	449	247	
	III	288	216	223		III	369	247	237		III	450	268	258
2, 8	I, 8	289	191		3, 11	I, 0	370	242		3, 2	I, 3	451	258	
	II	290	227			II	371	242			II	452	242	
	III	291	227	215		III	372	263	249		III	453	242	247
2, 9	I, 8	292	201		3, 12	I, 0	373	268		3, 3	I, 3	454	237	
	II	293	237			II	374	278			II	455	206	
	III	294	196	211		III	375	263	270		III	456	206	216
2, 10	I, 8	295	227		3, 1	I, 1	376	216		3, 4	I, 3	457	211	
	II	296	232			II	377	247			II	458	227	
	III	297	211	223		III	378	268	244		III	450	191	210
2, 11	I, 8	298	227		3, 2	I, 1	379	247		3, 5	I, 3	460	106	
	II	299	252			II	380	258			II	461	206	
	III	300	237	239		III	381	216	240		III	462	232	211
2, 12	I, 8	301	237		3, 3	I, 1	382	227		3, 6	I, 3	463	206	
	II	302	227			II	383	237			II	464	216	
	III	303	252	239		III	384	258	241		III	465	232	218
2, 1	I, 9	304	242		3, 4	I, 1	385	237		3, 7	I, 3	466	247	
	II	305	258			II	386	237			II	467	242	
	III	306	237	246		III	387	237	237		III	468	221	237
2, 2	I, 9	307	232		3, 5	I, 1	388	288		3, 8	I, 3	469	221	
	II	308	211			II	389	258			II	470	221	
	III	309	196	213		III	390	258	268		III	471	216	219
2, 3	I, 9	310	242		3, 6	I, 1	391	247		3, 9	I, 3	472	252	
	II	311	191			II	392	247			II	473	247	
	III	312	206	213		III	393	232	242		III	474	263	254
2, 4	I, 9	313	191		3, 7	I, 1	394	237		3, 10	I, 3	475	263	
	II	314	242			II	395	252			II	476	237	
	III	315	227	220		III	396	247	245		III	477	263	253
2, 5	I, 9	316	216		3, 8	I, 1	397	247		3, 11	I, 3	478	242	
	II	317	216			II	398	258			II	479	263	
	III	318	227	220		III	399	232	246		III	480	273	259
2, 6	I, 9	319	206		3, 9	I, 1	400	252		3, 12	I, 3	481	268	
	II	320	175			II	401	232			II	482	252	
	III	321	196	192		III	402	263	249		III	483	258	259
2, 7	I, 9	322	206		3, 10	I, 1	403	263		3, 1	I, 4	484	258	
	II	323	211			II	404	221			II	485	237	
	III	324	216	211		III	405	237	240		III	486	247	247

TABLE 4.—Continued

3, 2	I, 4	487	263	
	II	488	216	
	III	489	227	235
3, 3	I, 4	490	247	
	II	491	221	
	III	492	258	242
3, 4	I, 4	493	232	
	II	494	221	
	III	495	221	225
3, 5	I, 4	496	227	
	II	497	242	
	III	498	221	230
3, 6	I, 4	499	242	
	II	500	258	
	III	501	252	251
3, 7	I, 4	502	258	
	II	503	232	
	III	504	232	241
3, 8	I, 4	505	211	
	II	506	237	
	III	507	227	225
3, 9	I, 4	508	232	
	II	509	247	
	III	510	263	247
3, 10	I, 4	511	263	
	II	512	268	
	III	513	263	265
3, 11	I, 4	514	268	
	II	515	263	
	III	516	258	263
3, 12	I, 4	517	268	
	II	518	258	
	III	519	247	258
3, 1	I, 5	520	242	
	II	521	268	
	III	522	232	247
3, 2	I, 5	523	237	
	II	524	237	
	III	525	216	230
3, 3	I, 5	526	221	
	II	527	242	
	III	528	263	242
3, 4	I, 5	529	237	
	II	530	242	
	III	531	227	235
3, 5	I, 5	532	247	
	II	533	232	
	III	534	247	242
3, 6	I, 5	535	237	
	II	536	237	
	III	537	247	240
3, 7	I, 5	538	247	
	II	539	227	
	III	540	232	235
3, 8	I, 5	541	247	
	II	542	263	
	III	543	237	249
3, 9	I, 5	544	232	
	II	545	237	
	III	546	227	232
3, 10	I, 5	547	237	
	II	548	242	
	III	549	242	240
3, 11	I, 5	550	247	
	II	551	268	
	III	552	252	256
3, 12	I, 5	553	247	
	II	554	263	
	III	555	273	261
3, 1	I, 6	556	237	
	II	557	263	
	III	558	227	242
3, 2	I, 6	559	242	
	II	560	263	
	III	561	196	234
3, 3	I, 6	562	201	
	II	563	237	
	III	564	232	223
3, 4	I, 6	565	232	
	II	566	237	
	III	567	237	235
3, 5	I, 6	568	237	
	II	569	232	
	III	570	247	239
3, 6	I, 6	571	258	
	II	572	252	
	III	573	247	252
3, 7	I, 6	574	252	
	II	575	242	
	III	576	242	245
3, 8	I, 6	577	232	
	II	578	252	
	III	579	242	242
3, 9	I, 6	580	232	
	II	581	252	
	III	582	263	249
3, 10	I, 6	583	252	
	II	584	252	
	III	585	242	249
3, 11	I, 6	586	268	
	II	587	273	
	III	588	258	266
3, 12	I, 6	589	278	
	II	590	263	
	III	591	247	263
3, 1	I, 7	592	247	
	II	593	273	
	III	594	242	254
3, 2	I, 7	595	247	
	II	596	237	
	III	597	252	245
3, 3	I, 7	598	211	
	II	599	221	
	III	600	227	220
3, 4	I, 7	601	201	
	II	602	211	
	III	603	216	209
3, 5	I, 7	604	180	
	II	605	227	
	III	606	237	215
3, 6	I, 7	607	237	
	II	608	237	
	III	609	242	239
3, 7	I, 7	610	221	
	II	611	227	
	III	612	232	227
3, 8	I, 7	613	242	
	II	614	232	
	III	615	242	239
3, 9	I, 7	616	252	
	II	617	247	
	III	618	237	245
3, 10	I, 7	619	242	
	II	620	227	
	III	621	242	237
3, 11	I, 7	622	247	
	II	623	247	
	III	624	247	247
3, 12	I, 7	625	258	
	II	626	252	
	III	627	278	263
3, 1	I, 8	628	232	
	II	629	268	
	III	630	206	235
3, 2	I, 8	631	221	
	II	632	237	
	III	633	273	244
3, 3	I, 8	634	268	
	II	635	237	
	III	636	242	249
3, 4	I, 8	637	232	
	II	638	206	
	III	639	237	225
3, 5	I, 8	640	237	
	II	641	227	
	III	642	206	223
3, 6	I, 8	643	211	
	II	644	227	
	III	645	232	223
3, 7	I, 8	646	227	
	II	647	232	
	III	648	221	227
3, 8	I, 8	649	227	
	II	650	232	
	III	651	232	230
3, 9	I, 8	652	237	
	II	653	232	
	III	654	242	237
3, 10	I, 8	655	247	
	II	656	247	
	III	657	263	252
3, 11	I, 8	658	268	
	II	659	268	
	III	660	268	268
3, 12	I, 8	661	258	
	II	662	273	
	III	663	258	263
3, 1	I, 9	664	...	
	II	665	237	
	III	666	242	240
3, 2	I, 9	667	216	
	II	668	185	
	III	669	232	211
3, 3	I, 9	670	221	
	II	671	216	
	III	672	232	223
3, 4	I, 9	673	221	
	II	674	227	
	III	675	201	216
3, 5	I, 9	676	211	
	II	677	221	
	III	678	211	214
3, 6	I, 9	679	211	
	II	680	196	
	III	681	221	209
3, 7	I, 9	682	221	
	II	683	227	
	III	684	201	216
3, 8	I, 9	685	201	
	II	686	180	
	III	687	227	203
3, 9	I, 9	688	252	
	II	689	232	
	III	690	232	239
3, 10	I, 9	691	221	
	II	692	237	
	III	693	227	228
3, 11	I, 9	694	258	
	II	695	258	
	III	696	221	246
3, 12	I, 9	697	227	
	II	698	258	
	III	699	242	242
4, 1	I, 0	700	237	
	II	701	242	
	III	702	237	239
4, 2	I, 0	703	227	
	II	704	227	
	III	705	232	229
4, 3	I, 0	706	232	
	II	707	211	
	III	708	211	218
4, 4	I, 0	709	227	
	II	710	211	
	III	711	268	235
4, 5	I, 0	712	242	
	II	713	237	
	III	714	268	249
4, 6	I, 0	715	247	
	II	716	252	
	III	717	242	247
4, 7	I, 0	718	258	
	II	719	252	
	III	720	242	251
4, 8	I, 0	721	242	
	II	722	237	
	III	723	242	240
9	I	724	263	
	II	725	252	
	III	726	242	252
10	I	727	247	
	II	728	227	
	III	729	252	242

TABLE 4.—Continued

11	I	730	252	
	II	731	227	
	III	732	216	232
12	I	733	242	
	II	734	258	
	III	735	258	253
4, 1	I, 1	736	232	
	II	737	268	
	III	738	242	247
2	I	739	216	
	II	740	247	
	III	741	273	245
3	I	742	258	
	II	743	232	
	III	744	268	253
4	I	745	247	
	II	746	242	
	III	747	221	237
5	I	748	247	
	II	749	216	
	III	750	263	242
6	I	751	263	
	II	752	216	
	III	753	268	249
7	I	754	258	
	II	755	268	
	III	756	283	270
8	I	757	283	
	II	758	252	
	III	759	242	259
9	I	760	278	
	II	761	263	
	III	762	216	252
10	I	763	273	
	II	764	258	
	III	765	247	259
11	I	766	268	
	II	767	247	
	III	768	247	254
12	I	769	263	
	II	770	258	
	III	771	283	268
4, 1	I, 2	772	288	
	II	773	237	
	III	774	247	257
2	I	775	247	
	II	776	252	
	III	777	247	249
3	I	778	221	
	II	779	221	
	III	780	216	219
4	I	781	227	
	II	782	237	
	III	783	232	232
5	I	784	227	
	II	785	242	
	III	786	257	242
6	I	787	257	
	II	788	237	
	III	789	247	247
7	I	790	252	
	II	791	257	
	III	792	232	247
4, 8	I, 2	793	232	
	II	794	237	
	III	795	237	235
9	I	796	247	
	II	797	196	
	III	798	232	225
10	I	799	232	
	II	800	227	
	III	801	216	225
11	I	802	237	
	II	803	242	
	III	804	257	245
12	I	805	232	
	II	806	211	
	III	807	227	223
4, 1	I, 3	808	206	
	II	809	206	
	III	810	211	208
2	I	811	216	
	II	812	242	
	III	813	232	230
3	I	814	206	
	II	815	247	
	III	816	221	225
4	I	817	211	
	II	818	227	
	III	819	237	225
5	I	820	242	
	II	821	232	
	III	822	237	237
6	I	823	252	
	II	824	263	
	III	825	263	259
7	I	826	252	
	II	827	221	
	III	828	257	243
8	I	829	247	
	II	830	242	
	III	831	257	249
9	I	832	232	
	II	833	247	
	III	834	242	240
10	I	835	232	
	II	836	247	
	III	837	232	237
11	I	838	237	
	II	839	247	
	III	840	206	230
12	I	841	232	
	II	842	227	
	III	843	263	241
4, 1	I, 4	844	252	
	II	845	242	
	III	846	227	240
2	I	847	257	
	II	848	263	
	III	849	252	257
3	I	850	216	
	II	851	242	
	III	852	227	228
4	I	853	216	
	II	854	227	
	III	855	227	223
5	I	856	242	
	II	857	237	
	III	858	227	235
6	I	859	237	
	II	860	221	
	III	861	227	228
7	I	862	237	
	II	863	227	
	III	864	237	234
4, 8	I, 4	865	263	
	II	866	216	
	III	867	206	228
9	I	868	206	
	II	869	221	
	III	870	191	206
10	I	871	232	
	II	872	206	
	III	873	185	208
11	I	874	247	
	II	875	237	
	III	876	232	239
12	I	877	237	
	II	878	268	
	III	879	232	246
4, 1	I, 5	880	201	
	II	881	211	
	III	882	206	206
2	I	883	242	
	II	884	247	
	III	885	232	240
3	I	886	232	
	II	887	232	
	III	888	206	223
4	I	889	232	
	II	890	253	
	III	891	247	244
5	I	892	237	
	II	893	237	
	III	894	242	239
6	I	895	232	
	II	896	227	
	III	897	227	229
7	I	898	258	
	II	899	242	
	III	900	242	247
8	I	901	247	
	II	902	232	
	III	903	221	233
9	I	904	232	
	II	905	216	
	III	906	211	220
10	I	907	232	
	II	908	221	
	III	909	206	220
11	I	910	258	
	II	911	242	
	III	912	252	251
12	I	913	221	
	II	914	216	
	III	915	216	218
4, 1	I, 6	916	221	
	II	917	227	
	III	918	258	235
2	I	919	211	
	II	920	201	
	III	921	201	204
3	I	922	191	
	II	923	185	
	III	924	206	194
4	I	925	252	
	II	926	242	
	III	927	211	235
5	I	928	252	
	II	929	252	
	III	930	227	244
6	I	931	258	
	II	932	247	
	III	933	258	254
7	I	934	237	
	II	935	258	
	III	936	221	239
4, 8	I, 6	937	221	
	II	938	216	
	III	939	252	230
9	I	940	252	
	II	941	232	
	III	942	221	235
10	I	943	216	
	II	944	232	
	III	945	237	228
11	I	946	247	
	II	947	258	
	III	948	263	256
12	I	949	304(?)	
	II	950	273(?)	
	III	951	221(?)	266
4, 1	I, 7	952	278	
	II	953	258	
	III	954	258	265
2	I	955	216(?)	
	II	956	237	
	III	957	242	232
3	I	958	185	
	II	959	206	
	III	960	216	202
4	I	961	191	
	II	962	227	
	III	963	232	217
5	I	964	232	
	II	965	232	
	III	966	216	227
6	I	967	211	
	II	968	247	
	III	969	242	233
7	I	970	237	
	II	971	232	
	III	972	211	227

Table 4.—Concluded

8	I	973	216	
	II	979	221	
	III	975	252	230
9	I	976	221	
	II	977	237	
	III	978	221	226
10	I	979	227	
	II	980	237	
	III	981	263	242
11	I	982	273	
	II	983	242	
	III	984	247	254
12	I	985	258	
	II	986	237	
	III	987	263	253
4, 1	I, 8	988	278	
	II	989	247	
	III	990	263	263
2	I	991	273	
	II	992	268	
	III	993	258	266
3	I	994	278	
	II	995	247	
	III	996	247	257
4	I	997	293(?)	
	II	998	252	
	III	999	258	268
5	I	1000	258	
	II	1001	252	
	III	1002	263	258
6	I	1003	283	
	II	1004	273	
	III	1005	273	276
7	I	1006	299	
	II	1007	288	
	III	1008	283	290
4, 8	I, 8	1009	283	
	II	1010	278	
	III	1011	237	266
9	I	1012	252	
	II	1013	278	
	III	1014	278	269
10	I	1015	258	
	II	1016	258	
	III	1017	253	356
11	I	1018	278	
	II	1019	268	
	III	1020	283	276
12	I	1021	278	
	II	1022	283	
	III	1023	278	280
4, 1	I, 9	1024	278	
	II	1025	247	
	III	1026	273	266
2	I	1027	304	
	II	1028	294	
	III	1029	232	278
3	I	1030	242	
	II	1031	252	
	III	1032	206	233
4	I	1033	221	
	II	1034	206	
	III	1035	258	228
5	I	1036	242	
	II	1037	273	
	III	1038	242	252
6	I	1039	232	
	II	1040	191	
	III	1041	242	222
7	I	1042	237	
	II	1043	242	
	III	1044	247	242
8	I	1045	242	
	II	1046	263	
	III	1047	221	242
9	I	1048	227	
	II	1049	237	
	III	1050	206	223
10	I	1051	232	
	II	1052	221	
	III	1053	263	239
11	I	1054	268	
	II	1055	247	
	III	1056	237	251
12	I	1057	263	
	II	1058	242	
	III	1059	288	264
5, 1	I, 0	1060	288	
	II	1061	268	
	III	1062	268	275
2	I	1063	227	
	II	1064	237	
	III	1065	247	237
3	I	1066	227	
	II	1067	227	
	III	1068	211	222
4	I	1069	221	
	II	1070	211	
	III	1071	206	213
5	I	1072	232	
	II	1073	206	
	III	1074	247	228
6	I	1075	242	
	II	1076	232	
	III	1077	247	240
7	I	1078	211	
	II	1079	242	
	III	1080	232	228
5, 8	I, 0	1081	253	
	II	1082	253	
	III	1083	216	241
9	I	1084	206	
	II	1085	237	
	III	1086	237	227
10	I	1087	243	
	II	1088	249	
	III	1089	283	258
11	I	1090	263	
	II	1091	227	
	III	1092	252	247
12	I	1093	232	
	II	1094	247	
	III	1095	227	235

1.9 to 2.0 calories, or even more. Still, by forming these less-accurate solar-constant values into large groups of days, according to magnitude, H. H. Clayton was able to correlate solar changes with weather elements.[9]

It now occurs to me that since the periodicities now discovered in the solar emission have been expressed as to form and amplitude, and since 1920 seem to be permanent as far as known in period, amplitude, and form, it may be worth while to synthesize monthly mean solar variation *backward* from 1920. This done, it would be possible to compare the values synthesized with monthly mean solar-constant values observed on Mount Wilson. If, on the whole, high, medium, and low solar constants as synthesized correspond to high, medium, and low Mount Wilson values, it will be a confirmatory evidence of the sun's real variability, of the constancy of periodicities, of their comprising nearly the total solar variation, and of the value of Clayton's work on the correlation of solar variation with weather.

Table 5 gives the synthesized monthly solar-constant values from

---

[9] Smithsonian Misc. Coll., vol. 68, No. 3, 1917.

August 1908 to December 1920. These results are given graphically in figure 5,C. These are actual estimated solar constants in calories per square centimeter per minute, not, as in table 4, percentage departures from 1.90 calories.

COMPARISON OF SYNTHETIC WITH MOUNT WILSON SOLAR-CONSTANT VALUES

From table 53, page 193, volume 4, Annals of the Astrophysical Observatory, I take monthly solar-constant values determined from Mount Wilson observations in the months May to November, 1908 to 1920. I omit four values, July and August 1912, because the sky was then very much fouled by dust from the volcano, Mount Katmai.[10] I also omit July values of 1910 and 1917 because they are very wild indeed, far beyond the limits of dispersal of the others.

Having plotted the Mount Wilson values and such parts of the synthetic series as corresponded in time with them, I saw that there was a gradual rise in values in both observed and synthetic series from 1908 to 1914. I drew straight lines best following this trend to represent the means of the values over that interval, and read off the departures of the individual solar-constant values on the plot from these lines. For the rest of the total interval, that is 1915 to 1920, I read departures from straight horizontal lines drawn in the mean of ordinates. The plot was in arbitrary units, with the units for ordinates in the synthetic plot twice as large as those for the Mount Wilson data. These departure values follow in table 6.

Taking the sums of the data in the columns of table 6 they yield: Mount Wilson $\div$ synthetic $= \frac{503}{284} = 1.77$. Recalling the ratio of units, 2 to 1, it appears that the dispersal of Mount Wilson data is 3.54 times as great as that of the synthetic data. The synthetic curve 1920-1950, however, as plotted in figure 4, shows practically the same range of variation as does the curve of original modern observations. Hence it appears that the Mount Wilson solar-constant observations of 1908 to 1920 are probably $3\frac{1}{2}$ times less accurate than the modern work set forth in table 4.

Taking account of the numbers of departures of the same sign in the columns of table 6, and the numbers of them of opposite signs, the sums are 28 and 21.

Taking the sums of departures that are of the same sign in both columns, the results are 324 for Mount Wilson and 170 for the syn-

---

[10] See Smithsonian Misc. Coll., vol. 60, No. 29, 1913.

TABLE 5.—*Synthesized solar constant, 1908-1920*

Values to be prefixed by 1.9

1908	Aug.	49	1912	Jan.	45	1915	Jan.	45	1918	Jan.	47
	Sept.	49		Feb.	46		Feb.	50		Feb.	46
	Oct.	48		Mar.	48		Mar.	48		Mar.	43
	Nov.	46		Apr.	45		Apr.	51		Apr.	44
	Dec.	45		May	46		May	48		May	43
1909	Jan.	45		June	45		June	45		June	46
	Feb.	44		July	43		July	42		July	45
	Mar.	43		Aug.	44		Aug.	38		Aug.	46
	Apr.	40		Sept.	42		Sept.	40		Sept.	47
	May	39		Oct.	44		Oct.	42		Oct.	48
	June	39		Nov.	47		Nov.	43		Nov.	50
	July	42		Dec.	46		Dec.	45		Dec.	51
	Aug.	43	1913	Jan.	45	1916	Jan.	43	1919	Jan.	52
	Sept.	42		Feb.	47		Feb.	51		Feb.	49
	Oct.	45		Mar.	46		Mar.	53		Mar.	46
	Nov.	42		Apr.	48		Apr.	52		Apr.	47
	Dec.	40		May	45		May	47		May	48
1910	Jan.	40		June	46		June	42		June	46
	Feb.	41		July	47		July	40		July	44
	Mar.	43		Aug.	49		Aug.	36		Aug.	44
	Apr.	49		Sept.	48		Sept.	39		Sept.	48
	May	47		Oct.	46		Oct.	43		Oct.	47
	June	47		Nov.	45		Nov.	42		Nov.	44
	July	46		Dec.	43		Dec.	44		Dec.	41
	Aug.	47	1914	Jan.	46	1917	Jan.	43	1920	Jan.	43
	Sept.	46		Feb.	48		Feb.	44		Feb.	46
	Oct.	46		Mar.	48		Mar.	47		Mar.	45
	Nov.	44		Apr.	52		Apr.	46		Apr.	42
	Dec.	42		May	51		May	44		May	44
1911	Jan.	45		June	44		June	44		June	43
	Feb.	45		July	40		July	42		July	42
	Mar.	46		Aug.	41		Aug.	44		Aug.	41
	Apr.	48		Sept.	41		Sept.	43		Sept.	42
	May	52		Oct.	41		Oct.	46		Oct.	48
	June	48		Nov.	41		Nov.	50		Nov.	48
	July	47		Dec.	43		Dec.	48		Dec.	46
	Aug.	46									
	Sept.	45									
	Oct.	44									
	Nov.	40									
	Dec.	41									

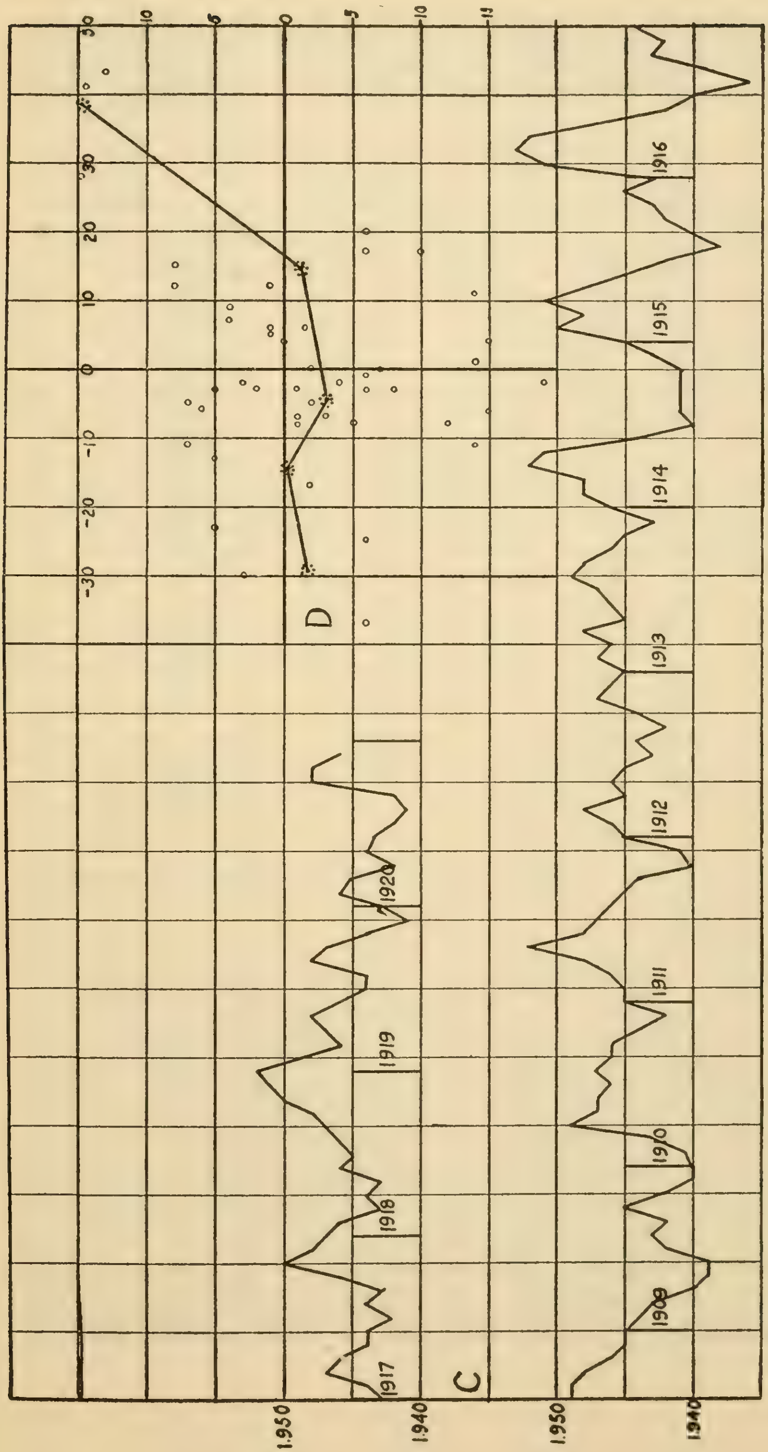


FIG. 5.—C, Solar-constant values in calories, as synthesized from 23 periodicities, 1908 to 1920. D, A comparison of mean monthly solar-constant departures from the mean, Mount Wilson (abscissae) vs. synthetic (ordinates).

thetic data. The corresponding sums for departures of opposite signs are 199 and 135. Thus, according to Mount Wilson, agreeing departures preponderate in total magnitude over disagreeing depar-

Table 6.—*Comparison of Mount Wilson and synthetic values*

	Mount Wilson	Syn.
1908		
Aug.	+45	+16
Sept.	+28	+15
Oct.	+43	+13
1909		
June	+17	− 6
July	− 3	− 1
Aug	+12	+ 1
Sept.	− 7	− 1
1910		
May	+12	+ 8
June	− 5	+ 7
July	−24	+ 5
Aug.	−11	+ 7
Sept.	−13	+ 5
Oct.	+ 3	+ 5
1911		
June	+15	+ 8
July	−13	+ 5
Aug.	− 2	+ 3
Sept.	+ 6	+ 1
Oct.	−17	− 2
1912		
May	+ 5	+ 1
June	− 8	− 1
1913		
Aug.	− 7	+ 5
Sept.	−30	+ 3
1914		
June	± 0	− 7
July	+ 4	−15
Aug.	+11	−14
Sept.	−11	−14
Oct.	− 6	−15
1915		
June	− 8	± 0
July	− 3	− 6
Sept.	+ 1	−14
Oct.	+17	−10
1916		
June	− 1	− 6
July	− 3	−10
Aug.	+ 2	−18
Sept.	− 8	−12
1917		
July	+20	− 6
Aug.	+ 6	− 2
Sept.	− 2	− 4
1918		
June	− 7	+ 2
July	+ 4	± 0
Aug.	− 3	+ 2
Sept.	+ 9	+ 4
1919		
June	+ 7	+ 4
July	± 0	− 2
Aug.	− 5	− 2
Sept.	− 6	+ 6
1920		
July	−25	− 6
Aug.	− 3	− 8
Sept.	−37	− 6

tures as $\frac{324}{199} = 1.6$. Similarly, for synthetic values the results are $\frac{170}{135} = 1.3$.

Finally, I show in figure 5,D, the Mount Wilson departures as abscissae against the synthetic departures as ordinates. The plotted points are greatly scattered, as the inaccuracy of Mount Wilson solar-constant values would lead us to expect. Yet, on the whole, the comparison indicates that high departures tend to occur simultaneously in both sets of data, and low departures similarly.

Thus four kinds of rough indications agree to confirm the view that the synthetic solar-constant values of 1908 to 1920 are supported as to their validity, at least in some degree, by the evidences from Mount Wilson observations. The four evidences are: 1. Both sets of data yield upward trends from 1908 to 1914. 2. Departures from representative lines have the same signs 28 times, opposite signs, 21.

3. The summation of departures of the same sign exceeds that for those of opposite sign about 1½ times. 4. The plot of departures indicates a positive correlation between Mount Wilson and synthetic solar-constant values.

The great inferiority in accuracy of Mount Wilson values of the solar constant forbids a high degree of correlation, even if the synthetic values are as correct from 1908 to 1920 as they are from 1920 to 1950. This inferiority arises from the fact that all the Mount Wilson values result from observations by the "long method." That method requires for accuracy a sky of constant transparency over several hours. If the sky improves, the solar-constant value is too high, and vice versa. Moreover, only one value was obtained per day with the "long method." In modern solar-constant work by the "short method," several values are obtained and combined on each day of observation. The sky is required to retain uniform transparency only during about 10 minutes of each observation. It might vary decidedly from one determination to another of the day's group, and yet all the solar-constant values of the day be closely agreeing.

SOLAR CONSTANT AND SOLAR CONTRAST

The Mount Wilson work offers another test of the probable validity of the synthetic solar-constant curve of 1908 to 1920. From 1913 to 1920 we were accustomed to produce drift energy curves in several wavelengths, observing intensities along the east-west diameter of an 8-inch solar image, on every day that we observed the solar constant of radiation. These U-shaped curves, which show the contrast in brightness between the center and edges of the sun's disk, were all measured as described in volume 4 of the Annals of the Smithsonian Astrophysical Observatory. We used an empirical formula to obtain a value to represent the average contrast between center and edge of the sun's disk on each day of observation. These data are given in tables 75 to 82 of volume 4 of the Annals.

It was thought probable that the "solar contrast" would be greater on days when the "solar constant" was higher. Some figures, indicating that this is so, are given in volumes 3 and 4 of the Annals.

Table 7, which follows here, is prepared from the "solar contrast" tables of the Annals, volume 4, and from table 6, just given, which presents synthetic solar-constant values of 1908 to 1920. To prepare the solar-contrast values for this use, means of the daily values are taken of every month given in Annals 4. Then, in order to eliminate systematic errors which might introduce inconsistencies, a separate mean value is computed for the available months of each year, 1913 to 1920. Differences from these yearly means are given in column 2 of table 7. To make the synthetic solar-constant values entirely comparable to these contrast values, separate means of them are taken for each year of the comparison, including only the months used in obtaining the separate contrast means. Differences from these synthetic solar-constant means, expressed in thousandths of a calorie, form column 1 of table 7.

TABLE 7.—*Comparison of synthetic solar-constant departures with solar-contrast values of 1913-1920*

Solar-constant departures in thousandths of a calorie.

Solar constant	Solar contrast
+17	+19
− 3	−32
−13	+14
+36	−35
+ 6	−24
−34	−18
−14	+28
+ 6	+49
+20	+10
0	−29
−40	−75
−10	0
+30	+ 4
−17	−18
+ 3	+15
− 7	+14
−14	−23
− 4	−12
+ 6	+ 8
+16	+16
+ 5	− 8
−15	−13
−15	+13
+25	+40
+ 3	+46
− 7	+18
+ 3	−70
+23	−13
− 4	+ 9

Counting the numbers of months when values in columns 1 and 2 have the same sign and opposite signs, the numbers (counting zero values into each group) are 18 and 13, respectively. So here is another straw pointing to the reliability of the synthetic solar-constant values. But more convincing, and more informing, is figure 6. Here the

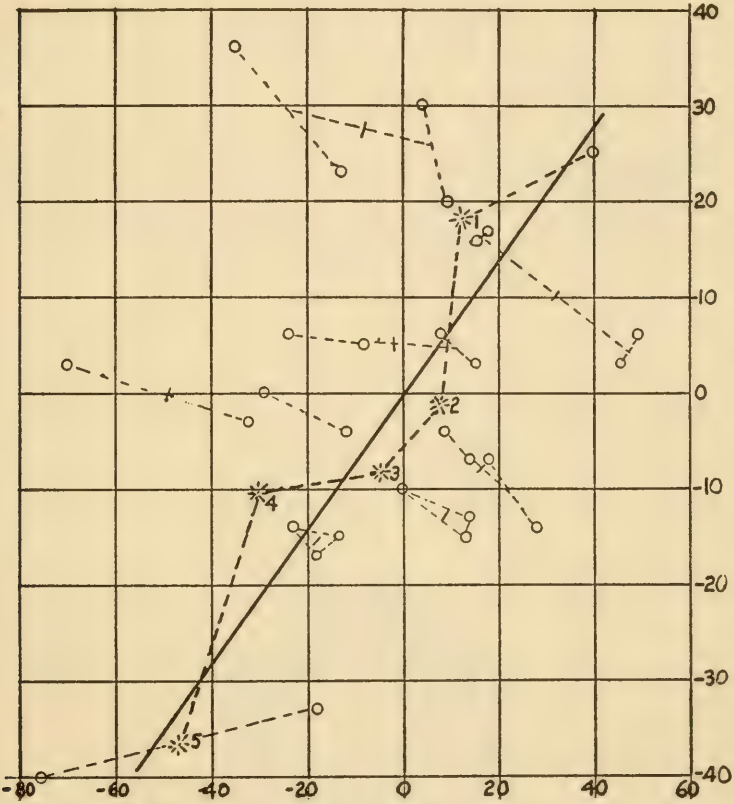


FIG. 6.—Mount Wilson solar contrast (abscissae) vs. synthetic solar constants (ordinates).

values in the columns of table 7 are plotted against each other, solar constants as ordinates, solar contrasts as abscissae. In order to bring out plainly the fact that higher contrast values attend higher synthetic solar-constant values, stars 1, 2, 3, 4, 5, have been plotted to give the centers of gravity of groups of 8, 8, 5, 5, and 2 months, respectively. A full heavy line has been drawn to show the trend of the results.

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 117, NUMBER 11

Roebling Fund

IMPORTANT INTERFERENCES WITH NORMALS IN WEATHER RECORDS, ASSOCIATED WITH SUNSPOT FREQUENCY

BY
C. G. ABBOT
Research Associate, Smithsonian Institution

(Publication 4090)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
MAY 20, 1952

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

Roebling Fund

IMPORTANT INTERFERENCES WITH NORMALS IN WEATHER RECORDS, ASSOCIATED WITH SUNSPOT FREQUENCY

By C. G. ABBOT
Research Associate, Smithsonian Institution

World Weather Records[1] comprise long tables of monthly weather records of pressure, temperature, and precipitation. At the bottom of each table are given normals of these elements, determined by averaging the long columns of monthly values for each month of the year. By subtracting these normal values from the numerous observed temperature values, tables of temperature departure are obtained. By dividing the numerous observed precipitation values by appropriate normal values, percentages of normal precipitation are tabulated.

By using percentages of normal precipitation thus obtained in a study of the effects of periodic solar variations on the precipitation of Peoria, Ill., important influences of sunspot frequency were uncovered. In the first place, the average percentage precipitation was about 9 percent higher when Wolf sunspot numbers exceeded 20 than when the Wolf numbers were below 20. In the second place, the average computed percentages showed large 12-month periodicities. The amplitude of these periodicities is about 8 percent when Wolf sunspot numbers exceed 20, and about 16 percent when the Wolf numbers are below 20.

The 12-month periodicities, just described, are roughly opposite in trends. With sunspot numbers above 20, as computed, high average percentage precipitation occurs in the first half of the year, low percentage precipitation in the second half. The maximum is in June, the minimum in October. With sunspot numbers below 20, low percentage precipitation occurs in the first half of the year, high percentage precipitation in the second half. The maximum is in August, the minimum in March.

---

[1] Smithsonian Misc. Coll., vol. 79, 1927; vol. 90, 1934; vol. 105, 1947.

SMITHSONIAN MISCELLANEOUS COLLECTIONS, VOL. 117, NO. 11

To determine these facts I used the normal values of precipitation published in World Weather Records for most of the time, but for recent years, for which World Weather Records are not available, I used the normals published by the U. S. Weather Bureau, which differ slightly. These normal values for Peoria are as follows, in inches of precipitation.

Fig. 1.—Twelve-month periodicities in precipitation at Peoria, Ill., depending on sunspot frequency, but hidden by using published normals.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Earlier...	1.75	1.70	2.80	3.28	3.94	3.71	3.75	3.44	4.24	2.44	2.32	1.66
Later....	1.79	1.95	2.76	3.15	3.70	3.66	3.76	3.10	3.79	2.92	2.31	2.04

The percentages of normal precipitation were computed for me by assistants, and I did not know until lately that two slightly different sets of normals were used. In further studies I intend to compute two sets of normals for Peoria from 1856 to 1950. One set will be suited to sunspot numbers above 20, the other to sunspot numbers below 20.

Separating the 82 years of the Peoria tabular monthly mean values of precipitation, 1858 to 1939, into two groups, 50 years of high sunspots, 30 years of low sunspots, and 2 years being omitted as mixed, I computed the following monthly mean percentage precipitation values, based on the above quoted normals.[2]

	Jan.	Feb.	Mar.	Apr.	May	June
Wolf number > 20...	105.6	107.0	107.9	108.5	109.1	108.9
Wolf number < 20...	91.1	89.8	89.2	91.8	93.0	91.7

	July	Aug.	Sept.	Oct.	Nov.	Dec.
Wolf number > 20...	105.6	102.4	101.9	101.2	103.4	102.3
Wolf number < 20...	98.0	105.0	104.8	102.8	101.9	98.7

These results are plotted in figure 1. The curve A corresponds to Wolf numbers >20, the curve B to Wolf numbers <20. One readily sees that high Wolf numbers attend higher average precipitation at Peoria; that strongly marked 12-month periodicities are hidden by tables of percentage precipitation as ordinarily computed from published normals; and that the amplitudes of these periodicities are large, and their trends roughly opposite, for sunspot numbers above and below 20.

It is quite obvious that no sound results on periodic fluctuations of Peoria precipitation can result from tabulating percentage precipitation computed from published normals. Take, for instance, the 7-month solar-radiation periodicity. Tabulations of numerous 7-month columns, covering many years, would be used. One or more of these columns would start with June in years of low sunspot activity. Curve B of figure 1 shows that in this column there would be a spurious increase of 13 percent from June to August, and a spurious decrease of 6 percent from August to December. Another column would start perhaps with August in some other year. This column would contain a spurious decrease of 15 percent to its end in February.

If such sunspot influences are hidden in the published normals for one weather element at one station, it is probable that similarly caused defects are hidden in published normals for all weather elements at all stations. Statistical meteorologists will do well to be on the watch for them.

---

[2] These computations employ the percentages of normals smoothed by 5-month running means.

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 117, NUMBER 12

TWO ABORIGINAL WORKS OF ART FROM THE VERACRUZ COAST

(With Three Plates)

BY
PHILIP DRUCKER
Bureau of American Ethnology

(Publication 4091)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
AUGUST 26, 1952

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

TWO ABORIGINAL WORKS OF ART FROM THE VERACRUZ COAST

By PHILIP DRUCKER

Bureau of American Ethnology

(With 3 Plates)

The two specimens described here were excavated at the site of Cerro de las Mesas, Veracruz, by the National Geographic-Smithsonian Institution Expedition to Mexico in 1941. Both were referred to in the published accounts of the work.[1] They could not be described adequately, however, at the time the reports were written, for both were badly broken, and their restoration was a long, painstaking process. This was particularly true of the pottery statue with which the preparators at the Museo Nacional de México struggled intermittently for several years before they found a way to bolster the fragments to support the figure's considerable weight. Both pieces are now among the collections of the Museo Nacional.

The specimens are important on two counts. From the cultural standpoint they reflect rather clearly the cultural heritage of their makers, and as objects of art both deserve consideration. As examples of artistic expression these two pieces rate high among the host of finer achievements of Middle American civilizations. Therefore, the accompanying descriptions and plates are presented for the benefit of students of Mesoamerican archeology and also for those interested in prehistoric American art.

THE TURTLE SHELL

The first piece to be described is a carved turtle shell (pl. 1, and fig. 1). It was found among the numerous mortuary offerings associated with burial II-18, in trench 30, which belongs to the Lower II period of the site. The small shell, about 15 cm. in length, was complete with both carapace and plastron. Six holes about the periphery of the carapace suggest that it was meant to be lashed onto something, but the use

---

[1] Stirling, M. W., Expedition unearths buried masterpieces of carved jade, Nat. Geogr. Mag., vol. 80, No. 3, pp. 207-302, 1941; Drucker, P., Ceramic stratigraphy at Cerro de las Mesas, Veracruz, Mexico, Bur. Amer. Ethnol. Bull. 141, pp. 9, 12, 1943.

of the object is unknown. Perhaps it was a ceremonial rattle. Restoration of the many fragments into which it had been broken revealed a complex design consisting of a number of symbolic motifs engraved on the carapace. The design appears to have been engraved with some rather sharp implement; then the areas adjoining the principal fields were scraped away to shallow bevels to give an impression of bold relief. The central figure of the design is the head of a man wearing an elaborate helmet consisting of a jaguar head, surmounted by a leering monkey skull. The jaguar's jaws are open so that the wearer's face appears between them. Such headgear was often used, we know, by Mexican priests on occasions of ritual. Considerable stylization has

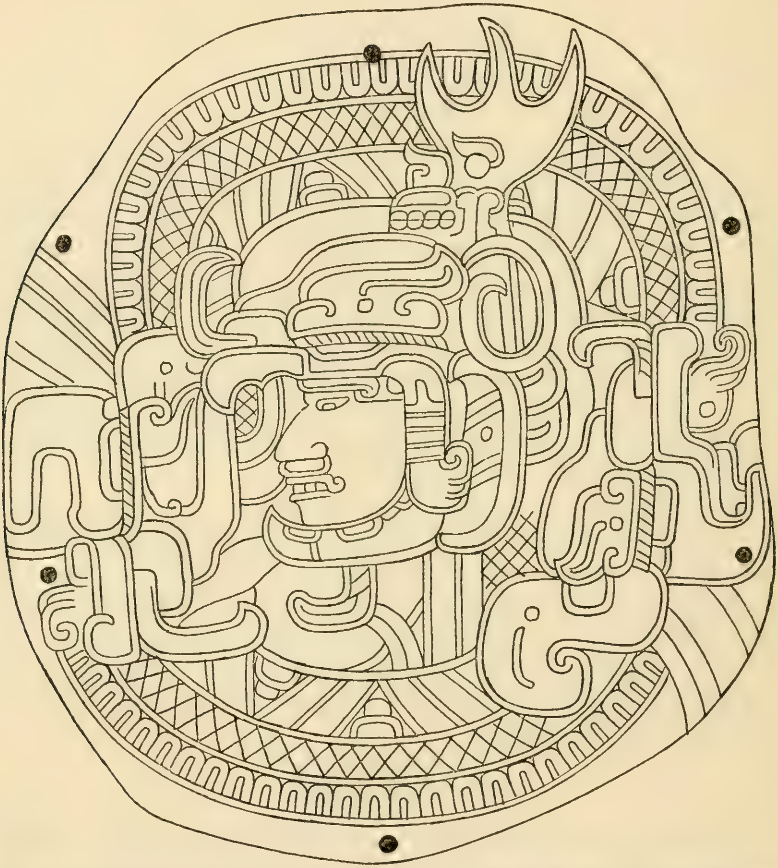


FIG. 1.—Design carved on turtle shell from Cerro de las Mesas. (From drawing by Covarrubias.)

taken place in the representation of the jaguar, but the beast may be recognized by the short nose, the low-domed, catlike forehead, and the large, round ears. The jaws have been modified until they differ somewhat from those usually seen in drawings from the area. They have a faint suggestion of the powerful beak of some raptorial bird. The significance of the monkey skull with its peculiar 3-tined crest is difficult to interpret.

Framing the central figure is a band consisting of two plumed serpents. The heads of these weird creatures are to be seen on either side of the head of the central personage with the helmet. The serpents' bodies are represented by bands covered with three parallel zones of small elements. The outermost of these shows unmistakably the broad belly scales, the cross hatching of the middle band representing the smaller scales of the sides, and the upper (or inner) zone indicating markings of the reptiles by opposed sets of sloping lines.

Good design is achieved by the contrast between the small compact elements of the serpent bodies and the more open areas of the central figure. There is a horizontal band set off by the plumed serpent heads, with their sweeping curves and open spaces, across the middle of the field that invariably leads the eye to the human face at the center, augmenting the emphasis of the location of the face on the high point of the shell's convexity. Were it not for this horizontal movement the components of the intricate pattern would have been lost in a confused mass of lines and small forms.

Another striking feature of the carving from the standpoint of design is its deliberate asymmetry that gives it movement and avoids the static monotony of perfectly balanced patterns. The bodies of the upper and the lower serpents are not in line. The left side of the lower one is offset markedly to the viewer's left; the right end, where it joins the head, is set over only slightly, producing a total effect of motion to the left. A similar trend is produced by the monkey skull and the plumes of the right-hand serpent which project beyond the central band and produce, with the rest of the open curvilinear areas of the central band, a triangle whose apex lies, or rather points, to the left—the same direction in which the central personage is facing. The plumes of the left-hand serpent were suppressed apparently because their use would have arrested the consistent leftward motion of the pattern.

A small area between the head and ear of the right-hand plumed serpent and the lower jaw of the jaguar headdress is partially cross hatched. It looks as though the artist had begun to fill in the entire strip between the central figure and the frame, then stopped. Why he did not complete this filler cannot be determined. It may be that he realized such a filled area would interrupt the transverse motion of the design.

All in all the design is well executed and obviously planned. Stylistically the carvings belong to the Highland tradition. The motifs: Personages wearing headgear representing the open fauces of an animal or monster, and plumed serpents, are common in the Highland from Teotihuacan to Aztec times. (They occur also in Maya art but the style is not in the least Mayan.) The treatment: A nonrealistic stiffness of the central figure, exuberant detail and filler, remind one strongly of paintings from Teotihuacan frescoes, and also certain Oaxacan stelae. Neither the characteristics of detail nor the general staid simplicity of Olmec art can be detected in the piece. Although the design is complex it lacks the interweaving of elements, the sinuous interlocked lines, of the Central Veracruz carving found on stone yokes and palmas, the style often called (or miscalled) "Totonac."

There is a noteworthy stylistic resemblance between the carving on the turtle shell and that of four Cerro de las Mesas stelae: those numbered 3, 5, 6, and 8.[2] Of all the better-preserved stone monuments from the site, these four form the most sharply defined group stylistically and, like the turtle shell, appear to derive their stimulus from Highland influences. This similarity suggests the provisional assignment of these stelae to the time horizon of the turtle shell, which, on the basis of the pottery associated with it in the burial offerings, can be dated as of the Lower II ceramic period.

THE STATUE OF XIUHTECUTLI

The clay statue shown on plates 2 and 3 was excavated by Stirling in Trench 34. It is to be attributed to the same temporal horizon as the turtle shell, Lower II. The large, heavy vessel that is supported on the head of the figure had been placed on a step and was buried by an enlargement of the mound. Portions of the body of the statue were inside the vessel, and pieces of clay arms and legs were stood vertically around the mouth. Within the largest fragment of the torso were bones of a human infant. Underneath the other fragments was the head.[3] In other words the object would seem to have been deliberately broken up so that all the pieces could be piled together as an offering during this particular enlargment of the mound.

---

[2] Stirling, M. W., Stone monuments from southern Mexico, Bur. Amer. Ethnol. Bull. 138, pls. 23, 24, and figs. 10c, 10a, 9, 11b, and 11c, 1943.

[3] Stirling, op. cit., 1941; Drucker, op. cit., 1943, pl. 8,c,f.

The shattered condition of the specimen when found made it difficult to recognize, in the field, the being represented; it was only when we began trying to fit parts together that we discovered that the bearded head actually belonged with the body fragments. Even then it was thought that the large vessel was a pedestal for the figure. After the figure had been restored at the Museo Nacional de México, however, Dr. Caso, Sr. Noguera, and others of the staff recognized that the statue represents Xiuhtecutli, The Fire God (also called Huehueteotl, The Old Old God), and, after examining the restored vessel, found clear indications of its former attachment to the head. After a number of trials, a base was designed which would support the figure adequately, along with an armature that sustains most of the weight of the heavy vessel—really a brazier—on the head. Xiuhtecutli, in his role as God of Fire, usually was portrayed supporting a vessel containing fire in just this fashion. It should be remarked that the complete figure, brazier and all, is between 80 and 90 cm. high, and in some areas the clay is nearly 2 cm. in thickness. The piece is therefore extremely heavy.

The statue had not been completely restored when the photographs shown in plate 2 were made. For that reason the flat tablets back of the head, which helped distribute the weight of the brazier to the shoulders, do not fit flush as they should (note daylight between the piece and the bottom of the vessel on the viewer's left, plate 2, b). Likewise, the flat strips between the figure's elbows and body and those on the knuckles were temporary braces of wood put on till the restoration of the figure could be completed. There should also be a headband about the head, with a wide flat bow, painted red, across the forehead, as in plate 3, which shows the statue as it is today in the Museo Nacional.

The basal portion of the torso, where the buttocks should be, is finished off square. I suspect the statue was built solidly in a bench or step, or on an altar, to keep it from overbalancing. The upper ends of the legs likewise are finished off square. They must have been fastened to the bench or altar or similar architectural feature.

The restored base for the figure is made so that the left leg rests within the curvature of the right. Actually, the left leg rested on top of the right, the edge of the foot attaching to the upper surface of the right leg at the point at which a small protuberance can be seen in the photograph (pl. 2, b). This seems a most uncomfortable postition. Perhaps it was used deliberately to increase the tension and feeling of strain the figure portrays. On the other hand, it may have been a customary local posture. People *can* get used to sitting that way, for I have seen Marshallese do so by the hour. This is only a random example; there is not the slightest intent to suggest any farfetched Oceanic influences.

At first glance the figure strikes one as being extremely realistic, but closer consideration shows it to contain a remarkable blend of realism and conventionalization. The sharp-peaked indentations above and below the eyes are completely nonrealistic, but the heavy shadows they produce give an effect of deep sockets from which the heavy-lidded eyes bulge. The exaggerated V-shaped cheekbones produce the effect of sunken cheeks, making the face that of an aged person. The deeply incised lines about the face suggest both wrinkles and lines formed by grimaces expressing physical strain. The formless tubular arms and legs, anatomic impossibilities, give the effect of the scrawny limbs of an old man. The body of the figure, with its shoulders hunched and back bent to an almost deformed angle to support a great weight, its sagging pectoral muscles and paunch from which the elasticity of youth have long since departed, is the most realistic unit of the piece. The effect of great physical effort and strain is achieved through a variety of ways, some already mentioned: The bulging eyes, the lines of the contorted features, the angle at which the head is held and the hunched-up shoulders, and, of course, the pronounced forward bending of the body. The original awkward position of the legs must have completed the strained, almost tortured, aspect of the figure.

The identity of the personage as Xiuhtecutli, The Fire God, who was also called Huehueteotl, The Old Old God, is quite clear, from the obvious indications of age and the characteristic brazier supported on his head. Xiuhtecutli was a Highland deity. According to Sahagun, he was the most important of the Aztec minor gods. His cult flourished from Teotihuacan through Aztec times in and around the Valley of Mexico, and Vaillant found him represented in the horizon of the Middle Cultures.[4] His appearance at a site in the coastal plain of Veracruz can only be interpreted as a reflection of the strong Highland influence on the early population of the Cerro de las Mesas region.

---

[4] Vaillant, G. C., The Aztecs of Mexico, p. 42, 1941. The small clay figurines representing sunken-cheeked aged persons, found occasionally in the merged Proto-Classic–Early Classic horizon of southern Veracruz and Tabasco (the period Middle Tres Zapotes and La Venta), apparently simply represent elderly persons, not a cult of Huehueteotl, for they lack the specific attributes pertaining to fire, etc., that characterize that Highland deity.

CONCLUSIONS

Both the specimens described here, with their pronounced Highland affiliations, emphasize a point brought out by the general pattern of ceramics from Cerro de las Mesas. Aztec influence, that is to say, Moctezuma's domination over the central Veracruz coast, when Cortes and his swashbucklers landed, was but one of history's repetitions. Highland cultures, richly and powerfully developed in the Mixteca-Puebla focus, had spilled down to the coast before, as demonstrated by the abundance of Cholulteca painted pottery that marks the beginning of the "Upper" culture horizon at Cerro de las Mesas. This earlier intrusion marks a Pan-Mexican period in which cultural dominance and expansion carried Mixteca-Puebla elements not only to central Veracruz and Yucatán, but to western Mexico as far as distant Sinaloa. But even before, during the long life of Teotihuacan culture, geographical distance could not restrict diffusion. From the times of the earliest occupation found at Cerro de las Mesas, the strongest influences determinable were those of Teotihuacan. Transplanted to a new setting, some of these Mexican Highland concepts attained new artistic heights on the Gulf coast, as the themes carved on the turtle shell and the statue of Xiuhtecutli clearly show.

Carved Turtle Shell from Cerro de las Mesas, after Restoration

a

b *c*

POTTERY STATUE OF XIUHTECUTLI, THE FIRE GOD

a, Facial detail, before restoration; *b, c,* statue as partially restored.

THE STATUE COMPLETELY RESTORED

Photograph courtesy National Geographic Society.

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 117, NUMBER 13

Charles D. and Mary Vaux Walcott Research Fund

PRIMITIVE FOSSIL GASTROPODS AND THEIR BEARING ON GASTROPOD CLASSIFICATION

(WITH TWO PLATES)

BY
J. BROOKES KNIGHT
Research Associate in Paleontology, U. S. National Museum

(PUBLICATION 4092)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
OCTOBER 29, 1952

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 117, NUMBER 13

Charles D. and Mary Vaux Walcott Research Fund

PRIMITIVE FOSSIL GASTROPODS AND THEIR BEARING ON GASTROPOD CLASSIFICATION

(With Two Plates)

BY

J. BROOKES KNIGHT
Research Associate in Paleontology, U. S. National Museum

(Publication 4092)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
OCTOBER 29, 1952

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

CONTENTS

Charles D. and Mary Vaux Walcott Reseach Fund

PRIMITIVE FOSSIL GASTROPODS AND THEIR BEARING ON GASTROPOD CLASSIFICATION

By J. BROOKES KNIGHT

Research Associate in Paleontology, U. S. National Museum

(With Two Plates)

INTRODUCTION

GENERAL CONSIDERATIONS

With only one exception that comes readily to mind, the various classifications of the class Gastropoda in current use are the work of neontologists. The living gastropods are classified on the basis of their morphology, largely the anatomy of the soft parts. The fossil forms, or at least the older ones, so far as they belong to genera that are now extinct, are given the scantest of notice and are distributed in an almost haphazard fashion among the families erected primarily for living forms. As neontologists have little familiarity with fossils, unless it be the more recent ones, they are not especially struck by the resulting incongruities. Of course they fail to take the fullest advantage of the information that the older extinct fossil forms can furnish as to the early history of the class and its bearing on phylogeny. Indeed the inaccuracy of such little knowledge as they have of the more ancient fossils is apt to lead them astray.

That the work of the neontologist is nevertheless of the highest importance is too obvious to need comment. He has the entire animal available to him, including the soft parts, and in the main he has made much of his opportunities.

The paleontologist, on his part, suffers from the severe handicap that he can never observe directly the soft parts of the forms that he studies. In a sense he is forced into the role of a mere conchologist. Unfortunately, many paleontologists, inadequately trained in zoology, surrender with resignation, if not with complacency, to what appear to be the necessities of the situation. Nevertheless, it is possible to infer from fossil shells somewhat more of the probable general anatomy of the soft parts than is commonly done and these

SMITHSONIAN MISCELLANEOUS COLLECTIONS, VOL. 117, NO. 13

inferences, if made with due caution, can be useful. Of course they do not stand on the same plane as direct observation; nevertheless to neglect them, or to refuse to give them recognition, however guarded, would be unscientific indeed.

The exception to my original statement that the classification of the Gastropoda is largely the work of neontologists is the work of Wenz, begun in 1938 and unhappily interrupted by his death soon after the close of the second World War (Wenz, 1938-1944). He lived to complete only that part dealing with the prosobranchs. Wenz was a paleontologist with an excellent training. He acquired some familiarity with the older fossil gastropods as a pupil of Prof. Emmanuel Kayser and especially of Prof. Ernst Koken, of Tübingen. His field of specialization since his student days was Cenozoic nonmarine gastropods, a field that did not qualify him particularly for the task he undertook. The novelties introduced by Wenz in 1938 into the classification of the Gastropoda were not in the highest categories but at the familial level. He made a distinct contribution in erecting many families, subfamilies, and superfamilies for extinct genera for which there had long been a need, but the inherent difficulties of working with skeletal material alone and his relative unfamiliarity with the older marine forms made many of his new families mixtures of incongruous elements, and their placement in the higher categories is not always fortunate.

Perhaps the outstanding contribution of Wenz's work in 1938 to the fundamentals of gastropod classification was his suggestion that the isolated, symmetrically paired dorsal muscle scars of *Tryblidium* (Tryblidiacea) might be a very primitive character suggesting the segmentation of the chitons (Wenz, 1938, p. 59). However, in 1938 he allowed himself to be influenced by this idea in constructing his taxonomic hierarchy only to the extent of erecting a separate superfamily, Tryblidiacea, for the genera with symmetrically paired dorsal muscle scars instead of including them with the superficially similar Patellacea, as had been done in effect by previous workers. As is generally recognized, the symmetry in the Patellacea is secondary and superficial, not primitive.

Two years later Wenz proposed a more radically revised classification of the major categories of the Gastropoda (Wenz, 1940). He recognized a major dichotomy within the Gastropoda (excluding the Loricata) between what he regarded as two subclasses, the Amphigastropoda (bilaterally symmetrical, primitively orthoneurous, with a saucer-shaped, conical, or symmetrically spiral shell) and the Prosobranchia (asymmetrical, chiastoneurous, with asymmetrically coiled shell). He elaborates somewhat his invaluable earlier views on the tryblidians but he does not follow the logic of his position and classify them with the chitons. Instead, because of the discovery of multiple paired dorsal muscle scars in the supposed bellerophont *Cyrtonella,* he classifies the bellerophonts with the tryblidians in a subclass, the Amphigastropoda. This action I do not regard as well taken (Knight, 1947b, p. 264, and appendix to this work). Naef, a neontologist, had made a somewhat similar division at an earlier date with the Planospiralia for the bellerophonts (he was unaware of the probable significance of *Tryblidium* and its allies or possibly even of their existence) and the Turbospiralia for the asymmetrical groups (Naef, 1911, p. 159). Naef's Planospiralia, unlike Wenz's Amphigastropoda, was looked on as streptoneurous and, of course, prosobranch.

In the interval between the first draft of the present paper and its completion, an interval required for the preparation of drawings, a significant paper on the aspidobranch Gastropoda and their evolution appeared. This paper, by the distinguished anatomist and physiologist, C. M. Yonge (1947), reports the results of some revealing investigations on the anatomy and functioning of the pallial organs of some aspidobranchs. Yonge does not stop with the recording of observations but proceeds to apply his findings to an interpretation of gastropod evolution just as I have done from a different set of observations. Both Yonge and I have accepted certain findings and interpretations from previous workers and to that extent have a common background. Hence it is not surprising that there is much basically the same in each interpretation. On the whole our acceptance or rejection of the suggestions of previous workers is gratifyingly similar. A minor difference is that he regards Wenz's suggestion that the tryblidians are pretorsional gastropods only as possible (Yonge, 1947, p. 485). With some rearrangements and differences in emphasis from Wenz I accept this as probable. Yonge regards the bellerophonts as prosobranchs, just as I do, and thus rejects Wenz's view that they were "primitively orthoneurous." However, he appears to harbor an unexplained and undocumented idea that although they are symmetrical prosobranchs they had a single dorsal and median retractor muscle (Yonge, 1947, p. 490, fig. 31a). It is my view that the bellerophonts are prosobranch gastropods that have undergone torsion and have retained a high degree of primitive bilateral symmetry including a single symmetrical pair of retractor muscles attached at the distal ends of the columella (Knight, 1947b).

Yonge proposes some phylogenies (Yonge, 1947, p. 490, fig. 31a) toward which I am compelled to be skeptical. I am skeptical of the supposed origin of the Neritacea and the pectinibranchs as branches arising independently and directly from the bellerophonts. The great expansion of the pleurotomarians in the Paleozoic when they overshadowed all other contemporaneous gastropods in diversity of form and number of genera and species provided possibilities that cannot be neglected. For example, the asymmetrical neritaceans and the pectinibranchs may have been derived from asymmetrical ancestors such as some of the numerous and varied pleurotomarians. The pleurotomarians (Pleurotomariacea) include much besides *"Pleurotomaria."* That the present-day *Theodoxus* and the pectinibranchs are not derived from the present-day *"Pleurotomaria"* one can readily concede. It is equally unlikely that the present-day *Haliotis, Scissurella,* the fissurellids, or the patellids are correctly derived from the present-day *"Pleurotomaria,"* as Yonge seems to imply. I am not even prepared to accept *Mikadotrochus beyrichi* (Hilgendorf), the species from which Yonge derives most of his ideas of pleurotomarian anatomy, as properly referred to the genus *Pleurotomaria* Sowerby. That all these may have had common ancestors more advanced than bellerophonts, i. e., advanced to the pleurotomarian stage or farther, seems probable.

The classifications of neontologists are based actually on comparative anatomy, that is to say on morphology, from which they attempt to infer phylogeny, but phylogeny, or descent with change in time, is held very much in the background as an ideal only. The paleontologist alone has spread before him the time sequence, the order in which forms appeared in time. This has been called chronogenesis. Chronogenesis is not a perfect tool, for the fossil record is far from complete and the recognition of phylogenies involves supposed relationships inferred from imperfectly known morphological criteria. Nevertheless, it is a useful tool, if used with caution, and is becoming more and more useful as our knowledge of the life of the past increases.

In summary, all classifications are provisional and hypothetical, based on inferences from more or less complete observations of various phenomena. Certainly any classification based wholly on neontological data or with inadequate attention to or understanding of paleontological data must be almost as defective in the very nature of the case as would be the converse. The present classification is offered as one that at least attempts to give full weight to paleontological data and their bearing on phylogeny. It is admittedly provisional.

PROPOSED CLASSIFICATION

Changes in classification.—The principal novelties of the classification given below consist of the following:

The Polyplacophora are returned to the Gastropoda as one order of a subclass, the Isopleura, proposed by Lankester in 1883. The order Monoplacophora (*Tryblidium* and its allies) is added to the Polyplacophora. I am allowing the Aplacophora to stand close to the Polyplacophora, as do most authors, although without strong conviction. They do not occur as fossils, and paleontology has no light to throw on them. They are probably degenerate, not primitive. These three orders will make up the Isopleura.

In the subclass Anisopleura, also proposed by Lankester in 1883, are included as superorders the Prosobranchia, Opisthobranchia, and Pulmonata, while to the primitive prosobranch superfamilies Bellerophontacea and Pleurotomariacea of the order Archaeogastropoda is added a third, the Macluritacea. Except as affected by the foregoing the remaining more advanced archaeogastropod superfamilies are left untouched as Wenz left them, not because Wenz's treatment is satisfactory but because a complete revision is beyond the scope of this paper. Such a revision is well under way, however, and perhaps in the not too distant future the results may be published.

Phylum Mollusca Cuvier
  Class Gastropoda Cuvier
    Subclass Isopleura Lankester
      Order Monoplacophora Wenz[1]
      Order Polyplacophora Blainville
      Order Aplacophora Jhering
    Subclass Anisopleura Lankester
      Superorder Prosobranchia Milne-Edwards
      Order Archaeogastropoda Thiele
        Superfamily Bellerophontacea Ulrich and Scofield[2]
        Superfamily Pleurotomariacea Wenz[2]
        Superfamily Macluritacea Gill[1]

Other archaeogastropod superfamilies are not considered here, nor are the following orders and superorders:

      Order Mesogastropoda Thiele
      Order Neogastropoda Wenz
    Superorder Opisthobranchia Milne-Edwards
    Superorder Pulmonata Cuvier
  Incertae sedis. *Pelagiella* Matthew, 1895, and allies. Possibly not gastropods.

---

[1] Considered in some detail.

[2] Only the earlier, more primitive genera and some living ones considered.

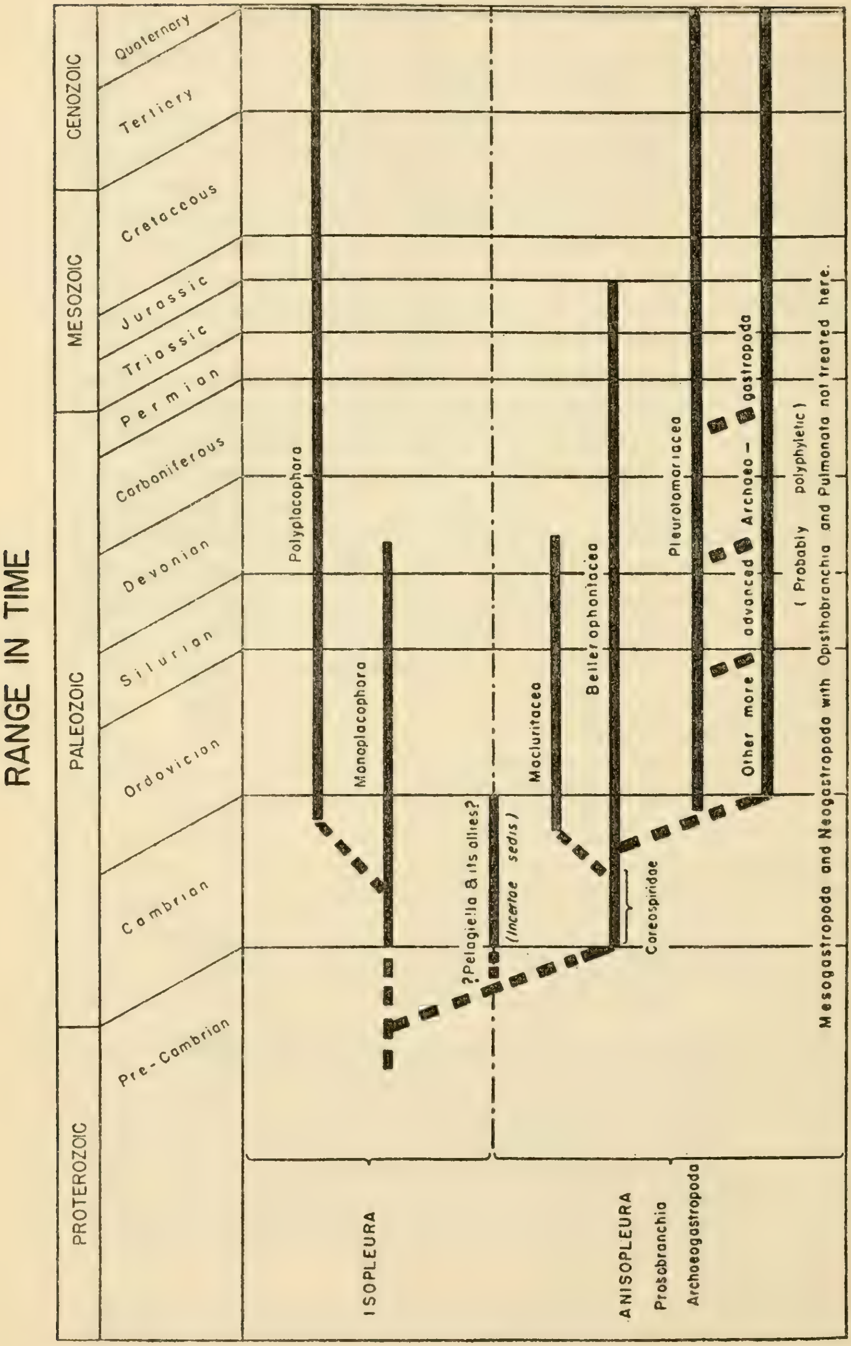


FIGURE 1

(See opposite page for explanation.)

Chronogenesis and range in time.—In order to give an over-all view of the range in time of the two orders of the Isopleura and the three most primitive superfamilies of the anisopleuran prosobranchs, a diagram is presented (fig. 1). It will be noted that the major dichotomy in time (as well as in morphology) is between the Isopleura and Anisopleura in the early Cambrian, at the beginning of the fossil record. It will be noted also that two of the three primitive superfamilies of the prosobranch Archaeogastropoda, the Macluritacea and Bellerophontacea, have been extinct since Devonian and Triassic times, respectively. Only the long-ranging Pleurotomariacea, late Upper Cambrian to Recent, has carried through in several specialized relic families. These give us some clue to the morphology of the soft parts and to the physiology and embryology of the primitive prosobranchs.

EXPLANATORY NOTES

Technical terms.—As far as possible the use of technical terms (other than the formal scientific names of systematic categories) has been avoided. With exceptions to be noted the morphological terms employed are so much in general use by both paleontologists and malacologists that it seems unnecessary to define them.

The term "hyperstrophic" is not a new one but experience suggests that many have only a hazy idea of its meaning. It refers to that

---

FIGURE 1.—Range in time of the more primitive categories.

For the benefit of the neontologist interested in geologic time in terms of years and unfamiliar with recent work, the following data are arranged from the Report of the Committee on the Measurement of Geologic Time of the Division of Geology and Geography, National Research Council, for 1949-1950 (p. 18):

Period	Beginning in approximate number of millions of years ago	Approximate length in millions of years
Quaternary	1	1
Tertiary	60	59
Cretaceous	130	70
Jurassic	155	25
Triassic	185	30
Permian	210	25
Carboniferous	265	55
Devonian	320	55
Silurian	360	40
Ordovician	440	80
Cambrian	520	80

Computed probable errors in beginnings: Quaternary ± 50 thousand years, Tertiary ± 1 to 2 million years, Mesozoic ± 5 million years, and Paleozoic ± 10 million years.

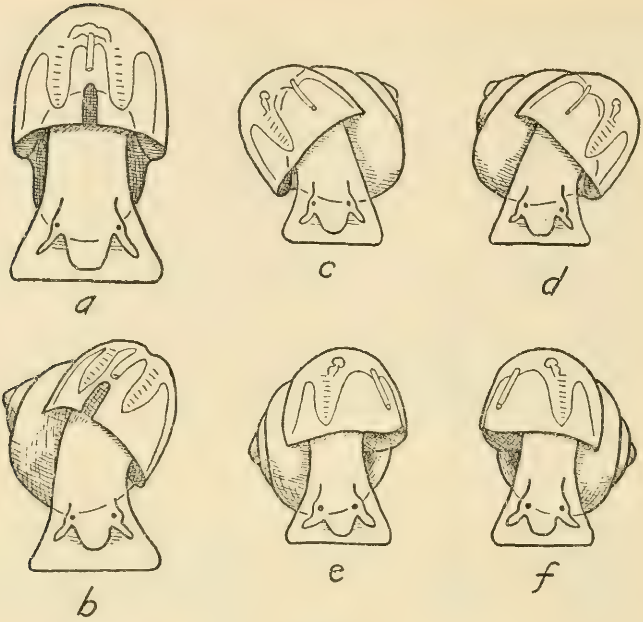


FIGURE 2

a, Isotrophic coiling. Symmetrically coiled in a plane with the sides mirror images of each other. The example is a diagrammatic restoration of a generalized bellerophont. Note the symmetrical and paired ctenidia, the rectum passing through the pericardium and terminating in the anus between the ctenidia and close to the slit, and the symmetrical and paired auricles of the heart.

b-f, Asymmetrical coiling. *b*, Orthostrophic coiling in the pleurotomarians. Although the shell is asymmetrical and orthostrophic the rectum still passes through the pericardium and terminates between the ctenidia close to the slit. Many of the organs such as ctenidia, auricles, etc. are paired. The diagram shows a dextral pleurotomarian. No certainly sinistral ones are known. *c, d*, Orthostrophic coiling at an advanced stage of asymmetry. In the dextral forms the right ctenidium and auricle are lost, the rectum has moved to the right and no longer passes through the pericardium, and the slit has disappeared. *c* shows a sinistral orthostrophic gastropod and *d* a dextral one. Note that the arrangement of the shell and the internal organs in each is the mirror image of the other. A tremendous majority of living gastropods are dextral orthostrophic.

e,f, Hyperstrophic coiling. *e*, sinistral and *f* dextral. Comparing the dextral and sinistral hyperstrophic forms with their orthostrophic counterparts, the relative positions of the corresponding internal organs are the same in each but the direction of asymmetry of the shell is reversed. In the dextral hyperstrophic form the spire protrudes to the left side instead of to the right. The internal organization is dextral, but the shell if oriented in the

[legend continued on opposite page]

sort of coiling in which the shell is inverted and what appears to be the spire is homologous with the base of orthostrophic forms. It is as though the normal spire were pushed through, protruding on the side that is normally the base and the side that normally has the spire resembles a base. The shell resembles superficially a sinistral shell but the soft parts are dextral. A hyperstrophic sinistral shell resembles a dextral one but the soft parts are sinistral.

The term "orthostrophic" is employed for the normal coiling of the great majority of asymmetrical gastropods both dextral and sinistral. The true sinistral gastropod is in all respects a mirror image of a dextral gastropod.

The term "isostrophic" is introduced as an adjective to describe the sort of coiling that is found in many nautiloid and ammonoid cephalopods, and particularly in the bellerophont gastropods. It may be exogastric as in the cephalopods or endogastric as in the gastropods. Isostrophic coiling is symmetrical with the left and right sides mirror images of each other.

Text figure 2 illustrates the different types of coiling described above.

The term "Cambrian" is employed here in the current American sense (Howell et al., 1944, pp. 993-1004) in which beds of Tremadocian age are excluded from the Cambrian. Those are placed as late Lower Ordovician. It is important that the European reader bear this in mind.

Illustrations.—In addition to certain diagrammatic drawings to illustrate various points under discussion I have included drawings of generalized restorations of a number of characteristic Paleozoic genera mentioned in the text. Many of these are yet unfamiliar to any but specialists and it is hoped that the drawings will be of assistance to the general reader in visualizing what must be unfamiliar genera to many. Although these were made from actual specimens of species, they are restorations intended to illustrate generic characters and are not accurate enough to be used for the identification of species.

References.—The list of references will be found on pages 55 to 56. In the text, references to the list are cited in parentheses by author and date. Since I published some years ago descriptions and

---

customary way with the spire upward appears to be sinistral. In this paper all illustrated species judged to be hyperstrophic are oriented with the spire downward for this brings the aperture to the same side as in a conventionally oriented orthostrophic shell. See plate 2 on which the Pleurotomariacea shown are dextral orthostrophic and the Macluritacea are dextral hyperstrophic.

figures of the type species of all names of genera based on Paleozoic species published before 1938 (Knight, 1941), no further references to such genera will be given here. References to Paleozoic genera published since 1937 appear in the list. For post-Paleozoic genera the reader is referred to Wenz, 1938-1944, which will suffice for many purposes. If this rather rare work is unavailable, many works on conchology or malacology will do.

ACKNOWLEDGMENTS

I am indebted to a number of colleagues who have read my manuscript at one stage or another of its development. Among these are Dr. G. Arthur Cooper, Dr. H. A. Rehder, and R. Tucker Abbott, of the U. S. National Museum, and William T. Clench, of Harvard University. Perhaps I am indebted most to Prof. Raymond C. Moore, of the University of Kansas, and to Dr. L. R. Cox, of the British Museum (Natural History). The former has lent encouragement over the five or six years that my ideas have been developing on paper. Both have given the paper critical readings and have furnished the stimulus of dissent from some of the views expressed. I alone am responsible for departures from the orthodox.

ARGUMENT

In order to arrive at hypotheses worthy of attention one must proceed from the known to the unknown, or from the better known to the less well known. Therefore it will be profitable to consider at this point certain selected zoological data, well known, perhaps, to the neontologist but relatively unfamiliar to many paleontologists. Later, paleontological data will be considered.

NEONTOLOGICAL CONSIDERATIONS

MORPHOLOGY OF LIVING POLYPLACOPHORA

The chitons are regarded morphologically as the most conservative in the basic pattern of their organization of all living gastropods, if not of all living mollusks. In respect to certain features, the division of the shell [3] into eight plates and the musculature to operate them, they appear to be highly specialized. Likewise the remarkable shell eyes or aesthetes appear to be developed in some genera, possibly in

---

[3] I am regarding the polyplacophoran shell as homologous with the shells of other mollusks. However, it should be noted that at least one recent worker regards it as only analogous (Thiele, 1931, p. 2). Perhaps on further study this very fundamental difference will be resolved.

response, as it were, to the loss of the sense organs of the head.[4] It is these specialized features, the modifications of the primitive basic plan, that distinguish them as chitons. The basic plan of organization is bilaterally symmetrical in all significant respects. There is a flat, creeping foot and well-differentiated head. The head lacks the usual sense organs, possibly due to specialized degeneration. The mouth is anterior and the anus posterior, the digestive tract passes through the pericardium. The gills appear to be true ctenidia and are arranged in pairs in a groove between the shell and the upper surface of the foot on each side of the body, dominantly in the posterior part (Yonge, 1939). The numerous paired ctenidia seem to be metameric repetitions of a primary pair that lie on each side of the anus and just behind the excretory pore (the postrenal gill). The heart is dorsal and posterior. The nervous system is not twisted and shares the bilateral symmetry of the rest of the body. Strictly speaking there is no pallial cavity, but it seems reasonable to regard the posterior and lateral parts of the groove between the shell and the foot that contains the ctenidia and associated organs as strictly homologous with the pallial cavity of more advanced gastropods.

There is no need here to go into a complete morphological description of the chitons. The features to which I wish to draw special attention are the complete bilateral symmetry of all parts and the posterior anus, gills, and heart. It is these features that are regarded as primitive and it is contended that it is the modification of these features in the ancestral stock from which the chitons were derived that gave rise to the Anisopleura, modification primarily through torsion and progressively greater asymmetry.

The chitons appear first in the fossil record in late Cambrian time and are living today. They were never abundant and for most of the time were very rare. They have varied throughout all that vast expanse of time very little indeed.

MORPHOLOGY OF LIVING PLEUROTOMARIANS

The pleurotomarians[5] are classified in the subclass Anisopleura, superorder Prosobranchia, order Archaeogastropoda. They first ap-

---

[4] Can it be that the microscopic tubules in the shell of *Tryblidium reticulatum* Lindström described and illustrated by Lindström in 1884 (p. 56) are the tubules of aesthetes instead of some unknown parasitic organism?

[5] The noncommittal vernacular name for this group is employed at this point in its broadest sense, as an informal synonym of Pleurotomariacea. The group has been treated at one time or another as a genus, as a family, or as a superfamily. Wenz in 1938 assigned a little over 200 genera and subgenera, fossil and living, to the Pleurotomariacea.

pear in the fossil record in late Upper Cambrian time.[6] They were the most numerous, varied, and abundant of all gastropods throughout succeeding Paleozoic time. They continue in diminishing numbers and variety through the Mesozoic and carry through to the present as a few genera, in a few families, the most abundant and diversified of which represent two late specializations for rock clinging (Haliotidae, Fissurellidae). Another living family, composed of rare and very tiny forms, is the Scissurellidae. The fourth family of living pleurotomarians, the Pleurotomariidae, is represented in present seas by four rarely seen but large and handsome deep-water species, of great morphological interest because they are seemingly little-changed descendants of early and primitive anisopleuran gastropods. Although entire specimens are very rare, there have been a number of successful dissections with which are associated the names of W. H. Dall, E. L. Bouvier and H. Fischer, and of M. F. Woodward. Dissections have been made also of some of the abundant but specialized Haliotidae, Fissurellidae, and Scissurellidae, but the Pleurotomariidae appear to be less conspicuously specialized for particular environments and therefore more significant for the present purpose.[7]

This is no place to consider the minor anatomical details of the pleurotomarians but certain major features are of importance for our purpose. First, in common with all anisopleurans in which the features are not obscured by later developments, all display the effects of torsion in that the primitively posterior anus and pallial complex

---

[6] The genera I refer to, four in number, include three with a deep U-shaped or V-shaped sinus in the outer lip regarded by most paleontologists as homologous to a slit. These are *Sinuopea* Ulrich, 1911 (pl. 2, fig. 1), *Schizopea* Butts, 1926 (pl. 2, fig. 2), and *Dirhachopea* Ulrich and Bridge, 1931. The fourth, *Taeniospira* Ulrich and Bridge, 1931, has a moderately deep pleurotomarian slit and a slit band.

[7] It will be well here to point out that primitive prosobranch gastropods have not a single retractor muscle but a pair of retractor muscles. For example, the living representatives of two of the four existing families of the Pleurotomarianea, the Scissurellidae and the Haliotidae, have a pair of shell or retractor muscles, and a third, the Fissurellidae, has a crescentic muscle accepted as compounded from an original pair. In the Bellerophontacea, supposedly the immediate forerunners of the pleurotomarians, there is likewise a single pair; and in the Neritacea, seemingly an ancient branch from the pleurotomarian stock, and the very primitive Macluritidae there is also a pair. In the living representatives of the Pleurotomariidae alone, of the supposedly primitive stocks, is there a single retractor muscle. This suggests strongly that in this respect these have lost one of the primitive muscles and have advanced far toward *Calliostoma* Swainson, 1840, in the Trochidae, to which they may be more closely related than to the more primitive pleurotomarians.

are found in an anterior position above the head as though they had been twisted into that position. All have a helicoidally coiled, asymmetrical shell at least in late larval stages. But in spite of torsional asymmetry and the beginnings of lateral asymmetry they retain, as a primitive character fully retained in no other group of living anisopleuran gastropods, paired visceral organs, including paired ctenidia, paired auricles of the heart, paired kidneys, etc. The digestive tract passes through the pericardium and the anus discharges between the two paired ctenidia. These are primitive characters and they remind one strongly of the bilaterally symmetrical pairing of the homologous organs in the isopleuran Polyplacophora. They suggest that the Anisopleura were derived ultimately from bilaterally symmetrical, isopleuran ancestors.

Recent and fossil pleurotomarians always, or nearly always, show one distinctive shell feature by which they may be recognized almost at a glance. This is an emargination in the outer lip of the shell. In some of the earliest species it takes the form of a rather deep U-shaped or V-shaped sinus. In others the sinus is V-shaped and it may culminate in a short slit or notch. Still later appear forms with a deep slit and still other modifications, such as a row of tremata, developed independently in several genera, or the apical hole in the shell of the typical fissurellids. In all living pleurotomarians that have been examined the discharge end of the anal tube lies close to the apex of the emargination. Yonge has shown from studies of living examples of *Haliotis* Linné, 1758 (Yonge, 1947, p. 449), of the anatomy of a preserved specimen of *Mikadotrochus beyrichi* (Hilgendorf) (op. cit., p. 454), and of the described anatomy of *Incissura lytteltonensis* Smith (op. cit., pp. 449-458), as well as of living examples of the more highly specialized Fissurellidae, that the respiratory current is created by cilia on the filaments of the ctenidia. The water is drawn into the mantle cavity above and on both sides of the head. It passes backward beneath the ctenidia, impinging on the osphradia enroute, then upward between the ctenidial filaments and outward through the slit or its equivalent. Close to the inner end of the slit (or row of tremata) is the anus at the distal end of the anal tube. The currents, possibly aided by contractions, carry the faeces out through the slit. This is a highly important matter of sanitation for any gastropod with the anus within the mantle cavity and directed anteriorly so as to discharge between a pair of ctenidia. Obviously such a mechanism would not be important for forms with a posterior anus, such as isopleurans, or for those such as the more advanced anisopleurans with an anterior anus but with only one ctenidium on the upstream side, as it were, of the ciliary currents passing through the mantle cavity, or secondarily with a more or less posterior anus as in the opisthobranchs.

ANISOPLEURAN ONTOGENY

There are inherent technical difficulties in the rearing and studying of such extremely small and delicate organisms as the early embryos of primitive gastropods. Because of the complexity of the transformations and the confusing differences in detail from one species to another it is difficult to make generalizations in terms that will be valid in detail for even the few forms for which much is accurately known of the early ontogeny. Furthermore it is difficult to avoid attributing to the embryo adult anatomical features which occur only as rudiments, often as only a few cells not obviously organized, if present at all in the embryo. For example, it is commonly thought that in the process of torsion the gastropod becomes so twisted that the pallial cavity with the pallial complex including anus, ctenidia, kidneys, heart, etc., is translated bodily from a posterior position to an anterior position above the head. In effect this is true but in detail it is not, for in such primitive genera as *Haliotis* and *Patella* Linné, 1758, for example, the "proctodaeum and the solid mesoderm rudiments of the kidneys are the only representatives of the pallial complex when torsion begins. Even in *Viviparus* Montfort, 1810,[8] in which the developmental stages are abbreviated owing to viviparity, the single ctenidium and the visceral part of the pleuro-visceral loop do not develop until . . . after torsion is complete" (Crofts, 1937, pp. 262-263). However, in spite of these difficulties a significant series of events does occur in a definite order.

The early trochophore larva has a dorsal shell gland and a stomodaeum (rudimentary mouth) situated immediately below the ciliated ring of the velum on the ventral side. The shell, secreted by the shell gland, develops from a small disc to a rather deep cup containing the dorsal hump. The proctodaeum (rudimentary anus) is moved ventrally toward the stomodaeum. In the process the rudimentary gut, still without open mouth or anus, is bent into a rough U-shape. This operation is called flexure and is regarded as distinct from torsion for which, however, it lays the foundation. The rudimentary foot appears between the stomodaeum and proctodaeum. The pallial cavity appears as an invagination posterior to the foot. In the meantime the shell

---

[8] For *Paludina*, the name employed by Crofts and other embryologists, I am substituting the name *Viviparus*, today regarded as the correct name of the genus concerned.

has continued to grow and, owing to secretion of shell matter more rapidly on the posterior margin, it takes on an exogastric roughly nautiloid form with the primitive apex directed forward.

A highly significant organ, the development of which is completed at the end of the pretorsional stage, is the single "velum retractor muscle" first carefully studied by Crofts in *Haliotis* (Crofts, 1937). The muscle before torsion is asymmetrically placed and slightly spiral in such a way that its retraction rotates the dorsal hump in a counterclockwise direction when viewed dorsally. In passing it will be advantageous to note that the velum retractor persists through life in *Haliotis* as the small left-hand shell muscle and that the hypertrophied right-hand shell muscle, homologous with the single columellar or retractor muscle in most gastropods, is not at this stage represented by a recognizable rudiment of even a single cell. It is probable that the left-hand retractor muscle in the adults of the more primitive aspidobranchs is entirely homologous with that of *Haliotis*. In more advanced types it is lost before maturity.

In *Haliotis* torsion begins at about 30 hours after fertilization of the egg. Crofts (1937, pp. 233-234) reports that the first 90° of torsion takes place in 3 to 6 hours as a result of contraction of the "velvum retractor muscle." The full 180° torsion is not completed until 8 or 10 days later and apparently results from differential growth.

There are curious differences in both the process and time of torsion as reported by different authors for different species and even for the same species. Some of these differences may be caused by the difficulties in observing accurately such small and refractory subjects, but most of them probably reflect actual differences between species. Nevertheless there is general agreement on the fact of 180° torsion at an early embryonic stage.

The torsion results in the pallial cavity's moving from a posterior to an anterior position relative to the foot. Although the organs of the pallial cavity have not yet appeared when torsion begins or are extremely rudimentary they eventually mature after torsion in an anterior position even though their primitive position must have been posterior. Likewise the commissures of the visceral nerve complex mature after torsion as though they had been crossed to a figure 8 during the process, although during torsion they were far too short and rudimentary to be crossed. Torsion, of course, affects relations of the shell to the head and foot so that its apex points to the rear of the head instead of forward.

Before torsion there is some asymmetry in one respect or another, in part no doubt anticipatory in nature and chargeable to acceleration, but after torsion asymmetry develops apace. It is only less marked in those forms that develop primitive paired organs than in those that develop only one member of the primitive pair, usually the definitive left member. The shell is no longer approximately bellerophontiform, but coils in a laterally asymmetrical, helicoid spiral with the spire pointing backward. That in certain groups the shell then becomes symmetrical (*Diodora* Gray, 1821, for example) or that secondary detorsion occurs (opisthobranchs) with a high degree of superficial secondary symmetry is irrelevant to our present discussion. Nor is it relevant that in a few forms the torsion is clockwise resulting in sinistrality (see fig. 3).

To recapitulate, the anisopleuran veliger larva is provided with a dorsal shell gland; the gland secretes a shell that grows by marginal accretion and soon becomes cuplike; concurrently the pallial cavity is invaginated and the body, with the rudimentary alimentary canal, is bent to a U-shape with the procotodaeum within the pallial cavity posterior to the stomodaeum and separated from it only by the rudimentary foot. The U-shaped bending constitutes *flexure*. The next step is *torsion* by which the dorsal hump with the pallial cavity is twisted 180° in a counterclockwise direction (as seen from above) relative to the foot, thus laying the foundation for the prosobranch and streptoneurous conditions. Next comes, as a separate step, the development of lateral asymmetry and the helicoid spire. There are in some advanced stocks still further developments, including detorsion which brings about the opisthobranch condition, euthyneury, and in extreme cases secondary symmetry of a high order.

PRELIMINARY INFERENCES FROM NEONTOLOGICAL CONSIDERATIONS

From anatomy.—It is inconceivable that the living anisopleuran gastropods, which show torsional and generally lateral asymmetry and which are members of the Mollusca, a phylum characterized by basic bilateral symmetry, can be at all primitive in respect to those features. The most ancient anisopleuran group with living representatives, the Pleurotomariacea, appears first in the late Cambrian. Living pleurotomarians show vestiges of bilateral symmetry in the retention of paired visceral organs along with full torsional asymmetry and laterally asymmetrical coiling. The Polyplacophora living today are equally as ancient as the pleurotomarians. They are obviously specialized in respect to the eight-pieced shell, but they retain

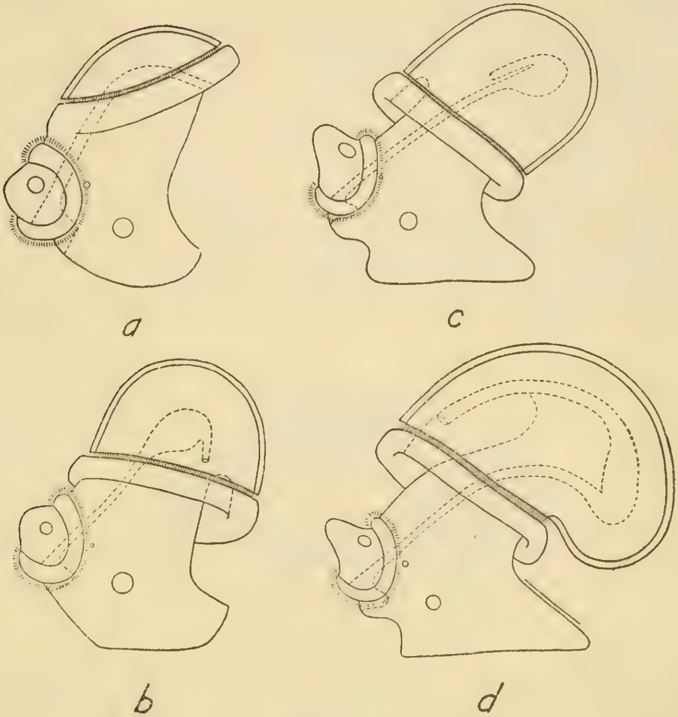


FIGURE 3

Torsion in the embryo of *Viviparus viviparus* (Linné). It should be noted that owing to the viviparity the developmental stages in *Viviparus* are abbreviated. Hence for this reason and because of the highly diagrammatic nature of the drawings (from Naef, 1911, fig. 8, in part) the picture presented is somewhat oversimplified. It is all the more comprehensible for those reasons.

a, Stage where flexure is in progress but torsion not begun. To the left of the figure is the ciliated velum, the cup-shaped shell is above and the rudimentary foot below. The digestive tract is dotted with the mouth below and to the left and the anus high and to the right of the figure.

b, The beginning of torsion. The mantle cavity has appeared and with the anus is turned a little to the right of the animal.

c, Torsion a little more than halfway completed. The anus and mantle cavity are now to the right and a little to the front.

d, Torsion completed. Note that the mantle cavity with the anus is now in front and above the head, it final position. The shell has become bellerophontiform.

strict bilateral symmetry. They cannot be ancestral to the pleurotomarians, but they very plausibly point the way to that more remote ancestor of both chitons and pleurotomarians which must be looked for first in Lower or Middle Cambrian rocks unless it became extinct before Cambrian time with its record irretrievable. Several very distinguished neontologists have speculated as to the probable nature of this common ancestor of both and, indeed, of all the Mollusca. The usual conclusion is that it was a mollusk with a single, low, conical shell, bilaterally symmetrical in all respects, with the anus and pallial complex in the rear, with a differentiated head and a flat creeping foot. In epitome, it would have the basic bilateral symmetry of the Polyplacophora but with a single shell, as in the Anisopleura, but neither coiled nor asymmetrical. Figure 4 shows a reconstruction of such a hypothetical ancestral gastropod, a reconstruction based on pure deduction before anyone had suspected the possibility that supposed Cambrian capulids or patellids that we now recognize as the Monoplacophora had just about the same anatomy. Figure 5 shows a restoration of a generalized monoplacophoran.

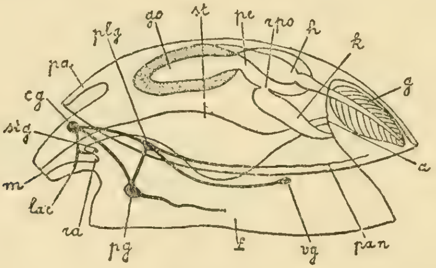


FIGURE 4

Scheme of a hypothetical primitive mollusk viewed from the left side. *a,* anus; *c, g,* cerebral ganglion; *f,* foot; *g,* gill, in the pallial cavity; *go,* gonad; *h,* heart; *k,* kidney; *lac,* labial commissure; *m,* mouth; *pa,* mantle; *pan,* pallial nerve; *pe,* pericardium; *pg,* pedal ganglion; *plg,* pleural ganglion; *ra,* radula; *rpo,* renopericardial orifice; *st,* stomach; *stg,* stomatogastric ganglion; *vg,* visceral ganglion. (After Pelseneer.)

From ontogeny.—Before torsion the cup of the larval shell deepens with flexure of the intestinal tract and because of more rapid growth at the posterior margin takes the form of the beginning of an isostrophic or bellerophonlike coil but with the apex or rudimentary coil forward. It seems reasonable to suppose then that the descendants of our hypothetical ancestral gastropod may have passed through similar stages in the initial process of becoming coiled. Indeed coiling could hardly have occurred in any other way. The development of a higher and higher shell and the initiation of coiling symmetrically in a plane are processes that lend themselves to gradual evolutionary development. If the fossil record is sufficiently complete, we

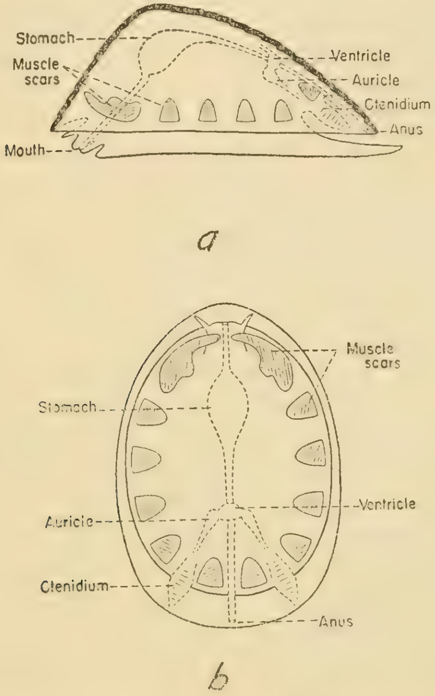


FIGURE 5

Schematic restoration of a generalized scenellid treated as though it were transparent. In making the restoration there were employed the concepts of untorted bilateral symmetry suggested by the muscle scars of *Archaephiala*. *a*, Left side view; *b*, from above. Except for the muscle scars, note the resemblance to the hypothetical primitive mollusk (fig. 4). The latter was suggested by Pelseneer without reference to scenellids which he regarded as anisopleurans (i .e., *Docoglossa*).

should expect to find among the earliest gastropods forms with complete bilateral symmetry and a low, cup-shaped shell with an apex somewhat in front of the center, others that maintain the bilateral symmetry with a higher, narrower shell and the apex partly coiled forward, and still others with a complete coil, all steps necessary to a gradual evolution. As will be shown in the following parts of this paper, that is precisely what we do seem to find in the earliest fossiliferous rocks.

The next ontogenetic step, the sudden torsional twisting, is spectacular and of the highest significance. Since torsion is not a phenomenon that lends itself to gradual step-by-step development it is highly probable that it occurred just as suddenly phylogenetically as it does today ontogenetically. It is possible, if not probable, that torsion originated as the result of a genetic mutation having its phenotypic expression effective at the veliger stage of the ontogeny (Garstang, 1929, p. 89). This is the view that was set forth by W. Garstang and that has radically altered the thinking of many students of the Gastropoda. If Garstang's view is true, an isopleuran parent may have produced anisopleuran offspring. What could only be regarded as a monstrosity if it had gone no farther was so successful that the strain that carried the genes as a part of its heritage prevailed in competition and eventually brought into being an entire new subclass. (Class in accordance with the usual classification.)

If torsion did arise suddenly in some such manner as Garstang postulated, then the adults of the first torted stock should have resembled their parent in every respect except that they had undergone torsion as larvae. They would have retained all their paired organs symmetrically developed and their shells would have retained their symmetry but with the apex or coil now in a posterior position. They would have retained other peculiarities of the parent stock such as the basic plan of ornamentation. The anus and pallial complex, however, would be above the head and directed forward because of torsion, and since the immediate parent with a posteriorly directed anus and pallial complex had and needed no special provision for clearing the pallial cavity of waste products, the newly torted offspring would be like the parent in this respect. That is to say, it would have no anal emargination in the lip of the shell. In the Early and Middle Cambrian are shells that seem to meet these specifications.

Since the newly acquired orientation results in a position of the anus and pallial complex that would seem to make it difficult to avoid fouling the ctenidia with waste products, we might expect that mutations providing a mechanism for ready disposal of the faeces and urine without fouling would have survival value. Hence it is not surprising to find in Upper Cambrian rocks the first bellerophonts with an anal emargination. It is then present in three bellerophont families. The forms without this sanitary provision disappear shortly thereafter.

The significant embryological studies of neontologists were made on asymmetrical anisopleuran gastropods, the asymmetrical development following closely on torsion. Consequently we should not be surprised to find that lateral asymmetry appeared in the paleontological record soon after the establishment of a line of isostrophic gastropods (bellerophonts) with only torsional asymmetry. This expectation is realized in the appearance of the first known pleurotomarians in late Upper Cambrian rocks.

RECAPITULATION

Summarizing our inferences from neontological data we arrive at the following hypotheses which may be tested against paleontological data. The first is that the Polyplacophora and the pleurotomarians were derived from a common ancestor with complete bilateral symmetry. We infer also that the Polyplacophora have evolved from that common ancestor through the segmentation of the shell but retention of bilateral symmetry. We may further infer that the pleurotomarians have evolved first through the introduction of torsional asymmetry by a single mutation phenotypically effective at the veliger stage of ontogeny (bellerophonts) and later through the initiation of the lateral asymmetry that characterizes all the Anisopleura other than the bellerophonts. (See fig. 6.) Lateral asymmetry is carried progressively much farther in more advanced groups. We may still further infer something of the probable characters of the isopleuran common ancestor of the Polyplacophora and the pleurotomarians and of the intermediate stages between the pleurotomarians and that ancestor.

The immediate predecessor of the pleurotomarians should have had all the characteristics of that group except lateral asymmetry. It should have had torsional asymmetry but lateral symmetry; it should have been coiled tightly or loosely or with a curved apex pointing to the rear in a plane, with each side the mirror image of the other (isostrophic). It should have had an anal emargination when fully established but not when it first suddenly came into being. It, in turn, should have had an immediate predecessor with a high, conical shell with curved apex as the first step toward isostrophic coiling. The high conical shell would of course have been deep and would have so crowded the multiple paired pedal muscles that there would have been room for only a few, perhaps only a single pair. If torsion had taken place the apex of the shell would have pointed backward, if not it would have pointed forward. The last-mentioned stage should have had as a predecessor an untorted mollusk with complete bilateral symmetry and a low, shallow conical shell with little or no flexure of the viscera and, of course, no torsion.

Since, by hypothesis, this most remote stage was ancestral to the Polyplacophora as well as to the Anisopleura it might conceivably display characters basic to the transverse segmentation of the shell into separate plates, characters such as multiple transversely paired pedal or shell muscles. It might have possessed in a rudimentary form traces of the tubules that carry the aesthetes in the tegumentum of modern Polyplacophora.

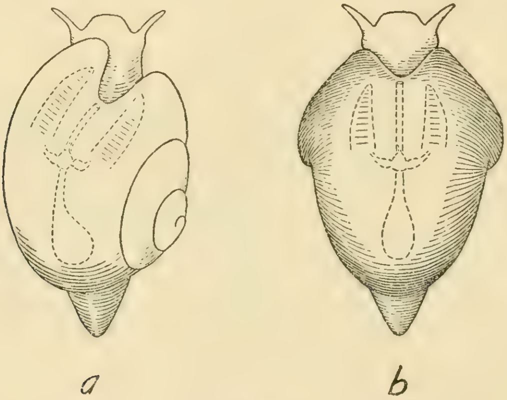


FIGURE 6

a, Schematic drawing of a primitive pleurotomarian seen from above (modified from Naef, 1911). The primitive anal emargination is shown as a U-shaped sinus. The anal tube leading from the stomach is shown as passing through the pericardium and terminating close to the emargination and between a pair of ctenidia.

b, Similar drawing of a primitive sinuitid bellerophont (also modified from Naef, 1911). It is thought to have been very like the primitive pleurotomarians but with complete lateral symmetry. Both have undergone torsion and the pallial complex is anterior instead of posterior.

PALEONTOLOGICAL CONSIDERATIONS

In order to dispel certain misconceptions widely prevalent in neontological circles and, alas, occasionally met with in paleontological circles, a few words in general terms about the gastropods of the Cambrian period may be helpful. These misconceptions arose largely through the efforts of paleontologists of an earlier day to place species, inadequately understood because of poor preservation or some other cause, in established genera, often in order to avoid erecting new genera for them. Since much of the evidence is not explicitly in the literature and cannot be introduced here without making this paper too diffuse, I am forced to speak dogmatically on some points.

There are no Platyceratidae known from rocks older than Middle Ordovician, and no Capulidae in the Paleozoic. That there are both, is a common error. Pleurotomarians do not occur throughout the Cambrian section so far as is known, and only the Late Cambrian bellerophonts are readily recognized as such. There are only four pleurotomarian genera known from Cambrian rocks. (*Pleurotomaria* Sowerby, 1821, is not among them and indeed did not appear in the Paleozoic.) These four are *Sinuopea* Ulrich, 1911 (pl. 2, fig. 1), *Schizopea* Butts, 1926 (pl. 2, fig. 2) (=*Rhachopea* Ulrich and Bridge, 1931, and *Roubidouxia* Butts, 1926), and *Dirhachopea* and *Taeniospira,* both of Ulrich and Bridge, 1931. The anal emargination is a deep, rounded sinus in *Sinuopea* and a deep angular sinus in *Schizopea* and *Dirhachopea,* perhaps culminating in a short notchlike slit in the latter. In *Taeniospira* there is a moderately deep slit and a typical slit band. All four genera are known from beds no older than the latest Cambrian Trempealeauan stage.

Six typical and unquestionable bellerophont genera are now known from the Cambrian and will the neontologist please note that *Bellerophon* Montfort, 1808, is not among them. These are *Owenella* Ulrich and Scofield, 1897, and *Cloudia, Anconochilus, Sinuella* (pl. 1, fig. 10), *Strepsodiscus* (pl. 1, fig. 8), and *Chalarostrepsis* (pl. 1, fig. 12) (all of Knight, 1947 and 1948). The first four have rounded sinuses as anal emarginations, the fifth a deep V-shaped sinus, and the last a deep slit. All these are of late Cambrian age. The earliest is *Strepsodiscus* of the early late Cambrian Dresbachian stage, and three of them, *Strepsodiscus, Sinuella,* and *Anconochilus,* occur earlier than any known pleurotomarian genera. Also there are two isotrophically coiled genera, *Coreospira* Saito, 1936 (pl. 1, fig. 7), and *Cycloholcus* Knight, 1947, both referred to the Coreospiridae. Although neither has an anal emargination, the Coreospiridae are here regarded as primitive bellerophonts. *Coreospira* first appeared close to the boundary between the Lower and Middle Cambrian, probably on the upper side.

There is also still another genus appearing still earlier and ranging throughout the Cambrian that must be considered in this connection. It is *Oelandia* Westergård, 1936, which is here placed in the Coreospiridae. It will be considered more in detail on a later page.

In addition to the bellerophont genera discussed, three genera of macluritoid gastropods occur in the last stage of the Upper Cambrian, the Trempealeauan, *Scaevogyra* Whitfield, 1878 (pl. 2, fig. 7), *Matherella* Walcott, 1912 (pl. 2, fig. 10), and *Kobayashiella* Endo, 1937. All other known Cambrian gastropods are referable to isopleuran monoplacophoran genera. Of these *Helcionella* (pl. 1, fig. 2), and *Scenella* Billings, 1872 (pl. 1, fig. 1), both put in their appearance along with *Oelandia* (pl. 1, fig. 5) in the Lower Cambrian and are thus among the earliest gastropods known. In addition to these there is that very puzzling, problematical group of gastropodlike shells, *Pelagiella* Matthew, 1895, and its allies, that range throughout the Cambrian. These, for reasons given later in this paper, may be regarded as an independent branch from some unknown gastropod ancestor or they may not be gastropods at all.

Although not yet described or announced in the literature chitons (Polyplacophora) are known from Upper Cambrian beds of the Trempealeauan stage.

CLIMBING DOWN THE FAMILY TREE

THE PLEUROTOMARIAN-BELLEROPHONT BRANCH TO THE ISOPLEURAN MONOPLACOPHORA

Continuing to proceed from the better known to the less well known, we will work backward from the living pleurotomarians, from which can be gleaned the basic anatomical details of the group, searching step by step for fossil forms that may be taken for representatives of the various stages in their evolution from their most primitive ancestral stock. The living pleurotomarians are referred currently to the Pleurotomariidae, the Scissurellidae, the Haliotidae, and the Fissurellidae.

In starting on our exploration it seems safe to assume that the basic organization of the most ancient pleurotomarian was essentially the same as that of its living representatives. Such a procedure permits us to drop rapidly down the gastropod family tree or backward in time something over 400,000,000 years to the late Cambrian when the first known pleurotomarians lived, continuing all the while along a branch that is easily recognized because its members show asymmetrical coiling and because of the anal emargination, a slit, sinus, or notch in the outer lip of the shell. From this vantage point in the remote past we may examine our surroundings, particularly those a little more ancient. The objects of our search are forms that resemble the pleurotomarians very closely but are still more primitive.

Contemporaneous with the earliest known pleurotomarians and in part preceding them are the bellerophonts.[9] All but the most primitive are so very similar to the pleurotomarians in a number of significant particulars that on comparative anatomy alone they must be regarded as quite closely related. The shells of the bellerophonts are coiled typically in a close spiral but the coiling is isostrophic rather than helicoidal; the whorl cavity is, of course, very deep and the two symmetrical retractor muscles are inserted one on each side deeply within the aperture at the two ends of the columella in such a position that their retraction would withdraw the head and foot within the aperture; there is an anal emargination, a U-shaped or V-shaped sinus or a slit, just as in the contemporary pleurotomarians. In fact the only obvious particular in which the bellerophonts differ from pleurotomarians is that the coiling is isostrophic and the shell is a symmetrical spiral. Clearly then, the bellerophont, like the pleurotomarian, was a prosobranch, but a symmetrical prosobranch. Since lateral symmetry is a primitive character in the mollusks this is precisely what one might expect in the immediate ancestor of the pleurotomarians which themselves retain more or less symmetrically paired organs. It is commonly believed by neontologists that asymmetry is an immediate and necessary result of torsion. No doubt the belief is well founded in the sense that torsion precedes asymmetry and is a prerequisite for it, but if the bellerophonts are prosobranchs as their morphology strongly suggests and if torsion is the factor that distinguishes a bellerophont from an immediate laterally symmetrical isopleuran ancestor, then, as the time factor insists, it is not necessary to suppose that asymmetry was an immediate consequence. Of course torsion furnished the unstable condition that ultimately led to asymmetry.

Again surveying our surroundings, this time from the apparent base of the bellerophont stem, we meet with two more genera that have the characters one would expect of the very primitive bellerophonts. One is *Cycloholcus* from the base of the Upper Cambrian Dresbachian stage and the other is *Coreospira* (pl. 1, fig. 7) (both referred to previously) from close to the boundary of the Middle and the Lower Cambrian, probably on the upper side of the boundary. Both of these forms are isostrophically coiled and thus in this respect are in accord

---

[9] Some views expressed by Thiele, 1935 (p. 1125), and Wenz, 1938 (pp. 58-60), on the probable anatomy and physiology of the bellerophonts will not, I think, bear close scrutiny. Since I do not wish to interrupt the present argument to give the reasons for my contrary views that the bellerophonts are prosobranchs instead of primitively orthoneurous "Amphigastropoda," as Thiele and Wenz supposed, I am discussing the matter in an appendix to this paper.

with the bellerophonts. Unlike previously recognized bellerophonts there is no emargination in the lip that corresponds to the anterior lip. This appears puzzling unless we remember that there is a feature we were to look for in the primitive bellerophont.

Further exploration turns up the genus *Oelandia* (pl. 1, fig. 5), a genus that may be interpreted most plausibly as being closely related to *Cycloholcus* and especially *Coreospira* (pl. 1, fig. 7). *Oelandia* has been associated commonly with *Helcionella* Grabau and Shimer, 1909 (pl. 1, fig. 2). For example, Wenz in 1938 (p. 88) places it in the subfamily Helcionellinae in the family Tryblidiidae. There is indeed a resemblance—a resemblance that appears to me to be honestly come by but still not decisive taxonomically. In *Helcionella* the apertural margins are in a flat or nearly flat plane. In *Oelandia* however the margins tend to be curved and one end, the end toward which the apex bends, is considerably extended and often tilted up as though to form a trainlike hood. If one attempts to think in terms of soft anatomy this hood seems anomalous over the head but fits nicely as a hood over the posterior train of the foot. Hence the extended or up-tilted end is here regarded as posterior. If this hypothesis is accepted the apex is posterior and *Oelandia* may be considered to be a very primitive isostrophic prosobranch gastropod in the Coreospiridae, one that has not yet advanced to the stage of close coiling. Of course the anal emargination has not yet appeared. *Helcionella* remains in the Isopleura with the nontorted Monoplacophora. *Oelandia* is an anisopleuran that may have been derived directly from *Helcionella* and retains its characteristic ornamentation. Torsion may have first taken place between these two genera in earliest Cambrian or in pre-Cambrian time. This possibility will be discussed again.

The Coreospiridae are bellerophonts in respect to the shell coiled or nearly coiled with lateral symmetry in a plane. In some other respects they resemble more closely the group that we next meet with, for although we have reached in *Oelandia* (pl. 1, fig. 5) close to the beginning of the fossil record we have not fully surveyed its contemporaries. There are still three kinds of gastropods or supposed gastropods represented with *Oelandia* in the Lower Cambrian rocks. One of these three, *Pelagiella* and its allies, seems anomalous from any viewpoint and will be reserved for later discussion. The other two fit into our picture very nicely. Both are cup-shaped and show complete bilateral symmetry. Their ornamentation consists of transverse undulations somewhat similar to those of *Coreospira* (pl. 1, fig. 7) and *Oelandia*. One, the genus *Scenella* Billings, 1872 (pl. 1, fig. 1), is cup-shaped with a conical shell and the apex tipped toward the narrower end. The shell of the other genus, *Helcionella* (pl. 1, fig. 2), is also cup-shaped, and includes species that are low and broad as well as others that are high and narrow. In both the apex points toward the narrower end of the aperture and in the high and narrow species it is almost hooked. None of these have the hoodlike train of *Coreospira, Oclandia,* and narrow bellerophonts in general.

Although we know nothing of the internal organization of either *Helcionella* (pl. 1, fig. 2) or *Scenella* (pl. 1, fig. 1) by direct observation, their external features such as shape and ornamentation suggest rather strongly that they belong to a family that continues into the Devonian. Specimens of an Ordovician genus of this family, *Archaeophiala*[10] Perner (pl. 1, fig. 3), preserve the muscle scars beautifully. The scars are strongly pigmented and for that reason are unusually sharp and clear. (See Knight, 1941, pl. 3, figs. 3a-b.) These scars are 12 in number and are arranged in a ring deep within the margin of the shell. Two of the scars are larger than the others and are made up of three parts. These tripartite scars, which occur at one end, may be regarded as compound and perhaps as representing the scars of three muscles each. The other 10 scars are simple and probably are the scars of single muscles. These 12 (or 16) scars are in bilaterally symmetrical pairs. The pair of large compound scars lies at the end toward which the apex lies and very nearly closes the circle at that end. The scars of the other five pairs follow symmetrically on either side until the circle is nearly closed at the other end. There is a line of much fainter, unpigmented scars outside of the principle ring. The six (or eight) pairs of pigmented scars were probably points of attachment for symmetrically paired muscles connecting the shell to the foot. One can hardly guess what function was served by the muscles that made the more obscure scars outside those of the main circle but these shadow scars appear to be characteristic of the group.

Two exceedingly important inferences are suggested by the scars of *Archaeophiala* (pl. 1, fig. 3). The first inference is that the soft anatomy was bilaterally symmetrical throughout, that is to say the animal had not undergone torsion. This is an inference primarily from the complete bilateral symmetry of the paired muscle scars,

---

[10] I am employing *Archaeophiala* rather than *Tryblidium* to typify the gastropods with paired muscle scars for the reason that its shape, which is essentially that of *Scenella* and the lower, cup-shaped *Helcionella,* suggests that it is the more primitive. Although their muscle scars are virtually identical, I am placing each in a separate family, as will be seen, since each seems to be a member of a different series, each with its characteristic shape.

supported by the lack of an area between scars at either end for a pallial cavity. The second inference is that the end that has the large compound muscle scars and toward which the apex lies is anterior. This follows as probable from a corollary to the principal of cephalization to the effect that "heteronomous segmentation is an expression of cephalization." If one takes these two inferences together with the previous inference that such Cambrian genera as *Scenella* (pl. 1, fig. 1) and at least the lower, cup-shaped species of *Helcionella* (pl. 1, fig. 2) are organized in a similar way we have a working hypothesis as to the organization of these very important early forms. It seems quite certain that the superficial resemblances of these Cambrian cup-shaped forms to the living prosobranch patellaceans or capulids or to the equally prosobranch Paleozoic platyceratids is as surely a matter of convergence as is the equally superficial resemblance of all of them to the pulmonate ancylids.

It seems probable that a prerequisite for torsion was a reduction in the hypothetical six or eight paired shell muscles to a single pair. What better mechanism to give mutations accomplishing such a reduction survival value could have been devised than the development of high, narrow shells, such as actually occurred in some Lower and Middle Cambrian species currently referred to *Helcionella* (pl. 1, fig. 4). In these the hypothetical six or eight pairs of muscles, if present, would be crowded together. Perhaps, owing to this crowding, mutations that would effect the reduction of the six or eight pairs to a single pair through the elimination of all but one of the pairs would have survival value. If the suggested reduction actually took place the foundation was laid for torsion. All that would be required further is that through a genotypically small mutation the rudiments of one muscle of the pair (the left one) should develop in the early veliger larva earlier than those of the other. As has been shown by Crofts (1937), the retraction of such a single asymmetrical "velum retractor muscle" in the early veliger is what actually initiates torsion in *Haliotis*. Undoubtedly when torsion first appeared in the remote ancestors of *Haliotis* the same mechanism was responsible for it.

Both *Helcionella* (pl. 1, figs. 2 and 4) and *Scenella* (pl. 1, fig. 1) appear in Lower Cambrian rocks. It seems probable that *Helcionella* and *Scenella* had a common ancestor in early Cambrian or in pre-Cambrian time. *Chuaria* Walcott, from pre-Cambrian rocks of the Grand Canyon region, has been suggested as the most primitive ancestral gastropod but the only known specimens of the only known "species," all of which I have examined, are so very poorly preserved that it is utterly impossible for me to recognize them as gastropods or anything else. The most I can say of the specimens is that they may be organic in origin.

In descending the family tree we have passed from the earliest forms that can be assigned to the Anisopleura with assurance, the bellerophont cyrtolitids and sinuitids, such as *Strepsodiscus* (pl. 1, fig. 8) and *Sinuella* (pl. 1, fig. 10) of the lower and middle Upper Cambrian, through the probably anisopleuran Coreospiridae, to the isopleuran *Helcionella* (pl. 1, fig. 2) and *Scenella* (pl. 1, fig. 1) of the Lower and Middle Cambrian. In doing so we have passed along two exclusively Cambrian limbs, the Coreospiridae and the Helcionellidae. The Coreospiridae resemble the bellerophonts externally except that there is no feature that can be assigned the function of the bellerophont anal emargination. The Helcionellidae resemble the Coreospiridae except that the direction toward which the apex bends is interpreted as anterior. As stated above, there are with the genus *Helcionella* (pl. 1, figs. 2 and 4), as currently understood, species that have a high shell with a strongly curved apex and others, more similar to the type species, with a low shell with the apex so short and blunt that in some specimens it is almost an overstatement to say that it is curved at all. These appear to make a continuous series. Our hypothesis requires that torsion was initiated somewhere between the untorted helcionellids and torted bellerophonts. The evidence for one point in the chain as against another is not very compelling. I have placed the dividing line between *Helcionella* (pl. 1, fig. 2) and *Oelandia* (pl. 1, fig. 5), placing the former in the Isopleura with the Monoplacophora and the latter in the Anisopleura with the bellerophonts. If anyone prefers to class the Coreospiridae with the Monoplacophora or *Helcionella* with the bellerophonts, I cannot quarrel too vigorously with the preference. There is insufficient evidence. As the muscle scars, which might give more objective evidence, are unknown in *Helcionella* and in both *Oelandia* (pl. 1, fig. 6) and *Coreospira* (pl. 1, fig. 7) we are left with little but interpretations from weak morphological data as basis for a decision, however tentative. What little objective evidence there is lies in the similarity of the ornamentation in the Helcionellidae and the Coreospiridae and in differences in the apertural margins. This suggests that both of them are allied to each other and to the Scenellidae where the ornamentation follows a similar pattern, but that for some reason, assumed to be torsion, the apertural margins are different. At whatever point torsion was introduced, our hypothesis requires that it was in the more or less advanced descendants of *Scenella* and *Helcionella* that conceivably retained a similar type of ornamentation.

Just as the neontologists have employed restorations of the hypothetical primitive mollusk with fruitful results, so the paleontologist with even more actual data, the fossil shells, may employ them also. Not only does the paleontologist have fossil shells that tend to support the scientific speculations of the neontologist but he has others to which he may attempt to fit the soft parts of a generalized gastropod and form judgments from the plausibility of the results as to what the animal as a whole may have been like. Some of these hypothetically restored gastropods tend to fill gaps between the untorted

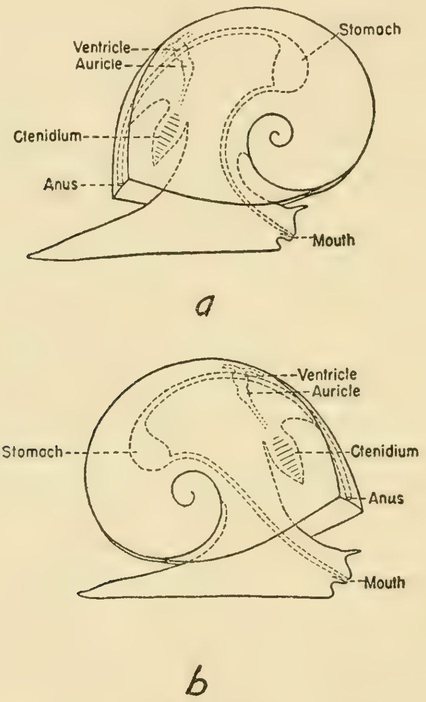


FIGURE 7

a, Schematic restoration of *Coreospira* as a monoplacophoran isopleuran.

b, Schematic restoration of *Coreospira* as an isostrophic anisopleuran, a bellerophont without an anal emargination. The latter seems a much more plausible restoration than the former. Of course, neither restoration may approximate the truth, but in that case *Coreospira* would probably not have been a gastropod. It is understood that such organs as ctenidia, auricles, etc., are paired in both restorations. The probable retractor muscles are not shown.

monoplacophoran and the torted bellerophont which in turn connects closely with the pleurotomarians.

For example, text figure 7 shows two restorations based on the known shells of *Coreospira* (pl. 1, fig. 7). Figure 7, *a,* shows the shell and hypothetical soft parts restored as an isopleuran monoplacophoran. Figure 7, *b,* shows the same restored as an anisopleuran bellerophont. Obviously the second yields a plausible picture of the probable relationship of shell and soft parts. It looks comfortable. The monoplacophoran restoration is too fantastic for even tentative acceptance. Even though one should restore the soft parts to display more primitive isopleuran features, a row of muscles, a very shallow posterior pallial cavity, etc., we still would have the coiled shell suspended above the head in a most unacceptable fashion, as well as a narrow, coiled visceral mass entirely incongruous on a monoplacophoran. Surely it is difficult to accept *Coreospira* as other than a primitive bellerophont.

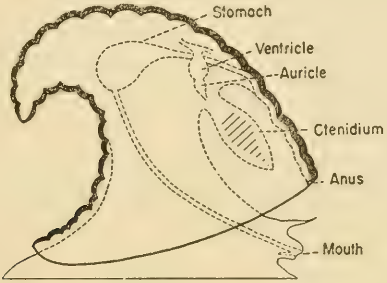


FIGURE 8

Oclandia restored as a bellerophont even more primitive than *Coreospira.* It presents a harmonious and plausible picture. A restoration as a monoplacophoran is quite as unacceptable as is the same restoration of *Coreospira.* As I have pointed out previously the trainlike hood over the posterior part of the foot is a critical feature—a feature that is shared with several bellerophont genera with narrow shells.

Figure 8 shows a restoration of *Oelandia* (pl. 1, fig. 5), believed to be a bellerophont even closer to the Monoplacophora than *Coreospira* (pl. 1, fig. 7).

THE POLYPLACOPHORAN BRANCH

The procedure of working backward may be likened to selecting one terminal twig of a tree from among very many, a twig on a branch that by preliminary inspection took its origin far down on the trunk, and then following that branch still farther down until one is led by the process to what appear to be the roots. But our metaphorical tree, from preliminary inspection in very poor light (for let us assume that we are feeling our way in the dark of the moon), seems to have more than one main branch. One of these which we will call the Polyplacophora, appears near the roots to lie close to the branch that we have been tracing backward with apparent success. Let us examine it further.

The chitons or Polyplacophora, far from abundant today, have always been rare in the fossil record. Nevertheless they are reported in the literature as distributed throughout geological time from rocks as early as Lower Ordovician and in the collections of the United States Geological Survey housed in the United States National Museum are specimens of unquestionable polyplacophoran plates from the late Upper Cambrian Eminence dolomite of Missouri. These specimens, belonging to species and perhaps genera yet undescribed, are nevertheless typically polyplacophoran in every detail including the peculiar surface sculpture, common to all chitons, possibly to be associated with the remarkable shell eyes, or aesthetes, developed in this group.

Thus our leap backward in time along the polyplacophoran limb of our metaphorical tree carries us almost exactly as far as our leap along the pleurotomarian limb, to latest Cambrian time. However, we find no obvious intermediate connections with any monoplacophoran. Our only clue appears to be offered by the paired multiple dorsal muscle scars of *Archaeophiala* (pl. 1, fig. 3) attributable by analogy to *Helcionella* (pl. 1, fig. 2) and *Scenella* (pl. 1, fig. 1), possibly reinforced by what appear to be tubules in *Tryblidium* very similar to those which carry the nerves for the aesthetes in chitons. In *Archaeophiala* (and in *Tryblidium*) the number of pairs is six[11] but the pair of large scars at the end regarded as anterior are compound and made up of three smaller elements so that the basic number of pairs might be regarded as eight. One might infer that the eight-segmented shell of the polyplacophoran was merely the single shell of the monoplacophoran separated into eight segments to correspond with the eight pairs of shell muscles.

---

[11] It may be significant that the embryos of living polyplacophorans first develop six shell plates. The other two, the terminal plates, are added at a later stage (Garstang, 1929, p. 78).

RECLIMBING THE TREE

For recapitulation it may be well to reverse our course and summarize our results by ascending the pleurotomarian branch of the family tree beginning with the Monoplacophora. We will still hold to this one line, lest we go entirely astray, and we will arrive at the present-day level along a limb with nothing more advanced than the highly specialized relics of the once great pleurotomarian stock.

Throughout rocks of Cambrian age we find what appear to be primitive gastropods with low, cuplike shells. The apex is subcentral or anterior and there is no posterior train. All have rather coarse transverse plicae or costae and finer ornamentation as well. They are believed to have six (or eight?) symmetrical pairs of adductor muscles and not to have undergone torsion. Typical of these early Cambrian genera are *Scenella* (pl. 1, fig. 1) and those species of *Helcionella* (pl. 1, fig. 2) that have the low cuplike form of the genotype. Probably these or similar forms were in existence in late pre-Cambrian time.

Concurrent with the more typical species of *Helcionella* (pl. 1, fig. 2) are other species, that should probably be referred to another as yet unnamed genus, which have very high, narrow shells (pl. 1, fig. 4). It is possible that in these forms the adductor muscles were so crowded that their number was reduced to a single pair, seemingly a prerequisite for the initiation of torsion. Likewise in the early two-thirds of Cambrian time are found species of *Oelandia* (pl. 1, fig. 6), much like *Helcionella* externally but with an extended or up-tilted margin under the apex that has the same shape as the posterior train found in narrow bellerophonts. Accepting it as homologous, we then must accept *Oelandia* (pl. 1, fig. 5) as having undergone torsion but in most other respects to have retained at least some of the external features of *Helcionella*. It is possible that it was the first bellerophont and first prosobranch. Its apex is posterior but still not truly coiled. However, close coiling is found in *Coreospira* (pl. 1, fig. 7) partly contemporaneous with all these but appearing first a little later and still without the anal emargination.

In late Cambrian time we find a number of bellerophonts each provided with an anal emargination: *Strepsodiscus* (pl. 1, fig. 8) and *Cloudia* in the Cyrtolitidae; *Sinuella* (pl. 1, fig. 10), *Owenella*, and *Anconochilus* in the Sinuitidae; and *Chalarostrepsis* (pl. 1, fig. 12) in the Bellerophontidae. With this beginning the bellerophonts deploy throughout Paleozoic time and have their last representatives in the Triassic.

In the latest Cambrian the first pleurotomarians put in their appearance, mostly primitive pleurotomarians with either rounded or angular sinuses, *Sinuopea* (pl. 2, fig. 1), *Schizopea* (pl. 2, fig. 2), and *Dirhachopea*. The anal emargination in *Taeniospira* is a true slit. The anal emargination became a true slit in Early Ordovician time in a number of genera, some as yet undescribed. During the remainder of the Paleozoic the pleurotomarians proliferate greatly and seemingly gave direct rise independently to a number of nonpleurotomarian aspidobranch stocks and through these to most if not all of the more advanced gastropods. They continue in declining numbers through the Mesozoic and Cenozoic and survive today in greatly reduced numbers as relic families adapted to special environments.

In late Cambrian rocks in beds almost contemporaneous with those containing the earliest known pleurotomarians, the first known polyplacophorans appear, typical chitons in all respects. These also continue to the present day but always as relatively few forms mostly adapted to rock clinging. They, like the anisopleuran branch, seem to have been derived from primitive, untorted monoplacophorans but through an entirely different set of modifications. The primitive isopleuran condition continued, for in the polyplacophorans there was no torsion, but the primitive single cuplike shell is replaced by eight transverse plates. Perhaps these eight plates represent the primitive shell which may have become divided transversely in accordance with the possibly eight pairs of shell muscles.

EXPLORATION OF OTHER EARLY BRANCHES

In our climb down two branches of the gastropod family tree, arriving along both at the same main stem, we have followed what appears to be a logical and straight course, paying no attention to other nearby branches. But there are other nearby branches not too far above the roots and it would be improper to leave them out of consideration altogether, especially as the light is very poor.

THE PATELLACEA

First there is the branch that we will call the Patellacea. It is well represented in our living faunas and goes far back into geological time. The patellaceans include simple, cuplike shells that show externally full bilateral symmetry and resemble very closely those that we are here regarding as monoplacophoran isopleurans. However, the anatomy and ontogeny of living representatives show unequivocably that the symmetry of the shell is superficial and secondarily derived. They are classified by neontologists as Archaeogastropoda in the Prosobranchia. Although primitive in many respects, they show in their soft parts and in their ontogeny both torsional and lateral asymmetry. Can it be that in following our branch backward in time we have become confused in the darkness and, instead of passing from the earliest bellerophonts to monoplacophorans, we have stepped across onto another superficially very similar but different branch? Can it be then that what we are calling monoplacophoran isopleurans are in truth nothing more than very ancient patellaceans? Except for Wenz, most previous authors have so regarded them. However, I think not, for there are characters in both groups, very obscure ones to be sure, that seem to indicate the contrary.

The significant clues have to do with the scars of the shell muscles in each group. In the patellaceans the muscle scars form a continuous horseshoelike crescent, open anteriorly, for the shell muscle does not intrude upon the region occupied by the anterior pallial cavity. The shell muscle is composed of closely applied bundles of muscle fibers and in some species this is reflected in the scar by knots, so to speak, in the continuous scar that suggest the discrete scars of the typical monoplacophorans. But these knots in the patellacean scar are not symmetrically paired while the discrete scars of the monoplacophorans are. They reflect the basic asymmetry of the patellaceans. Likewise the anterior opening of the patellacean scar seems to reflect the torsion of the primitively posterior pallial complex and cavity to an anterior position above the head. Although there is in the patellaceans a very thin scarlike line connecting the open ends of the horseshoe, it is apparently not the scar of the pedal muscle but merely the line of attachment of the mantle to the shell, analogous to the pallial line of the pelecypods. The monoplacophorans are here conceived to have included also forms with a continuous muscle scar, such as *Archinacella* Ulrich and Scofield, 1897, as well as those with discrete paired scars, but in both types the scars have elements that close or nearly close the circlet anteriorly and these elements seem to be continuations of the scars themselves. This suggests that these forms, like the Polyplacophora, do not have an anterior pallial cavity and supports our inference that the Monoplacophora have not undergone torsion. That the scars are narrower anteriorly may be accounted for if we imagine that the muscles attached at this part are extensions from the pedal muscles at each side arching over the head.

Although Wenz did not recognize them as such, it is my opinion that the late Paleozoic genera, *Metoptoma* Phillips, 1836, and *Lepetopsis* Whitfield, 1882, are not monoplacophorans but are referable to the Patellacea. Both have continuous, horseshoe-shaped muscle scars, completely open at the anterior end. I would also assign *Palaeoscurria* Perner, 1903, to the Patellacea. Perner described and figured for this genus an open horseshoe of almost discrete muscle scars but I have examined the types of his genotype species and can find no objective evidence for the existence of such a feature (Knight, 1941, p. 231). Nevertheless, there is no direct evidence for any other sort of scar, possibly because the matrix is too coarse to record such delicate features. However, the shape of the shell is so similar to that of *Lepetopsis* that I shall provisionally associate the two. The fossil record of the Patellacea is then continuous from at least Mississippian and perhaps from Silurian time to the present. I know of no Patellacea from rocks earlier than Silurian, nor do I know any forms transitional from pleurotomarian to patellacean unless the very imperfectly known *Halophiala* Koken, 1925, from Ordovician rocks may be so regarded.

MACLURITES AND ITS ALLIES

Beginning in the early Trempealeauan stage of the Upper Cambrian and ranging into the Middle Devonian are a series of genera that give the appearance, at least, of being coiled sinistrally. These genera are here united taxonomically not only by the apparent sinistral coiling, but by another feature as well. This feature, a difficult one to describe, consists in most of these genera of a peculiarity of the region surrounding the umbilicus or that part of the shell usually called the base whereby the "basal" part of the whorl profile is rather sharply arched, most conspicuously so where there is an open umbilicus. This sharp arching of the supposed basal part of the whorl resembles a notch keel with an internal channel. In many forms it is clearly the locus of a sinus in the lip. The following 17 genera, most of them commonly regarded as sinistral, make up the group I have in mind:

From the Upper Cambrian rocks

Kobayashiella Endo, 1937.
Matherella Walcott, 1912 (pl. 2, fig. 10).
Scaevogyra Whitfield, 1878 (pl. 2, fig. 7).

From Ordovician rocks

Antispira Perner, 1903.
Barnesella Bridge and Cloud, 1947 (p. 545).
Clisospira Billings, 1865.
Helicotis Koken, 1925.

Laeogyra Perner, 1903.
Lecanospira Ulrich, in Butts, 1926 (pl. 2, fig. 8).
Lesueurilla Koken, 1898.
Maclurites LeSueur, 1818 (pl. 2, fig. 12) (=*Maclurina* Ulrich and Scofield, 1897).
Macluritella Kirk, 1927.
Matherellina Kobayashi, (1933) 1937.
Mimospira Koken, 1925.
Palliseria Wilson, 1924 (pl. 2, fig. 11) (=*Mitrospira* Kirk, 1930).
Versispira Perner, 1903.

From Silurian rocks

Onychochilus Lindström, 1884 (pl. 2, fig. 9) (=*Palaeopupa* Foerste, 1893).

From Devonian rocks

Sinistracirsa Cossman, 1908 (=*Donaldia* Perner, 1903, preoccupied, and *Boycottia* Tomlin, 1931).
Omphalocirrus Ryckholt, 1860 (=*Coelocentrus* Zittel, 1882, *Polyenaulus* Ethridge, 1917, and *Arctomphalus* Tolmachoff, 1926).

Thus I have grouped together (with one or two superficially dextral genera) all the Paleozoic genera commonly regarded as sinistral except *Antitrochus* Whidborne, 1891, which I refer tentatively to the Trochonematacea, *Agnesia* Koninck, 1883, and *Hesperiella* Holzapfel, 1889, both pleurotomarians and possibly congruent, and *Cambodgia* Mansuy, 1914, a pseudomellaniid. Other typically dextral genera are known to have a few sinistral species, as well.

Up to this point I have spoken of the gastropods of the group we are considering as "apparently" sinistral, that is to say, when the shell is oriented in the arbitrarily conventional position [12] with the spire upward (or the umbilicus downward), the aperture is below and to the left rather than to the right as in the vast majority of gastropods. In the truly sinistral gastropod all organs of the body are reversed in position from that of the dextral gastropod beginning ontogenetically with the early cleavages of the egg. The reversal appears to be the result of a mutation that may occur in some individuals of normally dextral species, or that has become fixed in the heritage of some species in genera that are otherwise dextral, or of a few entire families.

Sinistrality is well known among living gastropods but relatively it is very rare. Likewise it is known among fossil Gastropoda. Of

---

[12] I employ the illogical conventional orientation preferred by English, German, and American authors.

the genera dealt with above *Antitrochus* and *Cambodgia* are probably sinistral. The pleurotomarians *Agnesia* and *Hesperiella* present a still different picture that I hope to discuss at another time. But in all cases sinistrality is a deviation from the basic plan and seemingly occurs only as the result of mutations that may or may not become fixed in the heritage of a group. It occurs sporadically in various only remotely related groups and is probably of no selective value, positive or negative, to its possessor. The rarity of sinistral gastropods is related to the primitive torsion and asymmetry of the Anisopleura. Presumably it was of such a nature as to produce dextral forms, and deviations from the plan require a relatively rare mutation in which all parts of the organism at all stages were reversed. Therefore the occurrence of a relatively large number of apparently sinistral forms classifiable into a relatively large number of genera very early in the history of the class is startling and affords grounds for suspicion that these forms are not truly sinistral.

Among living gastropods there is another phenomenon very much rarer than sinistrality which gives rise to a shell that has the appearance of being sinistral but the organs of the anatomy are not reversed from the position in dextral Gastropoda. The entire animal, including both soft parts and shell, is actually dextral in this case, and the shell is ultradextral or hyperstrophic, not sinistral. In other words, the normal spire has sunk inward, as it were, and may even be coiled in such a way as to produce an umbilicus. The normal base may be flat or protrude to resemble a spire in every respect. Hence a shell is produced that appears to be sinistral although it is actually dextral. The "spire" of such a shell is homologous with the base of what may be called a normal dextral shell and its "base" is homologous with the spire. (See fig. 2.)

Hyperstrophy is exceedingly rare among living gastropods, occurring most frequently as a specialization only in the embryonic nucleus of some opisthobranch gastropods and in the adult stage of a few end members of various highly specialized groups such as pteropods, Ampullariidae, and pulmonates. If it were to occur in adults of species with unknown soft parts it would be difficult to distinguish from sinistrality except on collateral evidence. One line of collateral evidence is that supplied by the peculiar angulation on the "base" of these early Paleozoic shells. If we regard these shells as hyperstrophic, the angulation is no longer anomalous. It becomes the trace of the dorsal anal emargination. There is another line of collateral evidence that is exceedingly pertinent to at least one of the Paleozoic genera that is included in the group we are discussing and it seems very strong evidence indeed. This evidence is furnished by the operculum which is preserved in this genus because it is calcified.

The gastropod operculum is basically corneous (conchyolin) but in some groups the corneous operculum is partially or wholly calcified and in some forms this makes the operculum very massive. Only where it is calcified is the operculum of fossil forms preserved. The embryonic operculum is a minute disk that grows by incremental additions to a margin or margins. Where the increments are added markedly to one side of the margin as against the other sides, growth may be in a spiral and such a spiral operculum, as seen on the external face of the operculum in dextral gastropods, always grows from the nucleus in a counterclockwise direction. In sinistral gastropods it is clockwise. Now, in one of the genera of Paleozoic gastropods of the group we are considering, the operculum was thick and calcified, consequently it is not only frequently preserved but in some specimens it has been found in place in the aperture. The genus is *Maclurites* LeSueur, 1818 (pl. 2, fig. 12). In *Maclurites* the operculum is in the form of an open spiral and the direction of coiling, as seen on its outer face, is counterclockwise. Hence, as pointed out by S. P. Woodward as early as 1854 (p. 202), the shell of *Maclurites* is not sinistral, as has often been supposed, but dextral and hyperstrophic. We do not know the operculum in any other of the genera included in the group under consideration. Nevertheless, as I have endeavored to show, the group we are considering appears to be a natural unit and we may therefore with reasonable assurance attribute to the other genera the character of hyperstrophy that the angulation on the "base" of the whorls suggests and that the operculum of *Maclurites* seems to confirm.

Assuming that we have solved the problem of the coiling in the group under consideration, namely that it is hyperstrophic dextral rather than sinistral, we are faced in consequence with an even more difficult problem. What is the meaning in terms of soft anatomy and of phylogeny of a rather large group of dextral hyperstropic forms introduced so very early in the history of the Gastropoda? Since this group seemingly became extinct before the close of Devonian time, it left no recognized descendants among living gastropods that might throw some light on its organization. As suggested above, hyperstrophy is very rare among living gastropods and occurs only as a secondary acquisition in groups far removed from any possible connection with our early Paleozoic group. We can only surmise what the anatomy of the soft parts of the Paleozoic forms might have been. The shells are coiled and coiled asymmetrically. These facts suggest torsion and possible asymmetry in the primitively paired organs. But, as the shells are hyperstrophic and appear in the fossil record shortly before the first known pleurotomarians, the asymmetry possibly may be very different from that of the main line of gastropod descent. Figure 9 shows hypothetical restorations of the hyperstrophic genus *Palliseria* (pl. 2, fig. 11) a close relative of *Maclurites* (pl. 2, fig. 12). Accepting the notch keel surrounding the umbilicus as the locus of the anus we find very little room for a right ctenidium and tentatively assume that this and its associated organs had been lost. The operculum of *Maclurites* is not only that of a dextral shell but it shows a startling resemblance to that of the recent *Nerita* in that there are points of attachment for a pair of retractor muscles. A single pair of retractor muscles is a primitive feature shared with the bellerophonts, the more primitive pleurotomarians and the neritaceans. The line of speculation that seems most plausible to me is that this group branched off from the early bellerophonts at some such stage as is represented by *Strepsodiscus* (pl. 1, fig. 8), a bellerophont that commonly shows some asymmetry in a sinistral or hyperstrophic sense. This would accord with chronogenesis, for *Strepsodiscus* precedes in the fossil record *Scaevogyra* (pl. 2, fig. 7), the earliest hyperstrophic gastropod, and both precede the earliest pleurotomarian. If this is true the somewhat angular "base" of *Scaevogyra's* whorl is homologous with the angular dorsum of *Strepsodiscus*. It is further supposed that asymmetry arose in the group under consideration as an early genetic response to the mechanical difficulties of isostrophic coiling as in the main line of gastropod descent that began with the pleurotomarians, but independently and probably in a somewhat different way, and that this, in turn, resulted in the asymmetrical, hyperstrophic shell.

PELAGIELLA AND ITS ALLIES

Doubts have been expressed that the members of this group are actually gastropods in spite of the very close resemblance of their shells to those of gastropods. Thus Wenz wrote in 1938 (p. 95) of *Pelagiella:* "Systematische Stellung Fraglich; vermutlich uberhaupt nicht zu den Gastropoden gehörig." The late Dr. E. O. Ulrich is said to have held the opinion that they were "pteropods," that is to say, allied to the hyolithids.[13] The hyolithids are no longer regarded as true pteropods or even as gastropods for that matter. The true pteropods are highly specialized opisthobranch gastropods of Tertiary

---

[13] Oral communication from Dr. Josiah Bridge.

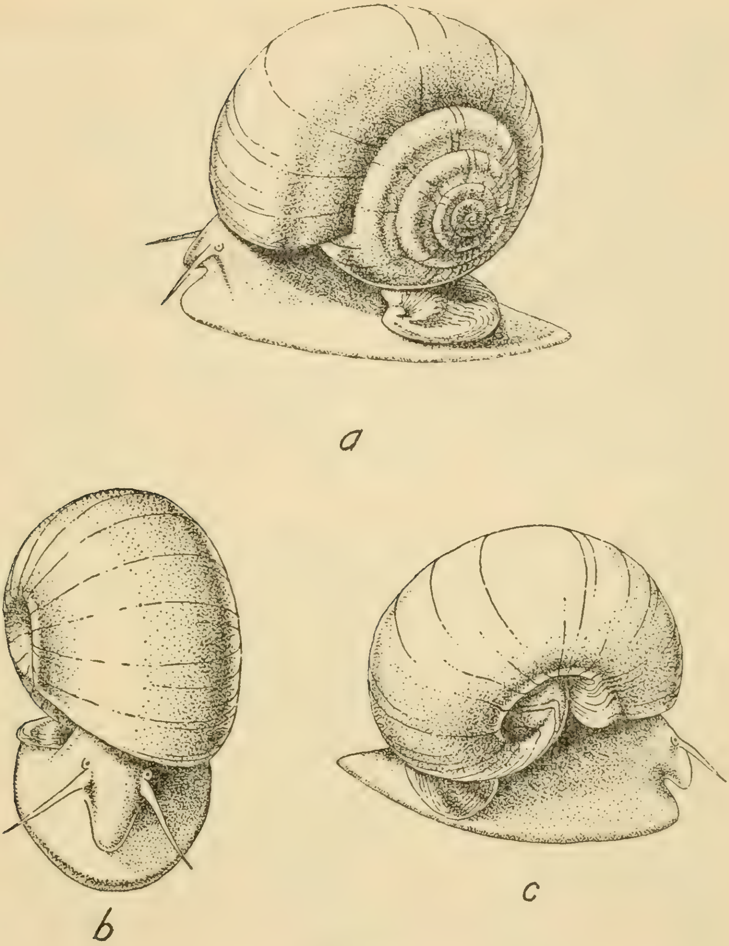


FIGURE 9

Three views of a restoration of *Palleseria longwelli* (Kirk), about × $\frac{3}{4}$.

a, View of the left side. Note the direction of coiling and the protruding, spirelike base.

b, Anterior view.

c, View of the right side. Note here and on the anterior view (*b*) the umbilicus occupying the side where a spire would be in a dextral orthostrophic gastropod. Note especially that the ridge surrounding the umbilcus is the locus of a notch. This notch, an anomalous feature if the shell is regarded as sinistral, is believed to be the anal emargination. If this is correct there is very little space for the primitive right ctenidium and probably it has been lost.

and Recent times, in many respects the farthest removed from the primitive stock of any of the class.

Matthew, in erecting the genus in 1895, seemed to regard *Pelagiella* as a heteropod. The heteropods are again a highly specialized group of late Cretaceous to Recent times, although being prosobranch, not quite so far removed morphologically from the primitive stock as the opisthobranch pteropods. These quite unacceptable assignments serve to accentuate the difficulties in finding a place for these forms in the Gastropoda. My own difficulties derive from the fact that if *Pelagiella* and its allies are gastropods, the hypotheses I have been setting up cannot include them, except peripherally. Otherwise these hypotheses must be abandoned or extensively modified in such ways that they would meet with greater difficulties in other directions than the difficulty presented in removing this obviously questionable group to a peripheral position or eliminating it from the Gastropoda altogether.

Pelagiella and its allies occur in company with the first recorded monoplacophoran gastropods in the rocks of early Cambrian time and are not only coiled but asymmetrically coiled. Thus, if they are gastropods, they appear superficially to have advanced well beyond the isopleuran monoplacophoran stage, the anisopleuran isostrophic stage, and even beyond the pleurotomarian stage of the main line of gastropod evolution. Therefore, since they are contemporaneous with the earliest known monoplacophorans, and the earliest and most primitive known representatives of one of the two hypothetically more primitive stages and precede the others by a considerable interval of geological time, the difficulties are obvious.

I do not wish to consume space in laboring the problem at too great length for, with our present lack of knowledge of their anatomy and even of their conchology, it is not soluble. I am not prepared to abandon the hypotheses as to the derivation of the main lines of gastropod descent until other hypotheses are presented that better explain the observed facts. Although it is recognized that the fossil record is imperfect, I am not prepared to assume that it is so very faulty that its bearing on the broader aspects of chronogenesis is to be set aside. There are various other possibilities that might be called upon to account for *Pelagiella* and its allies as gastropods. For example, can it be that they represent a branch from the monoplacophoran stock that acquired torsion and asymmetry independently in pre-Cambrian time, perhaps bypassing an isostrophic stage? There is little evidence one way or another but I think it extremely unlikely. Or can it be that they are monoplacophorans that carried their tendency to coil anteriorly to such a point that the resulting inconvenience of a coil poised above the head gave survival value to any mutation that set the coil asymmetrically to one side, as it were? This again appears to be extremely unlikely. It would require a symmetrically coiled predecessor and no such form is known.

Finally then, I share the doubts of my predecessors, expressed or implied, that *Pelagiella* and its allies are gastropods, but I shall go further than they have gone in that I shall not attempt to force them into a phylogenetic classification of the gastropods that appears to have no place for them. I shall very tentatively assign them the peripheral position of a shoot from the same pre-Cambrian root as the main trunk of the gastropod family tree originating obscurely in pre-Cambrian and of otherwise little-understood affinities. It would be helpful if I could assign them elsewhere in the animal kingdom, but I cannot do so.

Before leaving the subject of *Pelagiella* and its allies it may be well to review briefly and in general terms their chief characteristics. The shells are coiled and of from one-half to about three whorls. The coil is always asymmetrical. For the most part they are small and many are minute, a millimeter or two in diameter. The apical end of the whorl, the nucleus, appears in some to be laterally flattened and somewhat blunt, reminding one of the tip of a ram's horn, and in some forms slightly swollen. The whorls are ovoid in section, the narrow end of the ovoid being at the periphery. The spire is always low, varying in that respect from depressed to umboniform. In the forms with a depressed spire the base is arched; in those with an arched spire it is flattish. The shells of any one species appear to be rather variable and it is probable that both dextral and sinistral forms occur in some species. The ornamentation consists of fine, faint lines of growth and, on some forms, a single faint revolving lira, seemingly both above and below the periphery. The growth lines are somewhat drawn back at the rounded periphery, thus suggesting a broad, peripheral sinus. No operculum is known and there is no information on muscle scars. In some specimens of *Pelagiella,* Matthews reports and figures a groovelike constriction in the shell (or its steinkern?) close to the apertural margin. It is not present on Matthew's primary types of *Pelagiella atlantoides* (Matthew), the genotype (Knight, 1941, p. 237), but does occur on rare specimens subsequently assigned to the species by Matthew. It may be a mark of maturity or old age. Possibly the constriction is seen only on the steinkern in which case it might mean only that the apertural margin was thickened within and the thickening is invisible on the outer surface of the shell.

This group, in which I include Cambrian species mistakenly referred by authors to such genera as *Straparollina* Billings, *Straparolus* Montfort, *Euomphalus* Sowerby, *Raphistoma* Hall, *Ophileta* Vanuxem, and *Platyceras* Conrad, is in urgent need of intensive study, as are all Cambrian gastropods and gastropodlike forms for that matter. Several names have been proposed for supposed genera, mostly on the basis of quite inadequate studies. Besides *Pelagiella* Matthew, 1895, there are *Parapelagiella* Kobayashi, 1939 (p. 287), *Protoscaevogyra* Kobayashi, 1939 (p. 286), and *Proeccyliopterus* Kobayashi, 1939 (p. 286). The last three seem to be erected on characters of very doubtful value or are differentiated from *Pelagiella* on mistaken concepts of the characters of *Pelagiella* itself.[14] Still another genus, *Semicircularea* Lochman, in Lochman and Duncan, 1944 (p. 44), was erected for the forms with only about one-half whorl often misidentified as *Platyceras* by previous authors. *Pelagiella* and its allies range throughout Cambrian and perhaps into early Ordovician time.

TAXONOMIC CONCLUSIONS

As a result of our findings on our descent of the family tree and of the paleontological and neontological considerations given above, we have arrived at tentative hypotheses that force on our attention certain taxonomic conclusions. The first is that, since the monoplacophoran gastropods seemingly share with the polyplacophorans the basic isopleuran plan of organization, the two should be brought more closely together than has been customary in most classifications. The second is that, since the Anisopleura as the result of mutation arose suddenly from a monoplacophoran ancestor, and since certain anatomical features of both are very similar, the relationship between them is too close to permit them to be arranged in separate classes comparable in degree of differentiation to the other molluscan classes. The third is that, although the isopleurans and the anisopleurans should be placed in a single class, the gulf between them, both anatomically and in time, is profound and that, therefore, it seems appropriate to rank each as a subclass. On the basis of these three considerations we present the following revised definitions of the class

---

[14] It is unfortunate that the belief that the supposed characters of two of them suggested that they were ancestral to later genera of quite different affinities and led to the fixation of those ideas in the names given them. The proposal of names embodying phylogenetic concepts is most unwise.

Gastropoda and its major subdivisions, the subclasses Isopleura and Anisopleura. There are also other conclusions as to the subdivisions of the next lower rank but consideration of these is postponed until the class and the two proposed subclasses are dealt with.

Class GASTROPODA Cuvier

So great is the range of special morphological modifications in the class that it is exceedingly difficult, if not impossible, to draw up a brief diagnosis that will cover all gastropods without excluding some forms that clearly must be included. The return of the isopleurans to the class, however necessary it appears, increases the difficulties, for we thereby reduce the convenient criteria of torsion and of a single shell to a status diagnostic of subdivisions of lower rank.

The gastropods may be defined as mollusks with a differentiated head, a flat creeping foot, and a single basically conical shell. In a few gastropods specialized for free swimming the foot may be modified into finlike organs, in the polyplacophorans the primitive single shell has been divided transversely into eight segments, and in some highly specialized forms the shell has disappeared in the adult. In many others the cone is attenuated and coiled. Primitively marine, they have become adapted also to fresh waters and to terrestrial life. They are found at nearly all latitudes and nearly all altitudes from the depths of the oceans to high mountains. They appear in the fossil record in Lower Cambrian rocks and are flourishing today.

Subclass Isopleura Lankester.—Gastropods that retain throughout life both in the shell and in the soft anatomy the primitive bilateral symmetry of the class. They are entirely marine and always rare. They first appear in the fossil record in Lower Cambrian rocks and carry through to the present. They probably originated in pre-Cambrian time.

Subclass Anisopleura Lankester.—Gastropods that undergo torsion during the veliger stage. The Anisopleura are often abundant and are tremendously diversified in morphology and in habitat. They first appear in the fossil record as primitive forms in Lower Cambrian rocks and are flourishing today.

MAJOR DIVISIONS OF THE SUBCLASS ISOPLEURA

Order Polyplacophora.—Isopleuran gastropods with the shell made up of eight plates arranged along the midline of the dorsum; head not provided with eyes; shell eyes, or aesthetes, may be present. Polyplacophora range from late Cambrian time to the present, are always marine and relatively rare.

The subdivisions of the Polyplacophora will not be considered here.

Order MONOPLACOPHORA.—Isopleuran gastropods with a single conical shell with the apex subcentral or pointed forward; some possibly with aesthetes. Marine, Lower Cambrian–Devonian.

Before considering the subdivisions of the Monoplacophora it may be well to repeat that I do not consider *Discinella* Hall, 1871, *Mobergella* Hedström, 1923, or *Barella* Hedström, 1930, to be monoplacophoran gastropods but hyolithoid opercula. *Conchopeltis* Walcott, 1879, I regard as probably a scyphozoan and certainly no mollusk. *Chuaria* Walcott, 1899, is entirely problematical. (Knight, 1941, p. 20.)

Family TRYBLIDIIDAE Pilsbry, 1899

Subfamily PALAEACMAEINAE Grabau and Shimer, 1909

Relatively low to high, cap-shaped shells with apex subcentral to slightly anterior. Muscle scars (observed only in *Archaeophiala*) discrete and arranged in six (or eight?) symmetrical pairs; ornamentation basically concentric undulations.

Genera

Scenella Billings, 1872 (pl. 1, fig. 1) (=*Parmophorella* Matthew, 1886), Cambrian.

Helcionella Grabau and Shimer, 1909 (pl. 1, fig. 2), throughout the Cambrian.

Palaeacmaea Hall and Whitfield, 1872, Upper Cambrian.

Archaeophiala Koken, in Perner, 1903 (pl. 1, fig. 3) (=*Scaphe* Hedström, 1923, *Scapha* Hedström, 1923, *Patelliscapha* Tomlin, 1929, and *Paterella* Hedström, 1930), Ordovician.

Calloconus Perner, 1903, Lower Devonian.

In the Silurian what appears to be a new genus hitherto unrecognized is represented by *Palaeacmaea? solarium* Lindström, 1884 (p. 59).

Subfamily TRYBLIDIINAE Pilsbry, 1899

Spoon-shaped shells with the apex at or overhanging the anterior end. Muscle scars (observed in *Tryblidium, Pilina, Drahomira, Proplina,* and partially in *Cyrtonella*) essentially similar to those of the foregoing family; ornamentation concentric-lamellar or radiating.

Genera

Tryblidium Lindström, 1880, Silurian.

Cyrtonella Hall, 1879, Devonian.[15]

---

[15] I have given my reasons for including *Cyrtonella* Hall in the Tryblidiidae elsewhere (Knight, 1947b, p. 267).

Helcionopsis Ulrich and Scofield, 1897, Ordovician.
Drahomira Perner, 1903, Ordovician.[16]
Vallatotheca Foerste, 1914, Ordovician.
Pilina Koken, 1925, Silurian.
Proplina Ulrich and Bridge in Kobayashi, 1933, Upper Cambrian—Lower Ordovician.[17]

Family HYPSELOCONIDAE, new

Narrowly conical shells with the apex over the narrower (anterior?) end but tilted slightly backward. Ornamentation growth lines or faint radiating undulations; muscle scars unknown.

Genera

Hypseloconus Berkey, 1898, Upper Cambrian–Lower Ordovician.[18]
Pollicina Holzapfel, 1895, Ordovician.

Family ARCHINACELLIDAE, new

Low conical shells with the apex at or overhanging the anterior end. Ornamentation growth lines or radiating lirae; muscle scar a broad, continuous ring, narrowing in front where it passes below the apex. Ordovician.

Genera

Archinacella Ulrich and Scofield, 1897.
?Ptychopeltis Perner, 1903.[19]

It is possible that *Helcionopsis* will find a place here rather than with the Tryblidiidae when its muscle scars are discovered.

Order APLACOPHORA.—In this order there is no shell, and it is consequently unknown as a fossil. I have no comments but retain it here.

---

[16] *Drahomira* is a name published, but not adopted, by Perner, 1903 (p. 23, footnote) for *Tryblidium glaseri* Barrande in Perner, 1903 (p. 23), genotype by monotypy. This name was overlooked by me in the preparation of "Paleozoic Gastropod Genotypes" (Knight, 1941). Seemingly it is the valid name for a distinct genus of this family.

[17] The muscle scars of *Proplina cornutaformis* (Walcott), the genotype and only species referred to the genus in published literature, are unknown. However, the material assembled for a monograph on Ozarkian and Canadian gastropods by E. O. Ulrich and Josiah Bridge is available to me and several species referred to the genus show them clearly.

[18] For comments on the supposed multiple paired muscle scars of *Hypseloconus* see Knight, 1941 (p. 158).

[19] Although Perner described a scar for *Ptychopeltis,* examination of his specimens failed to disclose valid evidence for it (Knight, 1941, p. 288).

SUBCLASS ANISOPLEURA LANKESTER

Except for reviving Lankester's subclass Anisopleura, equivalent without the Monoplacophora (Tryblidiacea of Wenz) to the class Gastropoda of Wenz, 1938, I am now proposing few changes. To the Bellerophontacea, which are retained as Prosobranchia, are added the family Coreospiridae with the genera *Coreospira* Saito (pl. 1, fig. 7), *Cycloholcus* Knight, and *Oelandia* Westergård (pl. 1, fig. 5), but not without a residuum of doubt, and the superfamily Macluritacea is erected in the Prosobranchia. The Macluritidae of Wenz form its nucleus and other families composed of related elements are assembled with it. The revised taxonomy of the group will be presented as a part of another paper. The included genera are listed on pages 36-37 of this paper. In all other respects the Anisopleura are left as Wenz had them but because of lack of opportunity for intensive study rather than because of detailed endorsement of his arrangements.

APPENDIX

INTERPRETATION OF THE BELLEROPHONTS

AMPHIGASTROPODA VS. PROSOBRANCHIA

The genus *"Bellerophon"* of the older workers and some neontologists (now expanded to a superfamily, the Bellerophontacea, with four families and something like fifty genera and subgenera) has been difficult to understand and to classify. Its isostrophic habit of coiling is almost unique in the Gastropoda. This and the fact that the entire superfamily has been extinct since Triassic time and affords no living examples from which soft parts can be demonstrated have seemingly left us with little information to go on. The broad morphological pattern of the soft parts must be inferred since it cannot be observed directly.

De Koninck in 1883 (p. 121) reaffirmed on a more rational basis his suggestion of 1843 (p. 337) that the bellerophonts were prosobranch gastropods. Before 1883 the bellerophonts had been regarded as cephalopods, or as heteropod gastropods. Some specialized forms such as *Pterotheca,* originally described as brachiopods or pelecypods, have been regarded as pteropods. Since that time they have been classified as prosobranch with the Docoglossa, or as a separate class of Mollusca, the "Amphigastropoda." I can subscribe to none of these views except perhaps the main thesis of de Koninck in 1883, although not to the details.

As stated previously, Wenz's great contribution to theory in 1938

(p. 59) was the idea that the Tryblidiacea were primitive untorted gastropods. This I applaud and accept. But he also regarded the bellerophonts as untorted gastropods similar to the Tryblidiacea, on the grounds of symmetry and an unsupported assumption that the slit and band are not to be compared with the seemingly homologous feature in the pleurotomarians. On this point I must part company with him. Curiously, if I read the story aright, Wenz seems to be following part way in the footsteps of many of his predecessors, who regarded the bellerophonts as prosobranchs on the grounds of the following chain of reasoning: The early cup-shaped shells are symmetrical and resemble the living patellids; therefore they are to be classified with the latter as Docoglossa and prosobranchs. The bellerophonts are also symmetrical; therefore they are closely related to the patellids and are also Docoglossa and prosobranchs.

But Wenz in recognizing the early cup-shaped mollusks, the Tryblidiacea, as nontorted gastropods changed the first premise of the customary chain of reasoning and the bellerophonts, still linked with these early cup-shaped shells, are, to Wenz, like them nontorted gastropods.

The weakness in both lines of argument is the overvaluing of the symmetry of bellerophonts as a criterion of relationship to the symmetrical cup-shaped shells whether patellids or tryblidians, the undervaluing of the many manifest differences between the bellerophonts and either of the other two, and the undervaluing of several manifest anatomical homologies between the bellerophonts and the asymmetrical but coiled prosobranch pleurotomarians.

Fundamental to the undervaluing of bellerophont-pleurotomarian homologies is a failure on the part of Wenz and some neontologists to recognize that torsion and the development of lateral asymmetry are two distinct processes. Undoubtedly torsion set up unstable conditions that favored the natural selection of mutations, such as lateral asymmetry, that would result in a more efficient organism, but lateral asymmetry is not to be confused with torsion or what I have called torsional asymmetry. Although torsion is a prerequisite for asymmetry, asymmetry does not necessarily follow from it. It is as though this school of thought believes that the muscular pull that initiates torsion also distorts the lateral symmetry. I know no evidence that supports such a view. It is true, of course, that except in the Isopleura all gastropods living today show lateral asymmetry at some ontogenetic stage and the lateral asymmetry is initiated in the veliger larva immediately after torsion. But it does not follow that it was always universally thus. The view that asymmetry was the immediate or concommitant mechanical result of torsion and in consequence became a part of gastropod heritage smacks somewhat of Lamarckianism and in any case cannot be sustained.

Returning to Wenz's views, in 1938 they seem to have been approximately as I have stated them above. On the basis of the lateral symmetry alone he felt that the bellerophonts were closely related to the tryblidians and consequently had not undergone torsion. Although he gave no systematic expression to these views at that time, classifying both the Tryblidiacea and Bellerophontacea as Prosobranchia, it was his opinion that both were probably out of place in that position.

Feeling insecure as to his interpretation of the bellerophonts he was quite rightly searching for corroborative evidence, and he felt that the discovery in the bellerophonts of multiple, paired dorsal muscle scars like those of the tryblidians would be strong supporting evidence, as indeed it would. In 1937 he wrote to me asking what I knew of bellerophont muscle scars and that started the chain of events about which I wrote ten years later (Knight, 1947). Briefly, a specimen of the supposed but somewhat atypical bellerophant *Cyrtonella mitella* (Hall) was discovered which seemed to support fully Wenz's views in that the unmistakable record of two pairs of dorsal muscle scars (not three as Wenz wrote) was clearly visible on that part of the steinkern that was exposed. Possibly other scars may be covered by matrix. Feeling that his views as to the close relationship of the bellerophonts and tryblidians were fully vindicated, Wenz published his paper giving systematic effect to those views by employing for them a subclass, the Amphigastropoda (Wenz, 1940).[20]

An interesting point about tryblidian muscle scars noted in *Tryblidium, Archaeophiala,* and *Cyrtonella* is that each scar has on the side toward the margin of the shell a smaller, fainter scar as though it were the shadow of the scar cast before it. Wenz, who had never seen the specimen of *Cyrtonella mitella* he figured, misinterpreted a pair of these shadow scars, shown in the photograph sent him by Yang, as a principal scar. This is why he mistakenly reported three visible pairs of scars. The physiological significance of the "shadow scars" is

---

[20] Actually the Amphigastropoda consisting of only the bellerophonts, was erected as a new class of mollusks by Simroth in 1906 (p. 839), who was followed by Thiele in 1935. Simroth's course, and especially Thiele's, was supported only by the gratuitous assumption that the soft anatomy was without torsion and bilaterally symmetrical. Amazingly, Thiele assumed also "eine änliche schwimmende Lebensweise—wie die Nautiliden" (Thiele, 1935, p. 1125) in which he was followed by Wenz.

obscure but their presence is an additional evidence that *Cyrtonella* is a tryblidian.

Although the paired dorsal muscle scars on the specimen of *Cyrtonella* were discovered in my laboratory and although it was on my suggestion that Yang disclosed the discovery to Wenz, my views as to its significance were quite different from those so promptly published by Wenz in 1940. The more probable interpretation that *Cyrtonella,* a genus that was even then somewhat doubtfully placed in the Bellerophontacea and quite as easily interpreted as a tryblidian, should be placed in the Tryblidacea instead of the Bellerophontacea seems never to have occurred to Wenz.

Fortunately I was able to discover the muscle scars of two unquestionable bellerophont genera a few years later, *Sinuites* (pl. 1, fig. 11) and *Bellerophon* (pl. 1, fig. 13) (Knight, 1947). They consist of a single symmetrical pair. Each muscle was attached to the opposite end of the colummella about one-half whorl within the aperture, a position that would permit them to serve effectively as pedal retractors. They are not dorsal and not multiple pairs. Both of those facts are seemingly fatal to Wenz's arguments as to the closeness of the relationship between the tryblidians and the true bellerophonts.

Wenz displays a number of views to which I must take exception. For example, he accepts the wholly conjectural and long-rejected views of Lang (1891) as to the gradual development of torsion in the gastropods. He treats the bellerophonts and pleurotomarians as being present in early Cambrian rocks. In terms of genera recognized by him, neither appeared until late Cambrian time. Under the influence of his overestimate of the significance of external lateral symmetry in the bellerophonts he fails to even consider the close homologies between bellerophonts and pleurotomarians. Finally, he seems to hold the view first proposed by Deshayes in 1830 (p. 135) and abandoned by most students well before the close of the nineteenth century that the bellerophonts "tended toward a freely swimming, nektonic mode of life" (translation from Wenz, 1938, p. 59). I know of no evidence whatever that would support such a view and would be interested indeed to learn of a molluscan swimming mechanism that would be powerful enough to sustain the massive shells of some bellerophonts above the sea bottoms. It seems highly probable that the bellerophont foot conformed in general to the pattern shown by other Archaeogastropoda. It was adapted to creeping, not to swimming.

I regard the bellerophonts as prosobranch Archaeogastropoda close to and probably ancestral to the pleurotomarians which they precede in the fossil record. The bellerophonts share with the pleurotomarians (1) a shell that typically has deeply hollow, usually closely coiled whorls, (2) a sinus or slit which, if a slit, generates a slit band, (3) a single pair of lateral retractor muscles,[21] and (4) seemingly a single pair of each, of ctenidia, auricles, etc. They differ principally in that the coil of the bellerophont shell is bilaterally symmetrical (isostrophic) and that of the pleurotomarian shell is an asymmetrical orthostrophic helicoid, in my view a difference of little significance for classification but of profound import for understanding gastropod evolution.

Comparing the bellerophonts with the tryblidians we find they have one feature, and only one, in common: externally the shell of each is bilaterally symmetrical. But in respect to the first three categories in the foregoing paragraph, the tryblidians have (with a very few exceptionally high conical shells) (1) a shallow cup- or spoon-shaped shell with the apex bent toward one end, but no coiling, (2) no sinus or slit, and (3) multiple (usually six or eight) symmetrical pairs of dorsal muscle scars.

Let us look for a moment at these points of agreement and disagreement. The agreement between the bellerophonts and pleurotomarians on points 1 and 3 can only mean that we have a shell with a deep body cavity into which the head and foot can be withdrawn by the retractor muscles which are properly placed in both for the operation. Point 2, the sinus or slit can only be an anal emargination, a feature that is known otherwise only in prosobranchs and especially in the Archaeogastropoda, and which is accepted by many neontologists such as Garstang, Yonge, Crofts, and many others as an adaptation for sanitation after torsion had created a need for it. The bilateral symmetry of the shell can no more be considered a character of subclass or even ordinal rank than that same symmetry can be employed to link two groups so different on other points as the bellerophonts and tryblidians.

Need we continue to point further fundamental differences between the pleurotomarians and bellerophonts on one hand and the tryblidians on the other, differences such as the impossibility of at least the low, cuplike tryblidians pulling their head and foot into the shell? In that respect they probably resembled the chitons and the secondarily symmetrical fissurellids and patellaceans. Since the muscle

---

[21] The living pleurotomariid genera or subgenera *Perotrochus* Fischer, *Entemnotrochus* Fischer (pl. 2, fig. 4), and *Mikadotrochus* Lindholm, "*Pleurotomaria*" of authors, have only a single retractor muscle, although other living pleurotomarian genera have a pair.

scars of the high and narrow species of *Helcionella* (pl. 1, fig. 4) in the tryblidians have never been observed, it is more difficult to speculate profitably as to whether the muscles are so placed that they could or could not have withdrawn the head and foot into the shell. It is possible that they could, especially if, as I am suggesting, the reduction of the pedal muscles from eight pairs to one pair may have occurred first in them. Need it be pointed out to those who regard the anal emargination in the bellerophonts as posterior that no known or reasonably imaginable nontorted mollusk has or needs a slit or sinus to provide egress for the contaminated water of a posterior anus? Certainly the chitons and the tryblidians do not. Again, have those who infer that bellerophonts are primitively orthoneurous nontorted "Amphigastropoda" ever tried to imagine the animal with its large, heavy coil anterior and overhanging the head? The shell in many bellerophont species is not only thick and heavy but may carry a massive parietal callus as well. To me such an arrangement appears highly improbable, bordering indeed on the fantastic. It is suggested that the reader turn to figure 7, *a,* on page 30, where a restoration of a small very primitive bellerophont, with no parietal callus, is presented as though it were primitively orthoneurous and exogastric, may help him to visualize it.

In summary, it appears to me that the evidence for the view that the bellerophonts were prosobranchs, is very strong and the evidence that they were primitively orthoneurous "Amphigastropoda" very weak indeed.

Soft anatomy of the bellerophonts.—We now know enough of bellerophont shell morphology and enough of the morphology of living examples of the obviously related pleurotomarians that we may speculate with considerable safety on the general nature of bellerophont soft anatomy and perhaps even on its physiology and habits.

One may be quite confident that they were aspidobranchs with a high degree of bilateral symmetry reflected in symmetrically paired ctenidia, osphradia, hypobranchial glands, auricles, kidneys, and perhaps even gonads. They probably crawled on the sea bottom on a generalized gastropod foot. It seems probable that like other aspidobranchs they fed chiefly on vegetable matter and were rhipidoglossate. Nothing is known of the bellerophont operculum, if there was one.

Perhaps a diagrammatic restoration of some of the more significant soft parts with an interpretation of the course of the water currents in the mantle cavity will save pages of words.

On figure 10 is shown a shell of a bellerophont species, *Knightites multicornutus* Moore, 1941 (p. 153), with the soft parts restored in

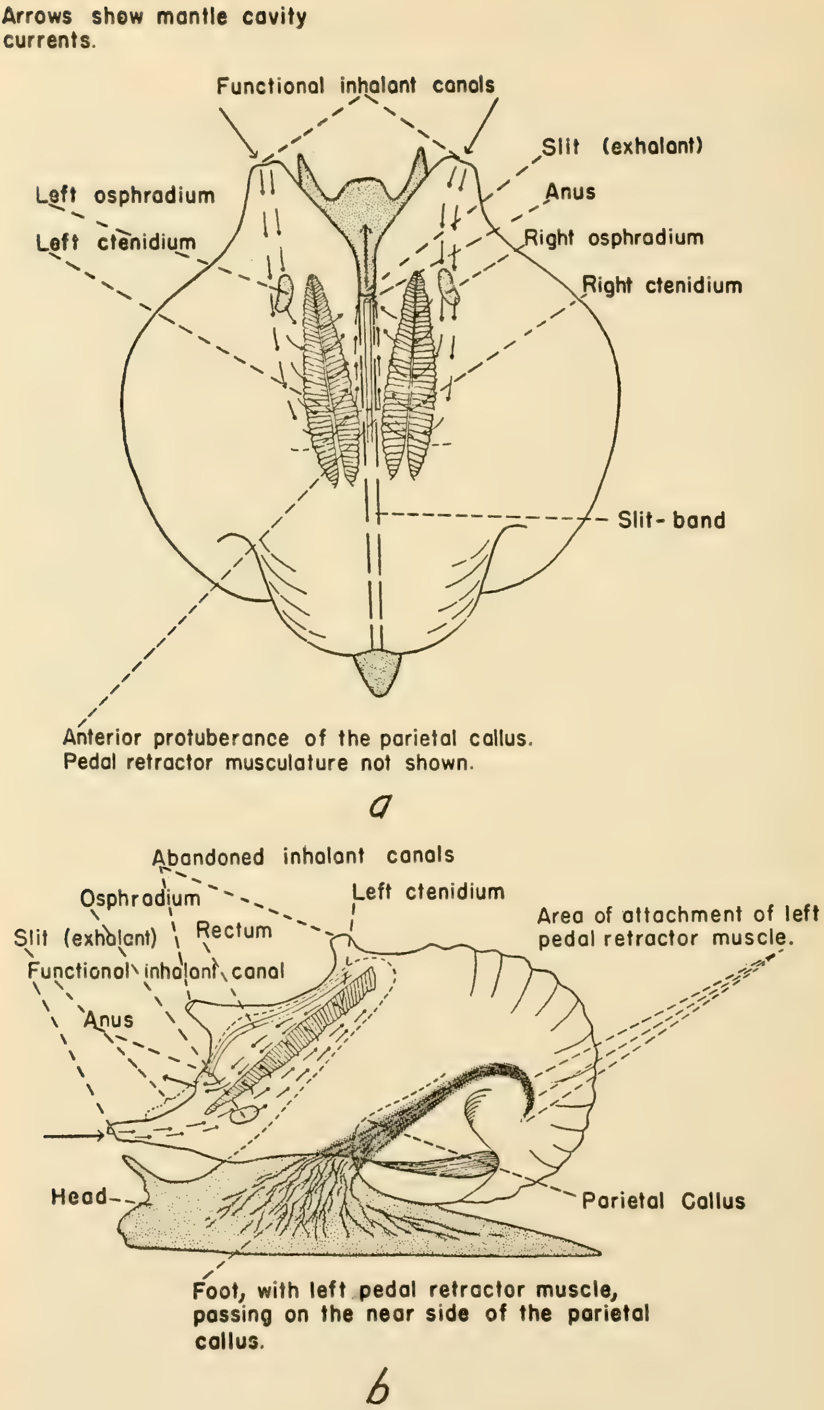


FIGURE 10

(See opposite page for explanation.)

terms of the above interpretation. It is a modification of figure 7d in Moore, 1941 (p. 158). I have abandoned the ideas expressed in figures 7a-c as untenable in the light of more accurate knowledge of the aerating currents in *Haliotis* than I then had. The extended periodic, paired canals on each side of the slit and slitband in *K. multicornutus* interested me very much. It occurred to me that they gave a clue to the region on the mantle lip through which passed the currents of water that aerated and flushed out the mantle cavity. The works of Yonge and Crofts on the aerating currents in various gastropods including the pleurotomarian *Haliotis* seem to reinforce the suggestion made by the canals of *K. multicornutus,* so that one can infer the probable course of the principal water currents in that species and probably in all generalized bellerophonts. This inferred circulation is in all respects that of a prosobranch and seems a reasonable approximation to the probable condition during life.

REFERENCES

CROFTS, D. R.

1937. The development of *Haliotis tuberculata,* with special reference to organogenesis during torsion. Philos. Trans. Roy. Soc. London, ser. B, No. 552, vol. 228, pp. 219-268.

GARSTANG, W.

1929. The origin and evolution of larval forms. British Assoc. Adv. Sci., Rep. 96th Meeting, pp. 77-98.

HOWELL, B. F., ET AL.

1944. Correlation of the Cambrian formations of North America. Bull. Geol. Soc. Amer., vol. 55, pp. 993-1004.

KNIGHT, J. BROOKES.

1941. Paleozoic gastropod genotypes. Geol. Soc. Amer. Spec. Pap. 32.

1947a. Some new Cambrian bellerophont gastropods. Smithsonian Misc. Coll., vol. 106, No. 17.

FIGURE 10

Two views of a diagrammatic restoration of *Knightites multicornutus* Moore (Bellerophontacea, Bellerophontidae), approximately × 2. The shell is drawn as though it were partly transparent so as to show some of the fleshy organs. The arrows show the probable path of the principal aerating and cleansing currents. Although most bellerophonts did not have inhalant canals as did *Knightites* it is thought that the path of the currents and regions of their entrance and exit were approximately the same as inferred for *Knightites.* In living *Haliotis* where the details are known the paths are homologous in every respect.

a, Dorsal view.

b, Left side view. The fibers of the left retractor muscle are shown in a highly schematic fashion as though they anastomose into the muscles of the foot (which are not shown).

1947b. Bellerophont muscle scars. Journ. Paleontol., vol. 21, pp. 264-267.
1948. Further new Cambrian bellerophont gastropods. Smithsonian Misc. Coll., vol. 111, No. 3.

KOBAYASHI, T.
1939. Restudy of Lorenz's *Raphistoma broggeri* from Shantung, with a note on *Pelagiella*. Jubilee publication in commemoration of Prof. H. Yabe's birthday.

LANKESTER, RAY.
1878. Mollusca. Encyl. Britt., 9th ed., vol. 16.

LINDSTRÖM, G.
1884. On the Silurian Gastropoda and Pteropoda of Gotland. Kong. Svenska Vet.-Akad. Handl., vol. 19, No. 6.

LOCHMAN, CHRISTINA.
1944. *In* Lochman and Duncan, Early Upper Cambrian faunas of central Montana. Geol. Soc. Amer. Spec. Pap. 54.

MOORE, R. C.
1941. Upper Pennsylvanian gastropods from Kansas. State Geol. Surv. Kansas Bull. 38.

NAEF, A.
1911. Studien zur generellen Morphologie der Mollusken. Teil 1. Über Torsion und Asymmetrie des Gastropoden. Ergebn. und Fortschcr. Zool., vol. 3, pp. 73-164.

PELSENEER, P.
1906. Mollusca. *In* Lankester, E. R., A Treatise on Zoology, pt. 5.

SIMROTH, H.
1906. *In* Bronn, H. G., Klassen und Ordnungen des Tier-Reichs.

THIELE, J.
1931-1935. Handbuch der systemtischen Weichtierkunde.

WENZ, W.
1938-1944. Gastropoda. *In* Schindewolf, O. H., Handb. Paläeozool., vol. 6, pt. 1, 1-7.
1940. Ursprung und frühe Stammes-geschichte der Gastropoden. Arch. Molluskunde, vol. 72, pp. 1-10.

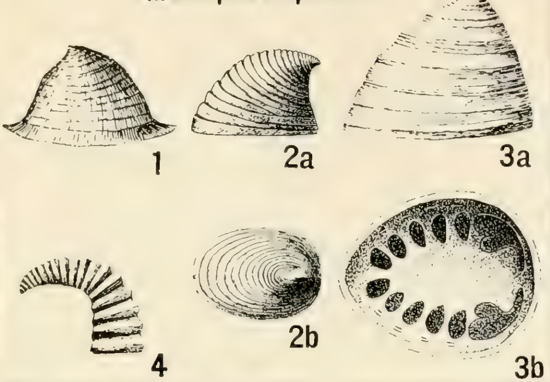
WOODWARD, S. P.
1851-1856. A manual of the Mollusca, or rudimentary treatise of Recent and fossil shells.

YONGE, C. M.
1939. On the mantle cavity and its contained organs in the Loricata (Placophora). Quart. Journ. Micr. Sci., vol. 81, pp. 367-390.
1947. The pallial organs in the aspidobranch Gastropoda and their evolution throughout the Mollusca. Philos. Trans. Roy. Soc. London, ser. B, vol. 232, pp. 443-518.

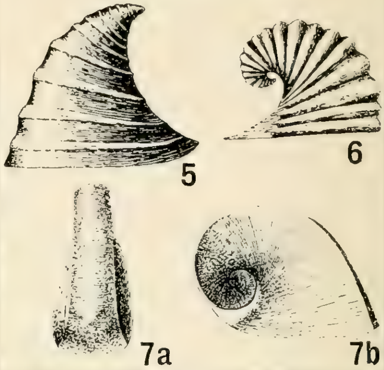
Just as this work reached page-proof stage, a copy of the "Traité de Paléontologie," published under the direction of Prof. Jean Piveteau, reached Washington (Traité de Paléontologie, vol. 2, 1952). The chapter on the Gastropoda is by Dr. Geneviève Termier (née Delpey) and Prof. Henri Termier of Algiers. Since I have discussed Mme. Termier's views on gastropods elsewhere (Geol. Mag., vol. 83, pp. 280-284, 1946), I shall say nothing further here except to reaffirm my almost complete disagreement.—J. B. K.

PLATES

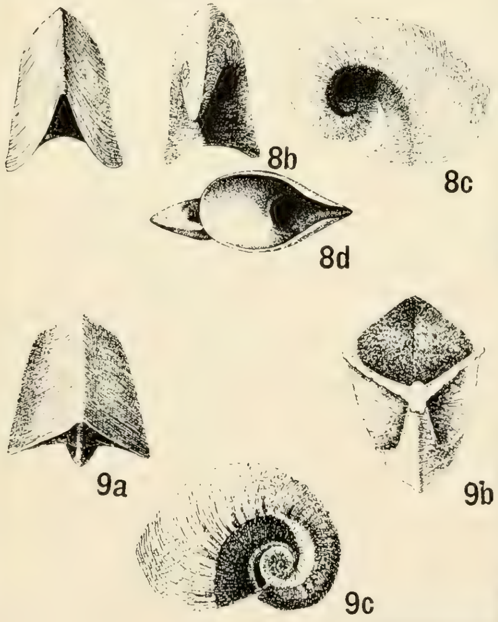
Monoplacophora



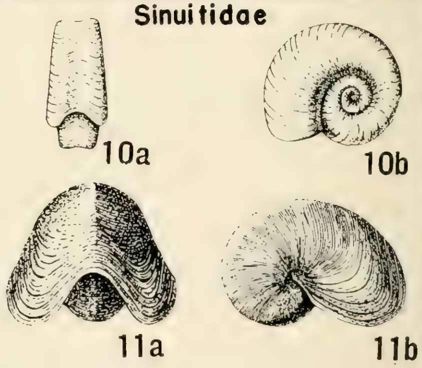
Coreospiridae



Cyrtolitidae



Sinuitidae



Bellerophontidae

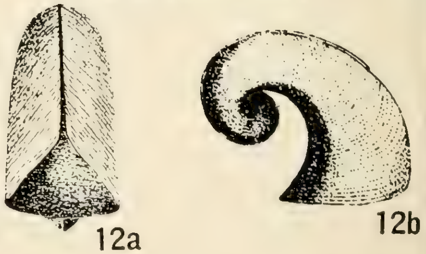


PLATE 1

1-3. Monoplacophora.

1. *Scenella reticulata* Billings. Lower Cambrian, Newfoundland. Left side. Adult. Approx. × 1. 2a, b. *Helcionella subrugosa* (Orbigny). Lower Cambrian, Troy, N. Y. a, Right side. b, View from above. An example of the low, cup-shaped species. Approx. × 1. 3a, b. *Archaeophiala antiquissima* (Hisinger). Upper Ordovician, Sweden. a, Right side. b, View looking directly into the cup of the shell showing the muscle scars (darkly pigmented) and the "shadow scars." This drawing was not made from the specimen but from photographs (Knight, 1941, pl. 3, fig. 3a-b). The shell is shown a little too narrow posteriorly. Approx. × 1. 4. *Helcionella?* sp. Middle Cambrian, Silver Peak Range, Nev. An example of the high, narrow species of *Helcionella?*. Approx. × 4.

5-7. Bellerophontacea, Coreospiridae.

5. *Oelandia acutacosta* (Walcott). Lower Cambrian, Manuels Brook, Conception Bay, Newfoundland. Left side view. Approx. × 4. 6. *Oelandia* sp. Middle Cambrian, Eagle, Alaska. Right side view. Approx. × 5. 7a, b. *Coreospira walcotti* Knight. Lower Middle Cambrian, Mount Stephen, British Columbia. a, View from above. Note the total lack of an anal emargination. b, Right side view.

8, 9. Bellerophontacea, Cyrtolitidae.

8a-d. *Strepsodiscus major* Knight. Upper Cambrian (Dresbachian), Colorado. a, Anterior view showing V-shaped anal emargination. b, Posterior view showing the slight asymmetry. c, Right side view. d, Apertural view of specimen oriented on its side. Compare with plate 2, fig. 7, *Scaevogyra swezeyi*. Approx. × 1. 9a-c. *Cyrtolites subplanus* Ulrich. Middle Ordovician, Tennessee. a, Anterior view, showing shallow V-shaped sinus. b, Apertural view from below. c, Left side view. Approx. × 1.

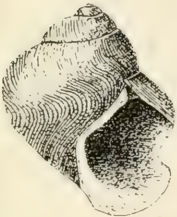
10, 11. Bellerophontacea, Sinuitidae.

10a, b. *Sinuella minuta* Knight. Upper Cambrian (Upper Dresbachian or Lower Franconian), near Burnet, Tex. a, Anterior view. Note U-shaped anal emargination. b, Left side view. Approx. × 10. 11a, b. *Sinuites cancellatus* (Hall). Middle Ordovician (Trenton), New York. a, Anterior view. Note U-shaped anal emargination. b, Right side view. Approx. × 1.

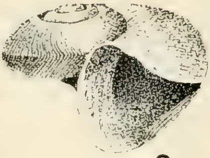
12, 13. Bellerophontacea, Bellerophontidae.

12a, b. *Chalarostrepsis praecursor* Knight. Upper Cambrian (Upper Franconian or Trempealeauan). a, Anterior view. Note that the anal emargination takes the form of a deep slit. b, Right side view. Approx. × 1. 13a-c. *Bellerophon* sp. Mississippian, Indiana. a, Right side view. b, Apertural view from below. c, Anterior view. Note short slit. Approx. × 1.

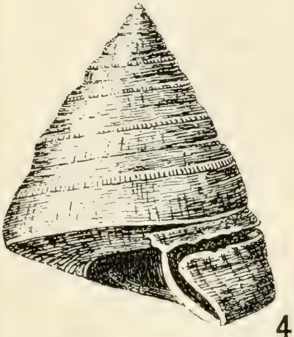
Pleurotomariacea

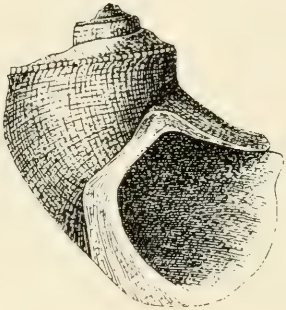

1a


1b


2


3

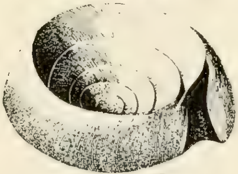

4


5


6

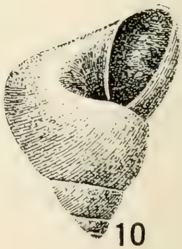
Macluritacea

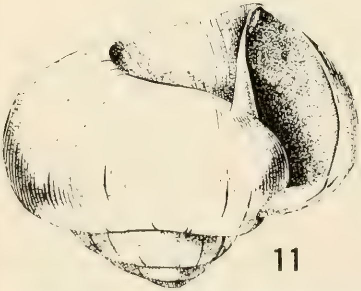

7

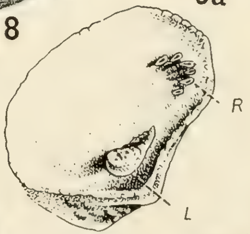

8


9a


9b


10


11



12a

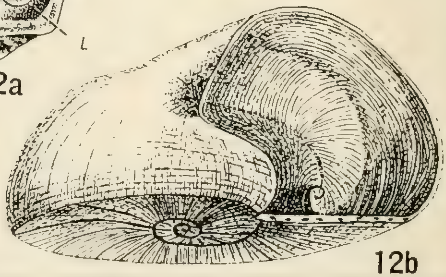

12b

PLATE 2

1-6. Pleurotomariacea.

1a-b. *Sinuopea sweeti* (Whitfield). Upper Cambrian (Jordan member, Trempealeauan), Wisconsin. a, Apertural view. b, Dorsal view. Note the U-shaped anal emargination and compare it with that of *Sinuites cancellatus* (pl. 1, fig. 11a). Approx. × 1. 2. *Schizopea typica* (Ulrich and Bridge). Lower Ordovician (Van Buren), Missouri. Note the deep V-shaped sinus. Approx. × 1. 3. *Loxoplocus* (*Lophospira*) *milleri* (Miller). Middle Ordovician (Trenton), New York. Note deep V-shaped sinus generating a band. Approx. × 1½. 4. *Entemnotrochus adansoniana* (Crosse and Fischer). Living, Caribbean Sea. This is one of the species miscalled "Pleurotomaria" by neontologists. Note the deep slit. Approx. × ¼. 5. *Phanerotrema labrosum* (Lindström) not Hall. Lower Silurian, Gotland. The slit, which generates a band, is short. Approx. × 1. 6. *Goniasma* sp. Pennsylvanian, Texas. Note the V-shaped sinus and the very short slit. This is an example of the Murchisoniidae. Approx. × 1½.

7-12. Macluritacea. All these are dextral and hyperstrophic. Hence the orientation, actually the same as for other dextral forms, appears to be up-side down. 7. *Scaevogyra swezeyi* Whitfield. Upper Cambrian (St. Lawrence Member, Trempealeauan). Note the sharp, V-shaped sinus culminating at the circumbilical carina. The sinus is the anal emargination without a reasonable doubt. It should be noted here that the thin shell with expanded aperture in Whitefield's restoration is an error. Wenz (1938, p. 239) grossly exaggerates the error. Approx. × 1. 8. *Lecanospira compacta* (Salter). Lower Ordovician (Roubidouxian), Quebec. Note the deep, V-shaped anal emargination and the circumbilical carina. Approx. × 1. 9a-b. *Onychochilus reticulatum* Lindström. Lower Silurian, Gotland. (After Lindström). a, A longitudinal section. b, Apertural view. Note that the anal emargination is obscure and that circumbilical ridge is rounded and troughlike. Approx. × 2. 10. *Matherella saratogensis* (Miller). Upper Cambrian (Little Falls, Trempealeauan), New York. As in *Onychochilus* the anal emargination is obscure and the circumbilical ridge rounded and troughlike. Approx. × 4. 11. *Palliseria longwelli* (Kirk). Middle Ordovician (Chazyan), Nevada. The anal emargination is angular and culminates at the angular circumbilical ridge. Approx. × ⅔. (See also text figure 9, p. 41.) 12a-b. *Maclurites logani* Salter. Middle Ordovician (Black River), Ontario. a, The operculum, inner surface. Note the attachment rugosities of the left (L) and right (R) retractor muscles. As in *Nerita* the attachment rugosity of the left muscle is an extended projection. b, The shell with the operculum in place, apertural view. The umbilicus is narrower and the circumbilical ridge more rounded than in some species. Note the counterclockwise spiral of the operculum, a feature diagnostic of a dextral gastropod. Approx. × ⅔.

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 117, NUMBER 14

Charles D. and Mary Vaux Walcott
Research Fund

NEW AND UNUSUAL SPECIES OF BRACHIOPODS FROM THE ARBUCKLE GROUP IN OKLAHOMA

(With Four Plates)

BY
G. ARTHUR COOPER

Curator, Division of Invertebrate Paleontology and Paleobotany
U. S. National Museum

(Publication 4093)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
SEPTEMBER 23, 1952

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 117, NUMBER 14

Charles D. and Mary Vaux Walcott Research Fund

NEW AND UNUSUAL SPECIES OF BRACHIOPODS FROM THE ARBUCKLE GROUP IN OKLAHOMA

(With Four Plates)

BY
G. ARTHUR COOPER

Curator, Division of Invertebrate Paleontology and Paleobotany
U. S. National Museum

(Publication 4093)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
SEPTEMBER 23, 1952

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

Charles D. and Mary Vaux Walcott Research Fund

NEW AND UNUSUAL SPECIES OF BRACHIOPODS FROM THE ARBUCKLE GROUP IN OKLAHOMA

By G. ARTHUR COOPER

Curator, Division of Invertebrate Paleontology and Paleobotany
U. S. National Museum

(With Four Plates)

The brachiopods described herein resulted from collecting by Dr. William E. Ham during the detailed mapping of the Arbuckle Mountains. As might be expected, the great care taken by Dr. Ham during the mapping to locate useful and easily recognizable fossils produced a number of new species and others that had hitherto not been seen in this region. Many of the occurrences produced beautifully silicified specimens which make possible easy recovery of excellent study material.

Since the appearance of Ulrich and Cooper's study of the Ozarkian and Canadian Brachiopoda, the stratigraphic sequence of the Arbuckle Mountains has been better defined by Decker (1939) and the brachiopods can now be assigned to their proper formations. The lists below include already known species and those described in this paper.

Fort Sill formation:
- *Billingsella corrugata* Ulrich and Cooper.
- *Plectotrophia bridgei* Ulrich and Cooper.
  - *laticosta* Cooper, new species.
- *Mesonomia magna* Cooper, new species.

Signal Mountain formation:
- *Apheoorthis ornata* Ulrich and Cooper.
  - *oklahomensis* Ulrich and Cooper.
  - *platys* Cooper, new species.
- *Billingsella rectangulata* Cooper, new species.
- *Cymbithyris hami* Cooper, new genus and species.
- *Fasciculina fasciculata* Cooper, new genus and species.
- *Finkelnburgia auriculata* Cooper, new species.
  - *biconvexa* Cooper, new species.
  - *extensa* Cooper, new species.

Palaeostrophia cf. *P. elax* (Clark).
Glyptotrophia rotunda Cooper, new species.

McKenzie Hill formation:
Finkelnburgia arbucklensis Cooper, new species.
    cf. *F. bellatula* Ulrich and Cooper.
    obesa Cloud.
Syntrophina campbelli (Walcott).
Tetralobula texana Ulrich and Cooper.

Cool Creek formation:
Finkelnburgia delicatula Cooper, new species.
    subquadrata Cooper, new species.
Imbricatia lamellata Cooper, new genus and species.
Clarkella species.
Diaphelasma oklahomense Ulrich and Cooper.
Syntrophinella deckeri Cloud.

Kindblade formation:
Finkelnburgia crassicostellata Cooper, new species.
    cullisoni Ulrich and Cooper.
    scenidioides Ulrich and Cooper.
Tritoechia delicatula Ulrich and Cooper.
    subaequiradiata Ulrich and Cooper.
    typica (Ulrich).
Oligorthis arbucklensis Ulrich and Cooper.
Diparelasma fasciculatum Cooper, new species.

West Spring Creek formation:
Diparelasma costellatum Cooper, new species.
    typicum Ulrich and Cooper.
Polytoechia subrotunda Ulrich and Cooper.
    subcircularis Cooper, new species.
Pomatotrema magnum Ulrich and Cooper.
    oklahomense Ulrich and Cooper.
    transversum Ulrich and Cooper.
Syntrophopsis laevicula Ulrich and Cooper.
    magna Ulrich and Cooper.
Finkelnburgia magna Ulrich and Cooper.
Tritoechia planodorsata Ulrich and Cooper.

Genus APHEOORTHIS Ulrich and Cooper, 1936

APHEOORTHIS PLATYS Cooper, new species

Plate 2B, figures 8-13

Shell small for the genus, wider than long, and subrectangular in outline; hinge forming the greatest width; cardinal extremities slightly auriculate. Sides nearly straight; anterior margin broadly rounded. Surface fascicostellate.

Pedicle valve gently convex in lateral profile and with the greatest curvature just anterior to the umbo; anterior profile broadly convex but with the median region somewhat narrowly convex; beak small; umbo narrowly convex. Fold marked by a median and two lateral fascicles, broad and low. Median region from umbo to anterior margin moderately swollen; flanks descending by a long, moderately steep slope to the margins. Interior with strong dental plates but only slightly thickened muscle area to form a spondylium discretum or the incipient stages of a pseudospondylium.

Brachial valve slightly convex in lateral profile and broadly but gently convex in anterior profile. Umbo smooth and slightly swollen; sulcus originating just anterior to umbo and widening and deepening to the anterior margin where it occupies one-third the valve width. Flanks gently swollen; slopes to posterolateral extremities short and gentle; cardinal extremities flattened. Interior with strong median ridge, small simple cardinal process on a moderately thickened notothyrial platform; brachiophores short and stout; adductor scars strongly impressed.

Measurements in mm.

	Length	Brachial length	Mid-width	Hinge width	Thickness
Pedicle valve,					
U.S.N.M. No. 116737a.........	9.0	?	9.8	10.0	2.2
Brachial valve,					
U.S.N.M. No. 116736b.........	?	7.0	9.6	9.4	0.9

Types.—Holotype: U.S.N.M. No. 116737a; paratype: U.S.N.M. No. 116736b.

Horizon and locality.—Signal Mountain formation (50 feet below the top) in Oklahoma, 2,100 feet north and 1,000 feet west of the southeast corner of sec. 26, T. 1 S., R. 1 W., Murray County.

Discussion.—This species is characterized by a fairly flat brachial valve, moderately convex pedicle valve and somewhat subdued ornamentation. This latter feature distinguishes this species from described species. Its ornamentation is much more subdued than that of *A. ornata* Ulrich and Cooper from the same formation.

Genus BILLINGSELLA Hall, 1892

BILLINGSELLA RECTANGULATA Cooper, new species

Plate 1A, figures 1-15

Shell moderately large for the genus, wider than long, subrectangular in outline. Hinge as wide as or slightly wider than the midwidth; cardinal extremities slightly auriculate; sides nearly straight; anterior margin broadly rounded; surface somewhat fascicostellate.

Pedicle valve nearly flat in the median region in lateral profile but with the umbonal and anterior marginal regions somewhat narrowly convex; anterior profile nearly flat to broadly and gently convex; umbo narrowly convex, the convexity continued to about the valve middle where it fades into the shell surface or slightly anterior to the middle: anteromedian region flattened; anteromarginal region gently but abruptly convex where a shallow, poorly defined sulcus appears; flanks bounding fold gently concave to nearly flat. Interarea orthocline; pseudodeltidium wide and strongly convex. Teeth strong, buttressed by excess shell suggesting short dental plates; adductor track moderately thickened anteriorly; pallial marks moderately strong.

Brachial valve deeper than the pedicle one, gently convex in lateral profile; broadly and moderately convex in anterior profile; umbo sulcate, sulcus wide and moderately deep to the valve middle but becoming shallow and even, or almost so, with the flanks at the front margin. Posterolateral areas flattened and with short steep slopes; flanks bounding sulcus moderately swollen. Interior with short, stout median ridge, lightly developed notothyrial platform and slender cardinal process. Chilidium only moderately developed.

Measurements in mm.

	Length	Brachial length	Mid-width	Hinge width	Thickness
U.S.N.M. No. 116722a..........	12.0	10.2	14.3	14.4	3.9
U.S.N.M. No. 116722b..........	13.5	11.0	14.8	14.9	4.3
U.S.N.M. No. 116722c..........	12.1	9.7	13.9	14.3	3.8

Types.—Holotype: U.S.N.M. No. 116722a; figured paratypes: U.S.N.M. Nos. 116722b, d, e, h, i, k; unfigured paratypes: U.S.N.M. Nos. 116722c, f, g, j.

Horizon and locality.—Signal Mountain formation (1-foot bed of limestone 100 feet above the base) in Oklahoma, 1,700 feet east and 1,300 feet north of the southwest corner of sec. 21, T. 1 S., R. 1 W., Murray County.

Discussion.—This species is characterized by its large size, rectangular outline, and moderately short interarea. The specimens illustrated are unusual in showing both valves in contact. *Billingsella* is generally loosely articulated and the valves fall apart after death.

Billingsella rectangulata is larger and squarer than *B. coloradoensis* and is differently ornamented. It approaches *B. corrugata* Ulrich and Cooper in size but lacks the concentric corrugations and acute cardinal extremities of that species.

CYMBITHYRIS Cooper, new genus

Shell attaining a width of about a half inch, wider than long, and with a wide hinge. Profile concavo-convex. Valves of unequal depth, the pedicle valve having the greater depth. Surface multicostellate.

Pedicle valve with pseudodeltidium and foramen as in *Billingsella;* teeth small, dental plates absent; musculature as in *Billingsella.*

Brachial interior with small flat brachiophores like those of *Billingsella;* median ridge short and low; cardinal process a simple ridge. Chilidium well developed.

Genotype.—Cymbithyris hami Cooper, new species.

Discussion.—The nearest relative to this genus is *Billingsella.* The two genera have the same type of pseudodeltidium, teeth, and muscular arrangement in the pedicle valve. They differ in that *Cymbithyris* has a concave brachial valve. The brachiophores are like those of *Billingsella* but other details of the brachial interior are obscure. *Cymbithyris* is thus a lateral development from *Billingsella.*

CYMBITHYRIS HAMI Cooper, new species

Plate 1B, figures 16-21

Shell subrectangular to quadrate in outline; hinge wider than midwidth; cardinal extremities somewhat auriculate; sides oblique; anterior margin narrowly rounded. Surface multicostellate.

Pedicle valve strongly convex in lateral profile; anterior profile narrowly convex in the median region and with steep lateral slopes. Umbo narrowly convex, the convexity extending to about the middle where it is dissipated in the median swelling of the valve; median region swollen, the broad swelling extending to the front margin. Flanks moderately swollen and with long, moderately steep slopes to the sides; posterolateral extremities somewhat flattened. Interarea moderately long, orthocline.

Brachial valve fairly concave in anterior and lateral profiles; umbo sulcate, sulcus extending from umbo to front margin, expanding anteriorly; flanks bounding sulcus moderately concave.

Measurements in mm.

Pedicle valves,	Length	Brachial length	Mid-width	Hinge width	Height	Thickness
U.S.N.M. No. 116724a....	12.4	?	13.7	16.6	4.5	?
U.S.N.M. No. 116724b....	12.7	?	14.3	16.5	3.8	?
U.S.N.M. No. 116724d....	9.5	8.2	?	?	?	2.2

Types.—Holotype: U.S.N.M. No. 116724d; figured paratypes: U.S.N.M. Nos. 116724a-c, e-f.

Horizon and locality.—Signal Mountain formation (limestone one foot thick 126 feet above the base) in Oklahoma, 1,700 feet west and 600 feet south of the northeast corner of sec. 28, T. 1 S., R. 1 W., Murray County.

Discussion.—No other species of this genus is known to which *C. hami* can be compared.

Genus **MESONOMIA** Ulrich and Cooper, 1936

MESONOMIA MAGNA Cooper, new species

Plate 1D, figures 27-34

Shell large for the genus, subrectangular in outline with the hinge forming the widest part; cardinal extremities auriculate; sides nearly straight; anterior margin broadly rounded. Anterior commissure uniplicate. Ornamentation consisting of costellae of varying sizes alternating with each other.

Pedicle valve unevenly convex in lateral profile and with the maximum convexity in the umbonal region; anterior profile broadly convex. Umbo narrowly swollen and forming a narrow fold to about the valve middle; anterior part of the median portion bent fairly abruptly in the direction of the brachial valve and forming a short, narrowly convex tongue; flanks bounding sulcus gently swollen; slopes to the posterolateral extremities short and gentle. Interior with small teeth and moderately thickened adductor track.

Brachial valve gently convex in lateral profile and broadly but gently convex in anterior profile; umbo sulcate, sulcus shallow and continued anteriorly to about the middle where it suddenly reverses to form a moderately broad fold; flanks gently swollen; interior with short, delicate brachiophores supported by shallow plates that unite under the thin cardinal process. Median ridge short and delicate.

Measurements in mm.

Pedicle valve,	Length	Brachial length	Mid-width	Hinge width	Thickness
U.S.N.M. No. 116694a.....	12.3	?	15.0	15.8	3.3
Brachial valves,					
U.S.N.M. No. 116694b.....	?	10.7	14.8	17.8	2.9
U.S.N.M. No. 116694c.....	?	11.1	15.8	17.2	2.7

Types.—Holotype: U.S.N.M. No. 116694a; figured paratypes: U.S.N.M. Nos. 116694b-d.

Horizon and locality.—Fort Sill formation (179 feet above the base) in Oklahoma, 1,000 feet south of the north quarter corner of sec. 29, T. 1 S., R. 1 E., Murray County.

Discussion.—This species is distinguished by its large size, gently sulcate pedicle valve, and the nature of the ornamentation. The species is most like *M. iophon* (Walcott) from the Mons formation of Alberta but is much larger and with less pronounced fold and sulcus. The ornamentation of *M. iophon* is stronger than that of the Arbuckle species and is not so strongly differentiated into strong and fine costellae.

FASCICULINA Cooper, new genus

Exterior somewhat resembling *Apheoorthis* and with unequally convex valves, the pedicle valve having the greater depth. Anterior commissure broadly sulcate; surface fascicostellate.

Pedicle valve with swollen median region serving as a fold; teeth small; dental plates well developed; muscle field orthoid and with the adductor track more or less elevated to form a pseudospondylium.

Brachial valve with sulcus originating at the beak and usually bounded by two strong costellae; cardinalia delicate; brachiophores short, small; sockets formed by small fulcral plates; brachiophore supports nearly erect to moderately oblique, attached directly to the floor of the valve but more or less joined by a callosity between them; cardinal process a simple ridge when present. Median ridge formed by inner swelling corresponding to sulcus; adductor callosities thick in old shells.

Genotype.—*Orthis desmopleura* Meek (as redefined by Ulrich and Cooper, Geol. Soc. Amer. Spec. Pap. 13, p. 131, 1938).

Discussion.—This genus can be recognized by its fasciculate exterior, usually weakly developed pseudospondylium, and discrete brachiophore plates. It may be easily confused with *Finkelnburgia* when the brachiophore plates are strongly oblique, but it differs from that genus in having a much stronger sulcus, one that extends from beak to anterior margin, much stronger ornamentation and generally weaker development of the pseudospondylium.

Fasciculina is like *Orusia* internally but is much differently ornamented. Furthermore in that genus the dental plates are short and no trace of a pseudospondylium has been seen.

Other species besides the genotype assigned to *Fasciculina* are *Eoorthis wichitaensis* Walcott and possibly *E. indianola* Walcott.

FASCICULINA FASCICULATA Cooper, new species

Plate 2A, figures 1-7

Small, subquadrate in outline, wider than long, and with the hinge forming the widest part; sides slightly oblique; anterior margin broadly rounded; cardinal extremities slightly auriculate. Surface fascicostellate.

Pedicle valve evenly and moderately convex in lateral profile and with the maximum convexity at about the middle; anterior profile fairly strongly and broadly convex; umbo narrowly convex, the convexity extended to the anterior margin as a low and broad fold having a median costella at the umbo and extending to the margin but with a broad fascicle implanted on each side of it. Flanks gently swollen and separated from the fold by a strong costella on each side giving the appearance of a fold within a broad median sulcus. Pseudospondylium moderately thickened and with the adductor track slightly elevated.

Brachial valve gently convex in lateral profile and broadly and gently convex in anterior profile; sulcus originating at the umbo and widening rapidly to the front margin where it occupies about half the width; posterior of sulcus marked by two costellae which bound a deep median sulcus within the broad sulcus; broad sulcus bounded by a strong costella on each side, and these oppose the depressions bounding the pedicle fold and the deeper inner sulcus opposes the fold within the pedicle depression. Flanks bounding sulcus, narrow, gently swollen. Interior with short delicate brachiophores and recumbent brachiophore plates.

Measurements in mm.

Pedicle valves,	Length	Brachial length	Mid-width	Hinge width	Thickness
U.S.N.M. No. 116738a........	6.4	?	7.9	7.9 plus	2.4
U.S.N.M. No. 116738b........	7.1	?	8.6	8.9	2.3
Brachial valve,					
U.S.N.M. No. 116738d........	?	5.7	7.8	8.1	1.7

Types.—Holotype: U.S.N.M. No. 116738e; figured paratypes: U.S.N.M. Nos. 116738b-d; unfigured paratype: U.S.N.M. No. 116738a.

Horizon and locality.—Signal Mountain formation (90 feet above the base) in Oklahoma, in the SE¼SW¼NE¼ sec. 16, T. 1 S., R. 1 W., 1,200 feet west of the east quarter corner, Murray County.

Discussion.—This species can be recognized by its strong costellae, alate cardinal extremities, fairly deep sulcus, and fairly well-developed pseudospondylium. It most resembles *F. desmopleura* (Meek) in its ornamentation but differs in its interior, the brachiophore supporting plates of the Arbuckle shell being more oblique and joined by a callus on the floor of the valve. Furthermore *F. fasciculata* has a moderately developed pseudospondylium whereas that of *F. desmopleura* is not strongly thickened.

This species differs from *F. wichitaensis* in being much smaller, having a more pronounced pedicle fold and stronger costellae.

Genus **FINKELNBURGIA** Walcott, 1905

FINKELNBURGIA ARBUCKLENSIS Cooper, new species

Plate 3H, figures 33-39

Shell of about medium size for the genus, wider than long; subrectangular in outline; sides nearly straight; hinge equal to or slightly narrower than the midwidth; cardinal extremities slightly obtuse or forming a right angle. Multicostellate with a few strong costellae standing out in a mat of fine ones.

Pedicle valve moderately convex in lateral profile but with the maximum curvature in the umbonal region; broadly and strongly convex in anterior profile; beak prominent; umbo and median regions swollen; flanks full with short steep slopes to the margins. Delthyrial cavity wide and deep; pseudospondylium with well-developed dental plates, narrow or broad adductor track but short median ridge. Pallial trunks wide and deeply impressed.

Brachial valve shallower than the pedicle valve, with gentle convexity in lateral profile and broadly convex in anterior profile. Sulcus poorly defined, shallow, extending from umbo to anterior margin; flanks gently swollen but median region somewhat flattened. Lateral slopes short and gentle. Interior with broad and short notothyrial cavity; adductor callosities not strongly developed but six pallial trunks deeply impressed.

Measurements in mm.

Pedicle valves,	Length	Brachial length	Mid-width	Hinge width	Thickness
U.S.N.M. No. 116741a.........	8.9	?	11.3	9.6	2.5
U.S.N.M. No. 116741b.........	8.0	?	10.3	10.3	2.2
Brachial valves,					
U.S.N.M. No. 116741c.........	?	8.8	12.0	10.5	2.3
U.S.N.M. No. 116741d.........	?	9.2	12.1	11.8	2.3

Types.—U.S.N.M. No. 116741b; figured paratypes: U.S.N.M. Nos. 116741a, c, d.

Horizon and locality.—McKenzie Hill formation (237 feet above the base) in Oklahoma, 1,500 feet east and 2,000 feet south of the northwest corner of sec. 28, T. 1 S., R. 1 W., Murray County.

Discussion.—This species is characterized by subrectangular outlines nearly rectangular or slightly obtuse cardinal extremities, poorly defined sulcus and closely crowded costellae. The species suggests *F. bellatula* Ulrich and Cooper but that is a smaller and somewhat less transverse shell with stronger costellae and more delicate pseudospondylium. *Finkelnburgia arbucklensis* is simliar to *F. helleri* Cloud but differs in being less transverse and in having a finer ornament, stouter cardinalia, and a narrower pseudospondylium.

FINKELNBURGIA AURICULATA Cooper, new species

Plate 2F, figures 29-38

Shell small, wider than long, and with the hinge wider than the midwidth; cardinal extremities mucronate; sides gently oblique; anterior margin broadly rounded; surface fascicostellate.

Pedicle valve deeper than the brachial valve; strongly convex in lateral profile; anterior profile strongly arched; umbo and median region strongly swollen; flanks swollen and with steep slopes to the margins. Interarea short, curved, apsacline. Interior with a deep pseudospondylium but with the adductor track only moderately thickened.

Brachial valve strongly convex in lateral profile; anterior profile strong and broadly convex and with steep lateral slopes. Umbo sulcate; sulcus widening and deepening anteriorly to the front margin. Flanks bounding sulcus fairly strongly swollen; brachiophores and supporting plates stout.

Measurements in mm.

	Length	Brachial length	Mid-width	Hinge width	Thickness
U.S.N.M. No. 116731a..............	6.1	5.7	7.4	7.9	4.7
Pedicle valve, U.S.N.M. No. 116731e..........	5.7	?	7.0	8.0	2.1

Types.—Holotype: U.S.N.M. No. 116731a; figured paratypes: U.S.N.M. Nos. 116731c-f; unfigured paratype: U.S.N.M. No. 116731b.

Horizon and locality.—Signal Mountain formation (6-inch bed of limestone 150 feet above the base) in Oklahoma, 300 feet west and 1,150 feet south of the northeast corner of sec. 28, T. 1 S., R. 1 W., Murray County.

Discussion.—This species is characterized by rectangular outline, strongly and subequally convex valves, and the sharp auriculation of the cardinal extremities. In the latter respect the species resembles *F. finkelnburgi* but it is much smaller and has straighter lateral margins and less extended cardinal extremities.

FINKELNBURGIA cf. F. BELLATULA Ulrich and Cooper

Plate 3G, figures 28-32

Finkelnburgia bellatula Ulrich and Cooper, Journ. Paleontol., vol. 10, No. 7, p. 622, 1936; Geol. Soc. Amer. Spec. Pap. 13, p. 134, pl. 25C, figs. 9, 10, 13-28, 1938.

Shell of about medium size for the genus, roundly subelliptical in outline with the hinge shorter than the midwidth which is the widest part; sides well rounded; anterior margin broadly rounded; cardinal extremities obtuse. Multicostellate, costellae of different sizes.

Pedicle valve gently convex in lateral profile but moderately convex in anterior profile; beak moderately protruberant; umbo narrowly swollen; entire valve fairly strongly inflated and with long convex lateral slopes. Interior with pseudospondylium short and weakly developed.

Brachial valve less deep than the pedicle valve, moderately convex in lateral profile; broadly and moderately convex in anterior profile; median regions inflated but posterior and median portion marked by a shallow and narrow sulcus which does not reach the margin. Anteromedian region swollen and conforming with the convexity of the rest of the valve; lateral slopes short and steep; interior with thick, erect brachiophore supports and thick cardinal process. Adductor platforms moderately developed.

Measurements in mm.

	Length	Brachial length	Mid-width	Hinge width	Thickness
Pedicle valve,					
U.S.N.M. No. 116747a........	8.4	?	10.1	7.0	2.2
Brachial valve,					
U.S.N.M. No. 116747b........	?	7.6	9.8	6.8	2.1

Hypotypes.—U.S.N.M. Nos. 116747a, b.

Horizon and locality.—McKenzie Hill formation (10 feet below the top) in Oklahoma, 2,200 feet north and 1,250 feet west of the southeast corner of sec. 7, T. 1 S., R. 1 E., Murray County.

Discussion.—The specimens here assigned to *F. bellatula* agree in outline and profiles and the ornamentation is well differentiated as in the type specimens. Furthermore the interiors agree in having a delicate pseudospondylium and the adductor platforms confined to the rear part of the shell.

FINKELNBURGIA BICONVEXA Cooper, new species

Plate 2E, figures 22-28

Shell of about medium size for the genus, wider than long, subrectangular in outline; hinge about equal to midwidth; cardinal extremities slightly auriculate; sides nearly straight; anterior margin broadly rounded; surface multicostellate, costellae crowded and of different sizes.

Pedicle valve deeper than the brachial valve, strongly convex in lateral profile; strongly convex in anterior profile and with long, steep, lateral slopes. Umbo, median region, and flanks strongly inflated. Pseudospondylium broad and low; adductor track thickened; median ridge short and thick.

Brachial valve moderately convex in lateral profile but broadly and strongly convex in anterior profile; beak prominent; umbo somewhat broadly and strongly swollen, the swelling continued anteriorly to the margin; anterior third somewhat flattened to approximate a median sulcus or definitely sulcate, the sulcus broad and shallow; flanks somewhat swollen and with short steep slopes to the margins. Interior with large and thick cardinalia; adductor platforms not developed.

Measurements in mm.

Pedicle valve,	Length	Brachial length	Mid-width	Hinge width	Thickness
U.S.N.M. No. 116733a........	8.1?	?	9.3	8.6	2.9
Brachial valve,					
U.S.N.M. No. 116733f........	?	6.8	9.3	8.6	2.3

Types.—Holotype: U.S.N.M. No. 116733a; figured paratypes: U.S.N.M. Nos. 116733c, e, f; unfigured paratypes: U.S.N.M. Nos. 116733b, d.

Horizon and locality.—Signal Mountain formation (218 feet above the base) in Oklahoma, 500 feet west and 750 feet south of the northeast corner of sec. 28, T. 1 S., R. 1 W., Murray County.

Discussion.—This species is characterized by strongly convex valves, closely crowded costellae, and a thick pseudospondylium. It is quite unlike other known Upper Cambrian Finkelnburgias except *F. osceola* which is larger and differently shaped, and *F. newtonensis*

(Weller) which is much smaller, less convex, and differently ornamented.

Of Canadian species this one is most like *F. wemplei* but differs in greater convexity, particularly of the brachial valve, and in having slight auriculations on the brachial valve.

FINKELNBURGIA CRASSICOSTELLATA Cooper, new species

Plate 1C, figures 22-26

Shells of intermediate size for the genus, wider than long, subrectangular in outline and with the hinge narrower than the maximum width which is at the middle; cardinal extremities obtuse; sides rounded; anterior margin broadly rounded; surface strongly costellate, costellae of unequal size.

Pedicle valve gently convex in lateral profile and with the most curvature just anterior to the middle; anterior profile moderately and broadly convex, umbo broadly swollen; median region gently convex; anterior half somewhat swollen and curved toward the brachial valve; flanks moderately swollen and with short, steep lateral slopes. Pseudospondylium broad and poorly developed; median ridge low and thick.

Brachial valve much less deep than the pedicle valve, gently convex in lateral and anterior profiles; umbo and median region gently swollen; sides gently swollen and with long, gentle, lateral slopes; interior with broadly recumbent brachiophore plates, and strong adductor callosities.

Measurements in mm.

	Length	Brachial length	Mid-width	Hinge width	Thickness
Pedicle valve,					
U.S.N.M. No. 116726a........	8.5	?	11.0	8.8	2.5
Brachial valve,					
U.S.N.M. No. 116726c........	?	7.5	10.9	10.2	1.8

Types.—Holotype: U.S.N.M. No. 116726a; figured paratypes: U.S.N.M. Nos. 116726b, c.

Horizon and locality.—Kindblade formation in Oklahoma, in the center NE¼SW¼ sec. 29, T. 1 S., R. 1 W., Murray County.

Discussion.—This species is characterized by strong costellae, a shallow brachial valve having large adductor platforms extending to about the middle and a fairly deep pedicle valve with broad, weakly developed pseudospondylium. The species suggests a small *F. magna* but it attains only about half the size of that species and also differs in the strength of its costellae. The interior of both valves is not so extravagantly developed as that of *F. magna,* but the structures are of the same broad character.

FINKELNBURGIA DELICATULA Cooper, new species

Plate 2D, figures 16-21

Small for the genus, wider than long with the hinge less than or about equal to the midwidth; cardinal extremities slightly obtuse or approximating a right angle; sides nearly straight; anterior margin broadly rounded; surface finely and closely costellate, but with scattered strong costellae.

Pedicle valve moderately convex in lateral profile and with the maximum convexity in the posterior third; anterior profile strongly convex; umbonal and median regions swollen; flanks descending moderately steeply to the margins; anterior somewhat flattened; interior with well-defined pseudospondylium with thickened and elongated adductor track supported by a short stout median ridge.

Brachial valve not so deep as the pedicle valve and moderately convex in lateral profile, broadly and moderately convex in anterior profile. Umbo sulcate; sulcus narrow and shallow, defined from umbo to anterior margin; flanks swollen and with short, moderately steep lateral slopes. Interior with moderately well-developed adductor platforms.

Measurements in mm.

Pedicle valve,	Length	Brachial length	Mid-width	Hinge width	Thickness
U.S.N.M. No. 116734a.........	7.6	?	9.0	8.8	2.5
Brachial valves,					
U.S.N.M. No. 116734f.........	?	6.1	8.3	7.8	2.0
U.S.N.M. No. 116734h.........	?	5.9	8.4	7.3	1.7

Types.—Holotype: U.S.N.M. No. 116734a; figured paratypes: U.S.N.M. Nos. 116734f, g; unfigured paratypes: U.S.N.M. Nos. 116734b-e, h.

Horizon and locality.—Upper Cool Creek formation in Oklahoma, one mile southeast of the windmill, center of sec. 5, T. 2 S., R. 1 E., Murray County.

Discussion.—Small size, fine costellae, subrectangular outline, and subauriculate cardinal extremities characterize this species. It is suggestive of *F. bellatula* in outline but has a somewhat wider hinge with definite auriculations and somewhat finer ornamentation. The interiors of the two species show differences. The muscle platforms of the brachial valve of *F. delicatula* occupy more of the interior than those of *F. bellatula* and the pseudospondylium of the pedicle valve is stouter than that of *F. bellatula.*

FINKELNBURGIA EXTENSA Cooper, new species

Plate 2G, figures 39-51

Shell of about medium size for the genus, width of hinge equal to about twice the shell length; cardinal extremities mucronate; lateral margins concave just anterior to the cardinal extremity; anterior margin broadly rounded. Surface marked by crowded costellae of unequal size, the larger ones in the minority, but numbering three or four to a millimeter at the front margin.

Pedicle valve unevenly convex in lateral profile, with the maximum convexity just anterior to the umbo; anterior profile narrowly convex in the median region and with abrupt slopes steep on the flanks of the median area but gentle to the margins. Beak prominent and elevated; umbo narrow and convex; median region strongly swollen from umbo to anterior margin; interior with pseudospondylium having an extravagantly thickened adductor and median ridge; pallial trunks deeply entrenched.

Brachial valve slightly less deep than the pedicle valve and having a moderately convex lateral profile in which the maximum convexity is located just anterior to the umbo; anterior profile broadly and moderately convex. Sulcus narrow and shallow, originating on the umbo and extending to the anterior margin, widening only slightly in its passage anteriorly; flanks bounding sulcus fairly strongly swollen; lateral slopes short, moderately steep. Interior with deep sockets, short and blunt brachiophores and strong, thick brachiophore plates. Cardinal process thin and delicate. Adductor platforms not strongly thickened.

Measurements in mm.

	Length	Brachial length	Mid-width	Hinge width	Thickness
Pedicle valves,					
U.S.N.M. No. 116728b........	6.8	?	8.8	13.3	2.9
U.S.N.M. No. 116728g........	8.9	?	12.2	18.9 +	4.0
U.S.N.M. No. 116728h........	7.2	?	7.9	12.0	2.6
Brachial valves,					
U.S.N.M. No. 116728a........	?	6.3	8.1	11.0	2.1
U.S.N.M. No. 116728d........	?	6.5	9.1	12.7	2.2
U.S.N.M. No. 116728f........	?	5.9	8.7	13.4	1.9

Types.—Holotype: U.S.N.M. No. 116728b; figured paratypes: U.S.N.M. No. 116728a, d-g, j; unfigured paratypes: U.S.N.M. Nos. 116728c, h, i, k.

Horizon and locality.—Signal Mountain (90 feet above the base) in Oklahoma, SE¼SW¼NE¼ sec. 16, T. 1 S., R. 1 W., 1,200 feet west of the east quarter corner, Murray County; 70 feet above the base, 2,300 feet west and 1,700 feet north of the southeast corner of sec. 8, T. 1 S., R. 1 W., Murray County.

Discussion.—This species is unusual for the great extension of its cardinal extremities and the deep impression of the pallial channels on the inside of the valves. It is most like the type species of *Finkelnburgia, F. finkelnburgi* Walcott, in the great extension of the cardinal extremities but is more extreme in this respect than any figured specimens of that species. *Finkelnburgia extensa* differs from *F. finkelnburgi* also in having finer ornamentation.

FINKELNBURGIA OBESA Cloud

Plate 3F, figures 20-27

Finkelnburgia obesa Cloud, Bull. Mus. Comp. Zool., vol. 100, No. 5, p. 458, pl. 1, figs. 8-18, 1948.

Shell of intermediate size for the genus, wider than long, suboval in outline with the hinge narrower than the greatest width which is just anterior to the middle; cardinal extremities obtuse; sides rounded; anterior margin broadly rounded. Surface multicostellate.

Pedicle valve moderately convex in lateral profile but with the maximum convexity in the umbonal region. Anterior profile broadly convex; beak prominent; umbo somewhat narrowly swollen but the swelling not continued to the middle; median region and flanks gently swollen; anterior half somewhat depressed to form a poorly defined sulcus. Interior with prominent and well-developed pseudospondylium having an elevated adductor track and a moderately high median septum.

Brachial valve gently convex in lateral profile and not having as much depth as the pedicle valve; anterior profile broadly and gently convex. Umbonal, median and flank regions swollen; lateral slopes short and steep. Interior with brachiophore plates stout and well-defined; cardinal process a thin ridge; adductor platforms moderately developed.

Measurements in mm.

Pedicle valves,	Length	Brachial length	Mid-width	Hinge width	Thickness
U.S.N.M. No. 116745a........	9.5	?	11.4	6.9	2.8
U.S.N.M. No. 116745b........	9.3	?	10.6	8.6	2.7
Brachial valves,					
U.S.N.M. No. 116745c........	?	10.4	11.6	8.7	3.0
U.S.N.M. No. 116745d........	?	8.9	11.5	8.0	2.4
U.S.N.M. No. 116745e........	?	8.4	10.5	7.2	2.3

Types.—Figured hypotypes: U.S.N.M. Nos. 116745b-e; unfigured hypotype: U.S.N.M. No. 116745a.

Horizon and locality.—McKenzie Hill formation (35 feet below the top) in Oklahoma, 2,200 feet east and 2,500 feet north of the southwest corner of sec. 2, T. 2 S., R. 1 E., Murray County.

Discussion.—Comparison of the McKenzie Hill specimens with Cloud's types of *F. obesa* indicates the exterior form to be very close. Comparison of the ornamentation is not possible in detail because the specimens from Oklahoma and Texas are badly worn. Those of the Arbuckle species were undoubtedly considerably water-worn before silicification. Details of the interior of the Texas species are not well preserved, but those that can be seen show close resemblance except for the fact that the Oklahoma specimens are somewhat thicker.

FINKELNBURGIA SUBQUADRATA Cooper, new species

Plate 31, figures 40-45

Shell large for the genus; wider than long and with the hinge slightly wider than the midwidth; cardinal extremities slightly auriculate; sides gently rounded; anterior margin broadly rounded. Surface strongly costellate, costellae of unequal size.

Pedicle valve considerably deeper than the brachial valve, strongly convex in lateral profile and with the maximum convexity in the umbonal region and just anterior thereto; anterior profile moderately and broadly convex. Beak small, slightly protruberant. Umbo swollen; median region from umbo to anterior margin swollen; flanks swollen and with short steep slopes to the margins. Pseudospondylium broad and with a long tonguelike adductor track; median ridge short and thick. Pallial sinuses (vascula media) wide and strongly divergent.

Brachial valve moderately convex in lateral profile; broadly and moderately convex in anterior profile. Umbo marked by a short, shallow sulcus; umbo and median region swollen, the swelling reflected in the flanks; lateral slopes moderately short and moderately gentle. Interior with small notothyrial chamber bounded by short brachiophore plates. Adductor callosities modestly developed.

Measurements in mm.

Pedicle valve,	Length	Brachial length	Mid-width	Hinge width	Thickness
U.S.N.M. No. 116743a....	12.8	?	15.5	14.7 plus	4.0
Brachial valve,					
U.S.N.M. No. 116743b....	?	10.2	13.7	13.6	3.0

Types.—Holotype: U.S.N.M. No. 116743a; paratype: U.S.N.M. No. 116743b.

Horizon and locality.—Cool Creek formation in Oklahoma, 900 feet west and 1,450 feet north of the southeast corner of sec. 3, T. 2 S., R. 1 W., Murray County.

Discussion.—This species can be recognized by its large size, subquadrate outline, strong costellae, thick and elevated pseudospondylium, and the broad, divergent pallial marks in the pedicle valve. *Finkelnburgia subquadrata* most strongly resembles *F. virginica* but is somewhat larger, is more quadrate, and has more distant costellae. Inside the brachial valve the adductor platforms of *F. virginica* are scarcely developed but in the Arbuckle shell they are strong. Inside the brachial valve the deep and wide vascula media are a feature peculiar to the Oklahoma species.

Genus PLECTOTROPHIA Ulrich and Cooper, 1936

PLECTOTROPHIA LATICOSTA Cooper, new species

Plate 4E, figures 23-35

Shell of about usual size for the genus, wider than long, subrectangular in outline; sides gently oblique to gently rounded; hinge slightly wider or slightly less than the midwidth depending on age; cardinal extremities slightly obtuse or slightly auriculate; anterior commissure gently uniplicate; surface marked by distant, rounded, elevated costellae crossed by prominent concentric lines of growth.

Pedicle valve unevenly convex in lateral profile and with the maximum convexity between the umbo and the middle, the anterior half flattened. Anterior profile with the median region somewhat narrowly convex and with steep sides. Beak small, umbo narrowly convex; posteromedian region swollen and with steep slopes to the cardinal extremities. Sulcus originating just anterior to the umbo, deepening and widening near the middle. Anterior tongue short and bluntly rounded. Interior with long and narrow pseudospondylium tapering anteriorly to a sharp point; median septum only slightly developed. Pallial marks not deeply impressed.

Brachial valve gently convex in lateral profile and with the maximum depth located just anterior to the umbo; anterior profile broadly, fairly evenly and moderately convex. Beak small, umbo somewhat narrowly swollen; median region broadly and strongly swollen; posterior marked by a short, shallow depression just anterior to the umbo, which is followed by the fold; fold originating just posterior to the middle, widening anteriorly, low and broadly rounded throughout. Flanks bounding fold gently swollen and with long gentle slopes to the margins. Interior with short brachiophores supported by short convergent supporting plates.

Measurements in mm.

	Length	Brachial length	Mid-width	Hinge width	Thickness
Pedicle valve,					
U.S.N.M. No. 117951d........	8.5	?	10.9	11.3	2.2?
Brachial valve,					
U.S.N.M. No. 117951b........	?	8.1	12.7	11.4	3.7
U.S.N.M. No. 117951g........	?	7.6	11.5	10.2?	2.3

Types.—Holotype: U.S.N.M. No. 117951g; figured paratypes: U.S.N.M. Nos. 117951a-f; unfigured paratypes: U.S.N.M. Nos. 117951h-k.

Horizon and locality.—Fort Sill formation (150 feet above the base) in Oklahoma, 2,500 feet east and 2,200 feet north of the southwest corner of sec. 26, T. 2 S., R. 4 E., South Ranch, Johnston County.

Discussion.—This species is especially characterized by its strong costellae, the low and broad fold, and the short blunt tongue of the pedicle valve. When compared with *P. bridgei* the Oklahoma specimens have a much less-elevated and less-carinate fold, a shallower sulcus on the pedicle valve, and a much shorter, blunter tongue on the pedicle valve. Inside the pedicle valve the pseudospondylium of *P. bridgei* is more elevated, has subparallel sides and a narrowly rounded front, whereas the same structure in *P. laticosta* is long, slender, tapers to a point, and is low throughout its extent.

Genus **TETRALOBULA** Ulrich and Cooper, 1936

TETRALOBULA TEXANA Ulrich and Cooper

Plate 4A, figures 1-7

Tetralobula texana Ulrich and Cooper, Geol. Soc. Amer. Spec. Pap. 13, p. 209, pl. 43B, figs. 17-22, 1938.—Cloud, Bull. Mus. Comp. Zool., vol. 100, No. 5, p. 462, pl. 2, figs. 15-16, 21, 22, 1948.

A few well-preserved specimens of this species are illustrated to show the occurrence of this easily recognized genus in Oklahoma. The species is characterized by its low fold which is located at the anterior margin only. In the pedicle valve the sulcus is broad and shallow and the tongue broad and rounded. In young specimens little trace of the fold can be detected.

Measurements in mm.

	Length	Brachial length	Mid-width	Hinge width	Thickness
Pedicle valve, U.S.N.M. No. 117950e	8.7	?	11.0	8.5	3.0
Brachial valve, U.S.N.M. No. 117950f	?	7.4	9.8	7.3	2.2

Figured specimens.—U.S.N.M. Nos. 117950a-f.

Horizon and locality.—McKenzie Hill formation (about 250 feet above the base) in Oklahoma, 2,100 feet west and 1,500 feet north of the southeast corner of sec. 36, T. 1 S., R. 1 E., Murray County.

Genus PALAEOSTROPHIA Ulrich and Cooper, 1936

PALAEOSTROPHIA cf. P. ELAX (Clark)

Plate 3A, figures 1, 2

Syntrophia elax Clark, Bull. Amer. Paleontol., vol. 10, No. 41, p. 15, pl. 3, fig. 1, 1924.

Palaeostrophia elax (Clark) Ulrich and Cooper, Geol. Soc. Amer. Spec. Pap. 13, p. 195, pl. 41A, figs. 1-11, 15, 1938.

Shell of about usual size for the genus, represented by three fragmentary specimens. Pedicle valve with wide and shallow sulcus occupying most of anterior region. Brachial valve with a broadly rounded fold. Interior with characteristic erect brachiophore supporting plates and elongate adductor tracks.

Figured specimens.—U.S.N.M. Nos. 116751a, b.

Horizon and locality.—Signal Mountain formation (63 feet below the top) in Oklahoma, 1,500 feet west and 1,900 feet north of the southeast corner of sec. 6, T. 2 S., R. 2 E., Murray County.

Genus GLYPTOTROPHIA Ulrich and Cooper, 1936

GLYPTOTROPHIA ROTUNDA Cooper, new species

Plate 2C, figures 14, 15

Small, transversely but broadly elliptical in outline; sides rounded; anterior commissure strongly uniplicate; surface marked by fine costellae cancellated by strong concentric lamellae.

Pedicle valve gently convex in lateral profile and strongly but broadly convex in anterior profile. Beak projecting; umbo narrowly rounded; median region swollen. Sulcus originating just posterior to the middle, deepening anteriorly but shallow throughout its length. Tongue short and narrowly rounded. Flanks swollen near the median region and with long steep slopes to the margins. Interior with broad, short sessile spondylium.

Brachial valve gently convex in lateral profile; broadly convex in anterior profile with the median region somewhat carinated and with long lateral slopes; umbo narrow and protuberant; median region inflated gently; fold originating at about the middle, low and subcarinate; flanks gently swollen. Interior with short, shallow brachiophore plates.

Measurements in mm.

	Length	Brachial length	Mid-width	Hinge width	Thickness
Pedicle valve, U.S.N.M. No. 116740b.........	6.3	?	8.1	6.8	2.2
Brachial valve, U.S.N.M. No. 116740d.........	?	5.4	7.8	6.0	2.2

Types.—Holotype: U.S.N.M. No. 116740b; figured paratype: U.S.N.M. No. 116740d; unfigured paratypes: U.S.N.M. Nos. 116749a, c, e.

Horizon and locality.—Signal Mountain formation (2-3½ feet above base of Butterly dolomite) in Oklahoma, SW¼SW¼SW¼ sec. 9, T. 2 S., R. 2 E., Murray County.

Discussion.—This species is ornamented like *G. imbricata* from the Mons formation near Lake Louise, Alberta, but differs in its less-transverse outline, less-deep pedicle sulcus, and more narrowly rounded fold on the brachial valve.

IMBRICATIA Cooper, new genus

Shells usually transverse, syntrophoid in profile and outline; anterior commissure moderately uniplicate; surface marked by strong concentric imbrications and fine costellae.

Interior of pedicle valve with small teeth and usually with a thick spondylium simplex, sessile at the rear but elevated anteriorly and supported by a short thick median ridge. Vascula media usually strongly developed.

Brachial valve with short, stout brachiophores and small sockets defined by small fulcral plates. Brachiophore supporting plates usually erect to moderately oblique, meeting the floor of the valve; brachiophore plates usually with thick ridges near the base of the plate which give them a saucerlike shape; no cardinal process. Adductor scars as in *Tetralobula* but usually not with strong callosities.

Genotype.—*Imbricatia lamellata* Cooper, new species.

Discussion.—This genus is essentially like *Tetralobula* but differs in having a more elaborate ornamentation which consists of fine radial costellae interrupted by strong concentric lamellae. Internally the two genera are similar but differ in details of the brachial interior. The brachiophore supporting plates are alike and were evidently the seat of attachment for diductor muscles. This is clearly shown by the presence of strong curving ridges near their base which gives them a saucerlike appearance. The adductor callosities of *Imbricatia* are not so strongly developed as those of *Tetralobula.*

Imbricatia is ornamented like *Stichotrophia* but differs from that genus in having brachiophore plates convergent toward the floor of the valve rather than strongly divergent. In *Stichotrophia,* furthermore, the brachiophore plates have adductor ridges suggestive of *Imbricatia* but they appear high above the floor so that the plate seems to consist of two elements. *Calliglypha* Cloud has imbricate ornamentation but in that genus the imbrications and radial lines produce small spines. Cloud's genus is readily differentiated internally because it is like *Diaphelasma.*

Other species formerly placed in *Tetralobula* can be assigned to *Imbricatia* as follows: *Imbricatia coloradoensis* (Ulrich and Cooper) from the Manitou limestone of Colorado; *I. imbricata* (Ulrich and Cooper) from the Hastings Creek formation near Philipsburg, Quebec; and probably *Tetralobula dorsosulcata* (Ulrich and Cooper) also from the Manitou limestone of Colorado.

IMBRICATIA LAMELLATA Cooper, new species

Plate 3E, figures 14-19; plate 4D, figures 17-22

Shell of about medium size for the genus, wider than long, roundly elliptical in outline; hinge wide; posterolateral extremities narrowly rounded; sides rounded; anterior margin broadly rounded; anterior commissure gently uniplicate; surface with strong concentric plaits which are finely costellated; costellae about eight in one millimeter at the front margin.

Pedicle valve moderately convex in lateral profile with the maximum convexity in the anterior half; anterior profile broadly and moderately convex, umbo and median region swollen; sulcus shallow, originating at about the middle; tongue short and narrowly rounded. Interior with spondylium sessile at rear but strongly elevated anteriorly; old shells with pallial marks strongly developed.

Brachial valve moderately convex in lateral profile, broadly and moderately convex in anterior profile. Fold variable, defined in the front third only and often appearing as an emargination in the anterior margin. Median region swollen; flanks moderately convex and with moderate slopes.

Measurements in mm.

	Length	Brachial length	Mid-width	Hinge width	Thickness
Pedicle valves,					
U.S.N.M. No. 116752b........	8.7	?	10.4	9.0	2.4
U.S.N.M. No. 116752c........	7.2	?	8.6	7.6	2.2
Brachial valves,					
U.S.N.M. No. 116752e........	?	7.6	10.6	8.4	2.8
U.S.N.M. No. 116752g........	?	8.2	10.9	7.5	3.0

Types.—Holotype: U.S.N.M. No. 116752g; figured paratypes: U.S.N.M. Nos. 116752a, b, 117949a-c; unfigured paratypes: U.S.N.M. Nos. 116752c-f, h.

Horizon and locality.—Middle of Cool Creek formation in Oklahoma, 100 feet north and 50 feet east of southwest corner of sec. 34, T. 1 S., R. 1 W., Murray County.

Discussion.—This species suggests *I. coloradoensis* and *I. imbricata* but differs from both of them. From the former it may be distinguished by its more transverse outline and less sharply folded brachial valve. It is closer to *I. imbricata* of Quebec in outline but is also somewhat more transverse than the species and has a much less conspicuous and shorter sulcus in the pedicle valve and a usually more modest development of the brachial fold.

Genus SYNTROPHINA Ulrich, 1928

SYNTROPHINA CAMPBELLI (Walcott)

Plate 3C, figures 4-8

Syntrophia campbelli Walcott, Smithsonian Misc. Coll., vol. 53, pp. 107, 108, pl. 10, figs. 9, 9a-c, 1908; U. S. Geol. Surv. Mon. 51, p. 801, fig. 73, 1912.

Syntrophina campbelli (Walcott) Ulrich and Cooper, Geol. Soc. Amer. Spec. Pap. 13, p. 218, pl. 46E, figs. 10-34, 1938.—Cloud, Bull. Mus. Comp. Zool., vol. 100, No. 5, p. 462, pl. 2, figs. 10-13, 17, 1948.

Shell small, roundly elliptical in outline, and with the maximum width at about the middle; sides strongly rounded; anterior commissure gently rounded, strongly uniplicate. Surface marked by concentric lines of growth.

Pedicle valve moderately convex in lateral profile and broadly and moderately convex in anterior profile. Umbonal and median region swollen; sulcus originating at about the middle, broad and shallow. Tongue moderately long and narrowly rounded. Flanks bounding sulcus gently convex and with long steep slopes to the margins.

Spondylium small, short, and supported by a short median septum. Teeth small, long, narrow.

Brachial valve about equal in depth to the pedicle valve, gently convex in lateral profile and most convex in the umbonal region; anterior profile broadly and moderately convex. Umbonal region swollen; fold originating at about the middle, low and broadly rounded; flanks bounding fold gently swollen and with steep slopes to the margins. Interior with broad and short brachiophores supported by convergent plates that meet the floor of the valve in close proximity. Sockets defined by small socket plates. Adductor scars not impressed.

Measurements in mm.

	Length	Brachial length	Mid-width	Hinge width	Thickness
Pedicle valve,					
U.S.N.M. No. 116749a........	7.1	?	10.4	5.5	2.5
Brachial valve,					
U.S.N.M. No. 116749g........	?	7.5	8.8	4.4	3.0

Types.—Figured hypotypes: U.S.N.M. Nos. 116749d-f; unfigured paratypes: U.S.N.M. Nos. 116749a-c, g-i.

Horizon and locality.—McKenzie Hill formation (360 feet above the base) in Oklahoma, 950 feet west and 2,050 feet north of the southwest corner of sec. 26, T. 6 N., R. 14 W., Kindblade Ranch, Wichita Mountains, Kiowa County.

Discussion.—These specimens are unusual in being preserved as silicified shells. Hitherto this species was known only from chert impressions. The specimens herein illustrated conform to the details of the species except for the small transverse plate in the apex of the brachial valve. This is lacking from the Oklahoma specimens.

Genus **CLARKELLA** Walcott, 1908

CLARKELLA species

Plate 3B, figure 3

The specimens of this interesting genus reported for the first time in Oklahoma are unfortunately very fragmentary. Part of a pedicle valve indicates a species with a deep and wide median sulcus having a prominent, impressed line running down the middle; the tongue is long and pointed. The spondylium is strongly elevated on a high median septum. The brachial valve had a prominent fold but its prominence did not arise until the anterior part of the shell. The posterior half is well rounded and without a fold. The interior shows the adductor callosities elevated on septa as usual for the genus, and the diductor ridges just below the notothyrial edge are well developed.

Figured specimen.—U.S.N.M. No. 116750a.

Horizon and locality.—Upper Cool Creek formation (300 feet below the top) in Oklahoma, at the south end of Falls Creek anticline, 2,200 feet north and 2,200 feet west of the southeast corner of sec. 21, T. 2 S., R. 2 E., Carter County.

Genus DIPARELASMA Ulrich and Cooper, 1936

DIPARELASMA COSTELLATUM Cooper, new species

Plate 3D, figures 9-13

Shell small, subcircular in outline with sides and anterior margins rounded; hinge narrow and cardinal extremities obtuse; surface costellate, three or four costellae to the millimeter at the front margin, the stronger ones concentrated at the sulcus.

Pedicle valve moderately convex in lateral profile and with the maximum convexity just anterior to the umbo; anterior profile strongly convex and with the median region somewhat narrowly rounded. Umbo narrowly swollen; median region swollen; anterior regions somewhat flattened; flanks sloping moderately steeply to the sides. Delthyrial cavity wide, bounded by strong dental plates.

Brachial valve having less depth than the pedicle valve and gentle convexity in lateral profile; anterior profile broadly and gently convex; umbo swollen and median and anterior regions moderately inflated; sulcus originating on the umbo, narrow and shallow, extending to the anterior margin. Flanks gently swollen; lateral slopes gentle.

Measurements in mm.

	Length	Brachial length	Mid-width	Hinge width	Thickness
Pedicle valve, U.S.N.M No. 116754a.........	6.3	?	7.6	5.0	2.3
Brachial valve, U.S.N.M. No. 116754b.........	?	6.0	7.6	4.9	1.2

Types.—Holotype: U.S.N.M. No. 116754a; figured paratypes: U.S.N.M. Nos. 116754b, c.

Horizon and locality.—West Spring Creek formation (419 feet below the top) in Oklahoma, 1,400 feet east and 1,700 feet north of the southwest corner of sec. 6, T. 3 S., R. 4 E., Johnston County.

Discussion.—This species is characterized by small size, moderate convexity, and fairly strong costellae. The species is most like *D.*

typicum of described species but is smaller, less convex, and more strongly costellate particularly in the median region.

DIPARELASMA FASCICULATUM Cooper, new species

Plate 4B, figures 8-12

Shell of about usual size for the genus, subcircular in outline; sides and anterior margin rounded; hinge narrower than the greatest shell width which is at the middle. Anterior commissure slightly sulcate. Surface costellate, fasciculate in bundles of two to four costellae.

Pedicle valve moderately convex in lateral profile and with the maximum convexity just anterior to the umbo, the remainder of the valve more gently convex; anterior profile narrowly convex in the median region and with steep lateral slopes. Umbonal and median regions swollen, the swelling extending anteriorly to the front margin to form a faint fold. Interior with dental plates well developed.

Brachial valve gently convex in lateral profile and with the maximum convexity just anterior to the umbo; anterior profile gently and broadly convex but with the median region slightly depressed. Umbo moderately swollen; sulcus originating just anterior to the umbo, shallow, widening anteriorly but remaining shallow throughout, and occupying about half the width at the front margin. Tongue short, broadly rounded; flanks bounding sulcus slightly swollen and with gentle slopes to the margins. Interior with short and delicate brachiophore plates and short, low median ridge.

Measurements in mm.

	Length	Brachial length	Mid-width	Hinge width	Thickness
Pedicle valve,					
U.S.N.M. No. 117948a.........	6.7	?	6.9	4.9	2.3
Brachial valve,					
U.S.N.M. No. 117948b.........	?	6.8	8.2	5.7	1.6

Types.—Holotype: U.S.N.M. No. 117948b; paratype: U.S.N.M. No. 117948a.

Horizon and locality.—Upper Kindblade formation (about 250 feet below the top) in Oklahoma, 700 feet east and 1,200 feet south of the northwest corner of sec. 5, T. 3 S., R. 4 E., Johnston County.

Discussion.—This species is characterized by its fasciculate costellae and the short brachiophore plates. It differs from *D. costellatum* in having the finer costellae concentrated in the sulcus and in having much more delicate cardinalia. It differs from all other described species in its fasciculate ornamentation.

POLYTOECHIA SUBCIRCULARIS Cooper, new species

Plate 4C, figures 13-16

Shell wider than long, circular in outline and with the hinge narrower than the greatest shell width which is at the middle; sides gently rounded; anterior commissure rectimarginate; surface multicostellate, seven costellae in one millimeter at the anterior margin.

Pedicle valve fairly evenly convex in lateral profile and with the maximum convexity at about the middle; anterior profile strongly convex; beak small, narrowly swollen; umbo somewhat narrowly swollen; median region inflated and most strongly convex near the center; sides steeply sloping to the margins; anterior slope long and less steep than the lateral slopes. Interarea long, curved, apsacline. Interior with strong dental plates, erect and subparallel; muscular area slightly elevated above the floor of the valve; diductor scars elongate; adductor region marked by a long narrow groove bounded by two plates convergent with the median septum and extending anterior to the delthyrial cavity. Dental plates extended as slightly divergent ridges anteriorly to the anterior end of the median septum. Pallial trunks not clearly defined anterior to the ends of the extensions of the dental plates.

Brachial valve with evenly and moderately convex lateral profile; anterior profile broadly and moderately convex; valve broadly elliptical in outline; umbo and median regions strongly swollen; lateral slopes steep and moderately long; anterior slope long, gently rounded and less steep than the lateral slopes. Interior with short convergent brachiophore plates, small cardinal process, short median ridge but lightly impressed pallial and muscular marks.

Measurements in mm.

Pedicle valves,	Length	Brachial length	Mid-width	Hinge width	Thickness
U.S.N.M. No. 117952a........	8.2	?	9.2	6.7	3.2
U.S.N.M. No. 117952c........	?	7.7	10.9	7.8	2.4

Types.—Holotype: U.S.N.M. No. 117952a; figured paratypes: U.S.N.M. Nos. 117952b, c; unfigured paratypes: U.S.N.M. Nos. 117952d-f.

Horizon and locality.—West Spring Creek formation (598 feet above the base) in Oklahoma, on Joins Ranch, 750 feet west and 1,550 feet south of the northeast corner of sec. 9, T. 2 S., R. 1 W., Murray County.

Discussion.—This species is characterized by its nearly circular pedicle valve, somewhat narrowly elliptical brachial valve, very fine costellae, and the low triseptate spondylium in the pedicle valve. This species suggests *P. alabamensis* and *P. fillistriata* in its fine costellae but differs from the former in being smaller, having a longer interarea which is less curved and a much lower spondylium. The Oklahoma species differs from *P. fillistriata* in having somewhat finer ornamentation and an extremely low spondylium, that of the Newala shell being strongly elevated.

SELECTED REFERENCES

Cloud, P. E.
1948. Brachiopods from the Lower Ordovician of Texas. Bull. Mus. Comp. Zool., vol. 100, No. 5, pp. 451-475, pls. 1-4.

Cooper, G. A.
1948. A new genus of Brachiopoda from the Longview limestone of Virginia. Bull. Mus. Comp. Zool., No. 6, pp. 473-474, pl. 4.

Decker, C. E.
1939. Two lower Paleozoic groups, Arbuckle and Wichita Mountains, Oklahoma. Bull. Geol. Soc. Amer., vol. 50, pp. 1311-1322.

Ulrich, E. O., and Cooper, G. A.
1938. Ozarkian and Canadian Brachiopoda. Geol. Soc. Amer. Spec. Pap. 13, pp. i-viii, 1-323, pls. 1-58.

Walcott, C. D.
1912. Cambrian Brachiopoda. U. S. Geol. Surv. Mon. 51, pp. 725-810, pls. 85-104.

EXPLANATION OF PLATES

Plate 1

Page

A. *Billingsella rectangulata* Cooper, new species........................ 3

1, Brachial view of a complete specimen showing pseudodeltidium, × 1; paratype, U.S.N.M. No. 116722b. 2-6, 8, Posterior tilted, pedicle, posterior, anterior, side, and brachial views, respectively, of the holotype, U.S.N.M. No. 116722a, × 2. 7, The holotype, × 1. 9, 10, Exterior and interior of the brachial valve, × 2, showing brachiophores; paratype, U.S.N.M. No. 116722k. 11, Interior of the pedicle valve showing teeth, vascula media, and thickening anterior to muscle scar, × 2; paratype, U.S.N.M. No. 116722e. 12, Another brachial interior showing notothyrial platform and median ridge, × 2; paratype, U.S.N.M. No. 116722i. 13, 14, Pedicle valve showing teeth and pallial marks, and same tilted to show callus supporting teeth, × 2; paratype, U.S.N.M. No. 116722d. 15, Another pedicle interior showing teeth; paratype, U.S.N.M. No. 116722h.

Signal Mountain formation (1-foot bed of limestone 100 feet above base), 1,700 feet east and 1,300 feet north of southwest corner of sec. 21, T. 1 S., R. 1 W., Murray County, Okla.

B. *Cymbithyris hami* Cooper, new species.............................. 5

16, Imperfect specimen showing both valves in contact and with missing parts restored, × 2; holotype, U.S.N.M. No. 116724d. 17, Exterior of a nearly complete pedicle valve, × 2; paratype, U.S.N.M. No. 116724a. 18, Exterior of another pedicle valve showing form, × 2; paratype, U.S.N.M. No. 116724b. 19, Exterior of a third pedicle valve, × 1; paratype, U.S.N.M. No. 116724e. 20, Interior of the brachial valve showing reduced brachiophores, × 2; paratype, U.S.N.M. No. 116724f. 21, Interior of the pedicle valve showing teeth and pseudodeltidium, × 2; paratype, U.S.N.M. No. 116724c.

Signal Mountain formation (limestone 1 foot thick 126 feet above base), 1,700 feet west and 600 feet south of the northeast corner of sec. 28, T. 1 S., R. 1 W., Murray County, Okla.

C. *Finkelnburgia crassicostellata* Cooper, new species.................... 13

22, Exterior of the pedicle valve showing costellae, × 1; holotype, U.S.N.M. No. 116726a. 23, Same, × 2, showing coarse and fine costellae. 24, Interior of the pedicle valve, × 2, showing broad pseudospondylium; paratype, U.S.N.M. No. 116726b. 25, 26, Exterior and interior, respectively, of the brachial valve showing ornamentation and adductor callosities, × 2; paratype, U.S.N.M. No. 116726c.

Page

Kindblade formation, in center NE¼SW¼ sec. 29, T. 1 S., R. 1 W., Murray County, Okla.

D. *Mesonomia magna* Cooper, new species.............................. 6

27, Exterior of the pedicle valve showing the ornamentation, × 1; holotype, U.S.N.M. No. 116694a. 28, 29, Exterior and interior, respectively, of the holotype showing details of the ornamentation, the teeth, and muscle region, × 2. 30, Brachial interior, × 2, showing cardinal process; paratype, U.S.N.M. No. 116694c. 31, Exterior of a nearly perfect pedicle valve, × 1; paratype, U.S.N.M. No. 116694b. 32, 33, Exterior and interior, respectively, of the preceding, × 2, showing ornamentation and brachiophores and their supporting plates. 34, Interior of a second pedicle valve showing vascula media, × 2; paratype, U.S.N.M. No. 116694d.

Fort Sill formation (179 feet above the base), 1,000 feet south of the north quarter corner of sec. 29, T. 1 S., R. 1 E., Murray County, Okla.

PLATE 2

A. *Fasciculina fasciculata* Cooper, new genus and species.................. 8

1, 2, Exterior and interior of the pedicle valve showing fasciculate costellae and cardinalia, × 2; holotype, U.S.N.M. No. 116738e. 3, Exterior of the pedicle valve, × 2, showing median fascicles; paratype, U.S.N.M. No. 116738b. 4, Interior of another pedicle valve showing pseudospondylium, × 2; paratype, U.S.N.M. No. 116738c. 5, 6, Same views as in figures 1 and 3 showing brachial and pedicle exterior, × 1. 7, Interior of a brachial valve showing cardinalia; paratype, U.S.N.M. No. 116738d.

Signal Mountain formation (90 feet above the base), SE¼SW¼NE¼ sec. 16, T. 1 S., R. 1 W., 1,200 feet west of east quarter corner, Murray County, Okla.

B. *Apheoorthis platys* Cooper, new species.............................. 2

8, 9, Exterior of the pedicle valve, × 1 and × 2, respectively, showing the ornamentation; holotype, U.S.N.M. No. 116736a. 10, Interior of the holotype showing pseudospondylium and vascula media, × 2. 11, 12, Exterior of the brachial valve, × 1 and × 2; paratype, U.S.N.M. No. 116736b. 13, Interior of the same brachial valve as the preceding showing the orthoid cardinalia, × 2.

Signal Mountain formation (50 feet below the top), 2,100 feet north and 100 feet west of the southeast corner of sec. 26, T. 1 S., R. 1 W., Murray County, Okla.

C. *Glyptotrophia rotunda* Cooper, new species 20

14, Exterior of the brachial valve showing fold and ornamentation, × 2; paratype, U.S.N.M. No. 116740d. 15, Exterior of the pedicle valve showing short and shallow sulcus, × 2; holotype, U.S.N.M. No. 116740b.

Page

Signal Mountain formation (2-3½ feet above base of Butterly dolomite), SW¼SW¼SW¼ sec. 9, T. 2 S., R. 2 E., Murray County, Okla.

D. *Finkelnburgia delicatula* Cooper, new species........................ 14

16, Exterior of the brachial valve, × 1; paratype, U.S.N.M. No. 116734f. 17, 18, Interior and exterior, respectively, of the same specimen showing details of the adductor callosities, the cardinalia, and the ornamentation, × 2. 19, Interior of another brachial valve, × 2, showing adductor callosities occuping center of valve; paratype, U.S.N.M. No. 116734g. 20, 21, Views of the exterior of the pedicle valve, × 1 and × 2, respectively; holotype, U.S.N.M. No. 116734a.

Upper Cool Creek formation, 1 mile southeast of the windmill, center of sec. 5, T. 2 S., R. 1 E., Murray County, Okla.

E. *Finkelnburgia biconvexa* Cooper, new species........................ 12

22, 23, Views of the exterior of the pedicle valve, × 1 and × 2, respectively, showing details of the ornamentation; holotype, U.S.N.M. No. 116733a. 24, Interior of the holotype showing the low pseudospondylium, × 2. 25, Incomplete pedicle valve showing pseudospondylium, × 2; paratype, U.S.N.M. No. 116733c. 26, Interior of an imperfect brachial valve showing cardinalia, × 2; paratype, U.S.N.M. No. 116733e. 27, 28, Interior and exterior of a brachial valve, × 2, showing cardinalia and details of the ornamentation; paratype, U.S.N.M. No. 116733f.

Signal Mountain formation (218 feet above the base), 500 feet west and 750 feet south of the northeast corner of sec. 28, T. 1 S., R. 1 W., Murray County, Okla.

F. *Finkelnburgia auriculata* Cooper, new species........................ 10

29-33, Brachial, anterior, posterior, side, and pedicle views, respectively, of the holotype, × 2; U.S.N.M. No. 116731a. 34, 38, Exterior and interior views of a pedicle valve, × 2, showing low pseudospondylium; paratype, U.S.N.M. No. 116731e. 35, Interior view of another pedicle valve showing auriculation of ears, × 2; paratype, U.S.N.M. No. 116731f. 36, 37, Interior views of two brachial valves, × 2, showing cardinalia and adductor callosities; paratypes, U.S.N.M. Nos. 116731d, c.

Signal Mountain formation (6-inch bed of limestone 150 feet above the base), 300 feet west and 1,150 feet south of the northeast corner of sec. 28, T. 1 S., R. 1 W., Murray County, Okla.

G. *Finkelnburgia extensa* Cooper, new species........................ 15

39, 40, Interior view of the same pedicle valve tilted and in normal view to show the teeth and pseudospondylium, × 2; holotype, U.S.N.M. No. 116728b. 41, 42, Interior view of a brachial valve, tilted and in normal view to show cardinalia, × 2; paratype, U.S.N.M. No. 116728a. 43, Interior

Page

of a pedicle valve showing deep pallial channels, × 2; paratype, U.S.N.M. No. 116728e. 44, Interior of a brachial valve having long auriculations and showing sockets and brachiophores, × 2; paratype, U.S.N.M. No. 116728f. 45, 46, Exterior and interior of pedicle valve showing large thick teeth, pseudospondylium, vascula media, and auriculations, × 2; paratype, U.S.N.M. No. 116728j. 47, Exterior of an exceptionally large and extended pedicle valve, × 1; paratype, U.S.N.M. No. 116728g. 48, 49, Same as preceding, × 2, to show details of ornamentation and some of the pallial marks. 50, 51, Views of the exterior of a brachial valve, × 1 and × 2, respectively, showing shallow sulcus; paratype, U.S.N.M. No. 116728d.

Signal Mountain formation (90 feet above the base), SE¼SW¼NE¼ sec. 16, T. 1 S., R. 1 W., 1,200 feet west of the east quarter corner, Murray County, Okla.

PLATE 3

A. *Palaeostrophia* cf. *P. elax* (Clark) 20

1, Exterior of an imperfect pedicle valve, × 1; figured specimen, U.S.N.M. No. 116751a. 2, Interior of the brachial valve showing the cardinalia, × 2; figured specimen, U.S.N.M. No. 116751b.

Signal Mountain formation (63 feet below the top), 1,500 feet west and 1,900 feet north of the southeast corner of sec. 6, T. 2 S., R. 2 E., Murray County, Okla.

B. *Clarkella* species 24

3, Interior of an imperfect brachial valve showing cardinalia, × 2; figured specimen, U.S.N.M. No. 116750a.

Upper Cool Creek formation (300 feet below the top), south end of Falls Creek anticline, 2,200 feet north and 2,200 feet west of the southeast corner of sec. 21, T. 2 S., R. 2 E., Carter County, Okla.

C. *Syntrophina campbelli* (Walcott) 23

4, Interior view of a brachial valve tilted to show the cardinalia, × 2; hypotype, U.S.N.M. No. 116749f. 5, Exterior view of preceding, × 2. 6, Interior view of a pedicle valve showing pseudospondylium and vascula media, × 2; hypotype, U.S.N.M. No. 116749e. 7, 8, Interior and exterior views of another pedicle valve showing vascula media and exterior sulcus; hypotype, U.S.N.M. No. 116749d.

McKenzie Hill formation (360 feet above the base), 950 feet west and 2,050 feet north of the southwest corner of sec. 26, T. 6 N., R. 14 W., Kindblade Ranch, Wichita Mountains, Kiowa County, Okla.

D. *Diparelasma costellatum* Cooper, new species 25

9, 10, Exterior views of the pedicle and brachial valves, respectively, × 1; holotype, U.S.N.M. No. 116754a, and paratype, U.S.N.M. No. 116754b. 11, 12, Exterior views of

Page

the same two specimens, × 2, showing details of the ornamentation. 13, Interior view of a brachial valve showing the cardinalia, × 2; paratype, U.S.N.M. No. 116754c.

West Spring Creek formation (419 feet below the top), 1,400 feet east and 1,700 feet north of the southwest corner of sec. 6, T. 3 S., R. 4 E., Johnston County, Okla.

E. *Imbricatia lamellata* Cooper, new genus and species.................. 22

14, 15, Exterior views of the pedicle and brachial valves, × 1; paratype, U.S.N.M. No. 116752b, and holotype, U.S.N.M. No. 116752g. 16, Exterior view of the preceding pedicle valve, × 2, showing the ornamentation. 17, Interior view of an old pedicle valve showing the pseudospondylium, vascula media, and other pallial marks, × 2; paratype, U.S.N.M. No. 116752a. 18, 19, Exterior and interior of the holotype, × 2, showing details of the ornamentation and the low adductor callosities.

Middle of the Cool Creek formation, 100 feet north and 50 feet east of the southwest corner of sec. 34, T. 1 S., R. 1 W., Murray County, Okla.

F. *Finkelnburgia obesa* Cloud.. 16

20, 21, Exterior views of the pedicle and brachial valves, respectively, × 1; hypotypes U.S.N.M. Nos. 116745b, d. 22, 23, Interior and exterior views of the same hypotype showing the pseudospondylium and vascula media, × 2. 24, 25, Interior and exterior views, respectively, of the brachial valve showing cardinalia and adductor callosities, × 2; hypotype, U.S.N.M. No. 116745d. 26, 27, Interior views of two brachial valves showing cardinalia, adductor callosities, and pallial markings; hypotypes, U.S.N.M. Nos. 116745e, c.

McKenzie Hill formation (35 feet below the top), 2,200 feet east and 2,500 feet north of the southwest corner of sec. 2, T. 2 S., R. 1 E., Murray County, Okla.

G. *Finkelnburgia* cf. *F. bellatula* Ulrich and Cooper..................... 11

28, 29, Brachial and pedicle exteriors, respectively, × 1; hypotypes, U.S.N.M. Nos. 116747b, a. 30, Interior of the preceding brachial valve showing the short adductor field and cardinalia, × 2. 31, 32, The preceding pedicle valve in interior and exterior views to show pseudospondylium and details of the ornamentation, × 2.

McKenzie Hill formation (10 feet below the top), 2,200 feet north and 1,250 feet west of the southeast corner of sec. 7, T. 1 S., R. 1 E., Murray County, Okla.

H. *Finkelnburgia arbucklensis* Cooper, new species...................... 9

33, 34, Views of a pedicle valve, × 1 and × 2, respectively, showing the ornamentation; holotype, U.S.N.M. No. 116741b. 35, Exterior of a brachial valve, × 1; paratype, U.S.N.M. No. 116741d. 36, 37, Exterior and interior views of the same brachial valve as the preceding, × 2, showing

Page

cardinalia, adductor field, and pallial markings. 38, Interior view of a pedicle valve showing the stout and low pseudospondylium and the deep vascula media, × 2; paratype, U.S.N.M. No. 116741a. 39, Interior view of a brachial valve, × 2, showing adductor field and cardinalia; paratype, U.S.N.M. No. 116741c.

McKenzie Hill formation (237 feet above the base), 1,500 feet east and 2,000 feet south of the northwest corner of sec. 28, T. 1 S., R. 1 W., Murray County, Okla.

I. *Finkelnburgia subquadrata* Cooper, new species........................ 17

40, Exterior of a pedicle valve, × 1; holotype, U.S.N.M. No. 116743a. 41, 42, Interior and exterior views of the holotype, × 2, showing short, thick pseudospondylium and deep, widely divergent vascula media. 43, Exterior of a brachial valve, × 1; paratype, U.S.N.M., No. 116743b. 44, 45, Exterior and interior of the same brachial valve as the preceding showing cardinalia and adductor callosities.

Cool Creek formation, 900 feet west and 1,450 feet north of the southeast corner of sec. 3, T. 2 S., R. 1 W., Murray County, Okla.

PLATE 4

A. *Tetralobula texana* Ulrich and Cooper.............................. 19

1, 2, Pedicle and brachial views, respectively, × 1, of adult specimens; figured specimens, U.S.N.M. Nos. 117950e, f. 3, Exterior of the pedicle valve showing the fine costellae, × 2; figured specimen, U.S.N.M. No. 117950a. 4, Exterior of the brachial valve, × 2; figured specimen, U.S.N.M. No. 117950f. 5, Exterior of a young brachial valve, × 3, showing ornamentation; figured specimen, U.S.N.M. No. 117950b. 6, Interior of the brachial valve showing the adductor callosities, × 3; figured specimen, U.S.N.M. No. 117950d. 7, Interior of the pedicle valve, × 3, showing the strong pallial trunks and the spondylium; figured specimen, U.S.N.M. No. 117950c.

McKenzie Hill formation (about 250 feet above the base), 2,100 feet west and 1,500 feet north of the southeast corner of sec. 36, T. 1 S., R. 1 E., Murray County, Okla.

B. *Diparelasma fasciculatum* Cooper, new species........................ 26

8, 9, Exterior views of the pedicle and brachial valves, respectively, × 1; paratype, U.S.N.M. No. 117948a, and holotype, U.S.N.M. No. 117948b. 10, 12, Same views of same specimens, × 2. 11, Interior of the preceding brachial valve, × 2, showing short brachiophore.

Upper Kindblade formation (250 feet below the top), 700 feet east and 1,200 feet south of the northwest corner of sec. 5, T. 3 S., R. 4 E., Johnston County, Okla.

Page

C. *Polytoechia subcircularis* Cooper, new species........................ 27

13, Exterior of the brachial valve, × 3, showing the fine costellae; paratype, U.S.N.M. No. 117952c. 14, Interior of the brachial valve showing the convergent brachiophore plates like those of *Tritoechia,* × 3; paratype, U.S.N.M. No. 117952b. 15, 16, Normal view and view of the valve tilted, respectively, to show the spondylium supported by the dental plates and a median septum, × 3; holotype, U.S.N.M. No. 117952a.

West Spring Creek formation (598 feet above the base), on the Joins Ranch, 750 feet west and 1,550 feet south of the northeast corner of sec. 9, T. 2 S., R. 1 W., Murray County, Okla.

D. *Imbricatia lamellata* Cooper, new genus and species.................. 22

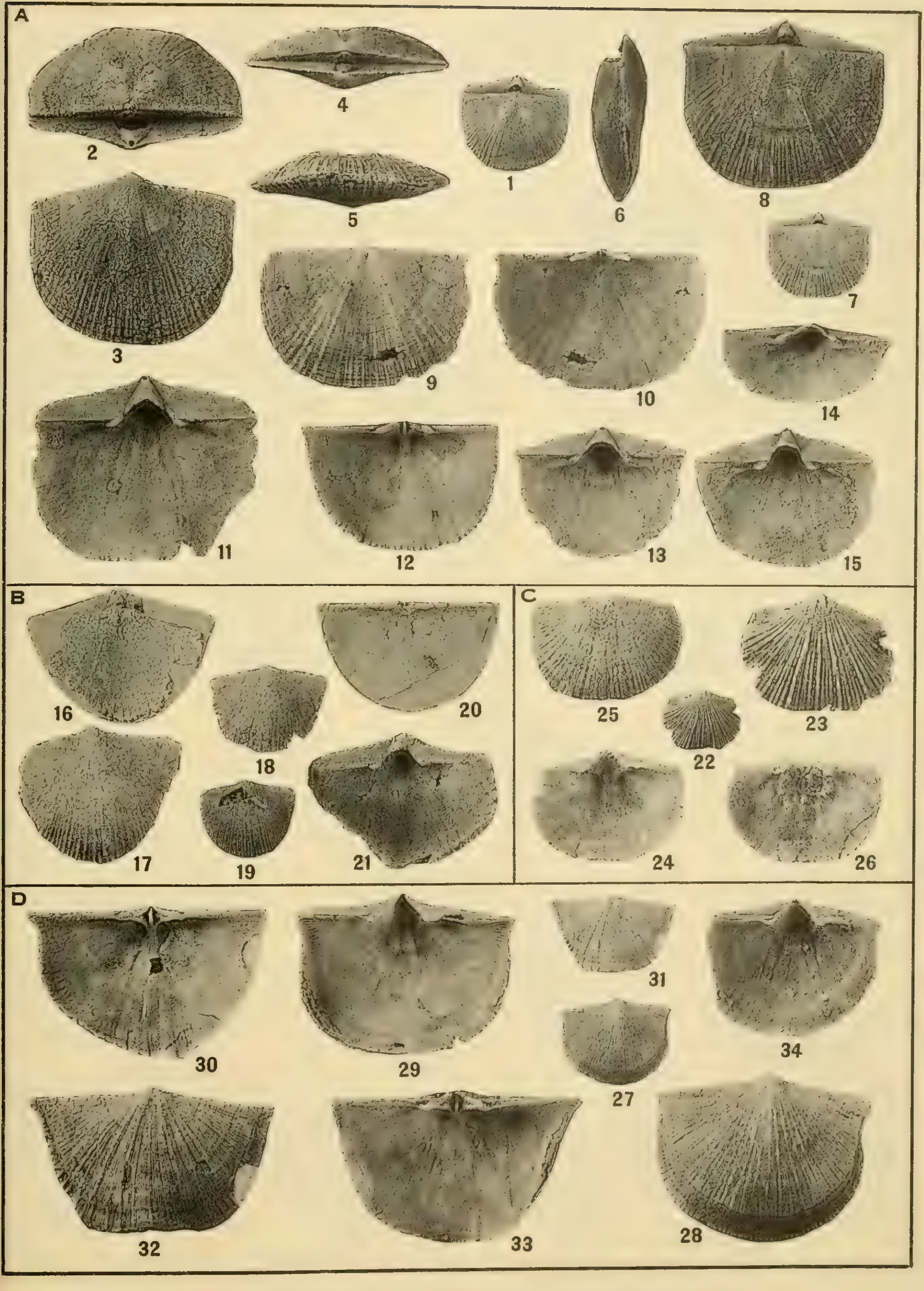
17, Exterior of the pedicle valve showing the imbrications, × 2; paratype, U.S.N.M. No. 117949a. 22, Interior of the same pedicle valve showing the spondylium, × 2. 18, 19, Exterior and side views of the brachial valve showing imbricate ornamentation, × 2; paratype, U.S.N.M. No. 117949c. 20, 21, Tilted and normal views of another brachial valve showing cardinalia, × 2; paratype, U.S.N.M. No. 117949b.

Cool Creek formation (300 feet below the top), center NE$\frac{1}{4}$ sec. 6, T. 2 S., R. 1 E., Murray County, Okla.

E. *Plectotrophia laticosta* Cooper, new species.......................... 18

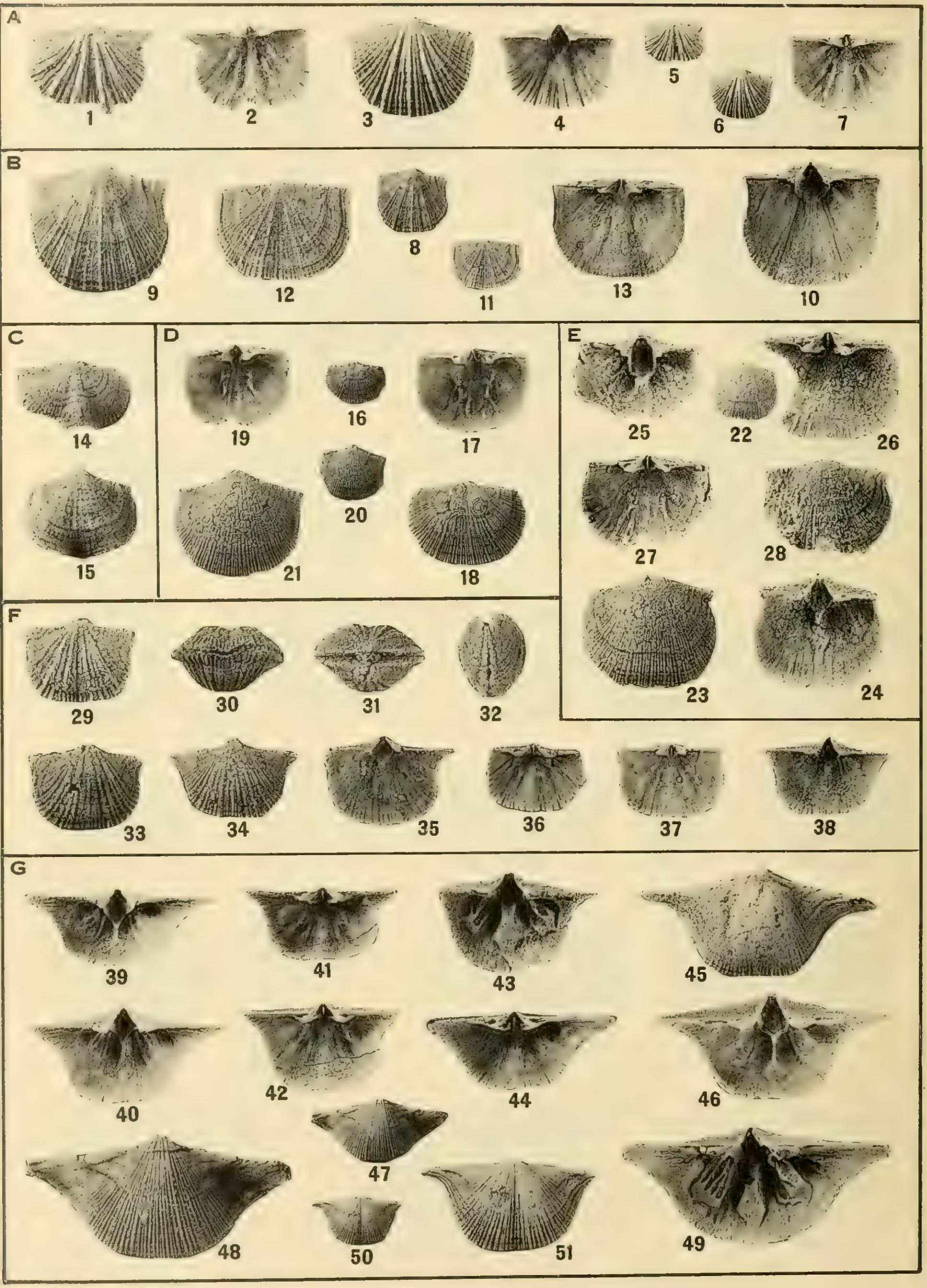
23, 24, Exterior views of the pedicle and brachial valves, respectively, × 1; paratypes, U.S.N.M. Nos. 117951d, c. 25, The same pedicle valve, × 2, showing sparse costellae. 26, Exterior of the brachial valve showing low fold and distant costellae, × 2; holotype, U.S.N.M. No. 117951g. 27, Another brachial valve showing the same features, × 2; paratype, U.S.N.M. No. 117951e. 28, 29, Exterior and side views of the brachial valve showing the low fold and distant costellae, × 3 and × 2, respectively; paratype, U.S.N.M. No. 117951f. 30, 31, Interior of the brachial valve showing the cardinalia, normal view, and the same valve tilted, respectively, × 2; paratype, U.S.N.M. No. 117951b. 32, 33, Tilted valve and normal view of the pedicle interior, respectively, showing tapering spondylium and adductor track, × 3; paratype, U.S.N.M. No. 117951a. 34, 35, Normal interior view and the same valve tilted, respectively, to show the converging brachiophore plates, × 3; paratype, U.S.N.M. No. 117951b.

Fort Sill formation (150 feet above the base), 2,500 feet east and 2,200 feet north of the southwest corner of sec. 26, T. 2 S., R. 4 E., Johnston County, Okla.



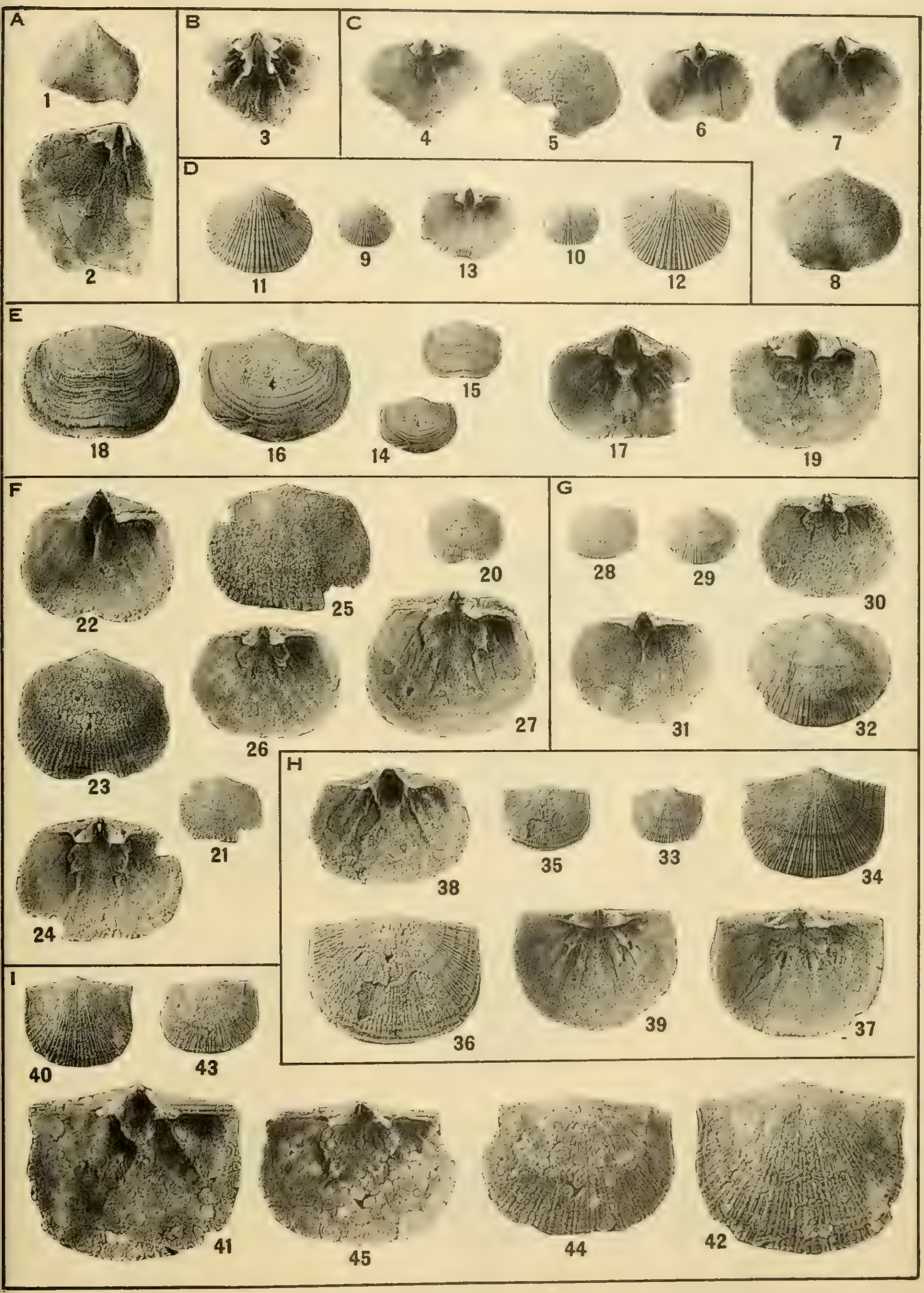
BRACHIOPODS FROM THE ARBUCKLE GROUP, OKLAHOMA

(SEE EXPLANATION OF PLATES AT END OF TEXT.)



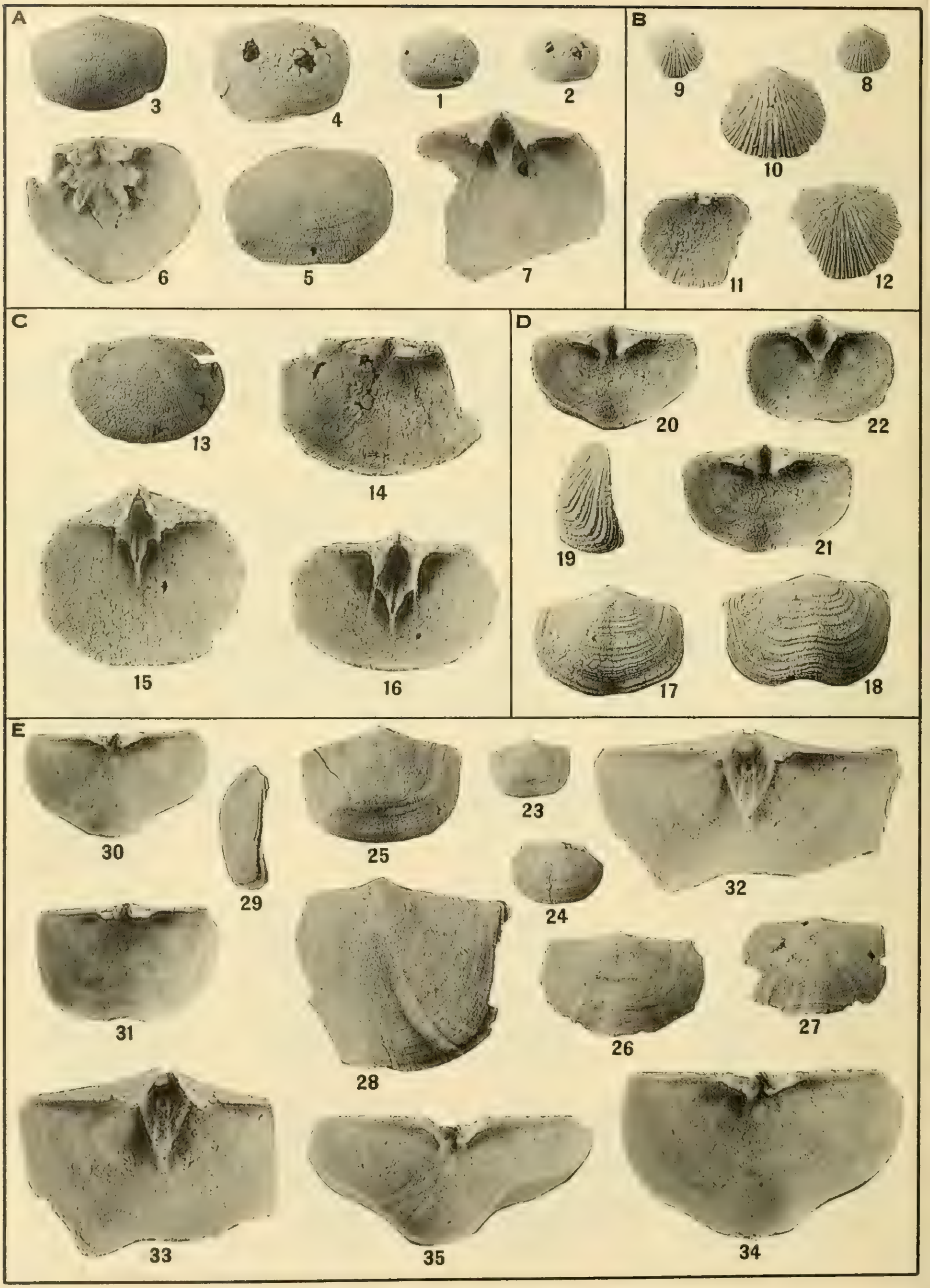
BRACHIOPODS FROM THE ARBUCKLE GROUP, OKLAHOMA

(SEE EXPLANATION OF PLATES AT END OF TEXT.)



Brachiopods from the Arbuckle Group, Oklahoma

(See explanation of plates at end of text.)



BRACHIOPODS FROM THE ARBUCKLE GROUP, OKLAHOMA

(SEE EXPLANATION OF PLATES AT END OF TEXT.)

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 117, NUMBER 15

Charles D. and Mary Vaux Walcott
Research Fund

THE FORAMINIFERAL GENUS TRIPLASIA REUSS, 1854

(WITH 8 PLATES)

BY
ALFRED R. LOEBLICH, JR.
AND
HELEN TAPPAN
U. S. National Museum

(PUBLICATION 4094)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
SEPTEMBER 9, 1952

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 117, NUMBER 15

Charles D. and Mary Vaux Walcott
Research Fund

THE FORAMINIFERAL GENUS TRIPLASIA REUSS, 1854

(WITH 8 PLATES)

BY
ALFRED R. LOEBLICH, JR.
AND
HELEN TAPPAN
U. S. National Museum

(PUBLICATION 4094)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
SEPTEMBER 9, 1952

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

Charles D. and Mary Vaux Walcott Research Fund

THE FORAMINIFERAL GENUS TRIPLASIA REUSS, 1854

By ALFRED R. LOEBLICH, JR., and HELEN TAPPAN

U. S. National Museum

(With Eight Plates)

INTRODUCTION

Thirty-seven species of *Triplasia,* including nine new species, are described herein, and most of these are figured, from strata ranging in age from Lower Jurassic to Recent. An examination of abundant material shows a definite gradation within many of the species from forms with a triangular section to 4-sided specimens. Furthermore, the early planispiral coil is extremely variable in size and prominence, and it may be lacking entirely. These gradations, which are more fully discussed under the species concerned, are also shown in the illustrations and have led the writers not only to agree with Bartenstein and Brand (1951) in suppressing the genus *Frankeina* as a synonym of *Triplasia* but also similarly to suppress the genera based on quadrate forms, *Centenarina* Majzon and *Tetraplasia* Bartenstein and Brand.

Triplasia Reuss was defined in 1854, the genotype species being *Triplasia murchisoni.* Ruess's original description stated (translation from German):

> Test free, regular, straight, inverted-ovate or somewhat elongate in outline, 3-sided. Chambers placed in a straight line upon each other, identical, somewhat equitant, not separated by constrictions. The final chamber is produced into a short central neck, which carries the round aperture.
>
> Differs from *Nodosaria* in the 3-sided form, with identical unconstricted, somewhat equitant chambers, and the rough, not glassy, shell wall, and from *Orthocerina* by the equitant chambers and the central prolongation of the final chamber.

Before additional species were described, Reuss defined the genus *Rhabdogonium* (1860), placing *Triplasia* in it as a synonym, and stating in part (translation from German):

> The most conspicuous character of *Rhabdogonium* is the presence of sharper longitudinal angles on the straight test. The four first-known forms possessed

only three such angles, were also triangular in section, wherefore I gave the genus the name *Triplasia.* Here belong: *Rh. murchisoni* m., from the Gosauschicten from the Austrian Saltz domain, *Rh. globuliferum, roemeri,* and *anomalum* m., which I forthwith describe from the Cretaceous of Westphalia and finally *Rh. acutangulum* m., an as yet unpublished species that I discovered in the Hils of Berklingen.

Later, however, I discovered 4-sided species that, except for the tetragonal cross section, agree fully with the aforementioned in their remaining characteristics, as *Rh. strombecki* and *mertensi* m., both also occurring in the Hils of Berklingen and not as yet published. For these the earlier name *Triplasia* obviously cannot now be employed, and I therefore am compelled to substitute a new one, *Rhabdogonium.* In this way the angled rhabdoidal form of the test would be clearly signified.

Reuss therefore renamed his genus when he discovered quadrate specimens which he thought to be congeneric. This cannot be done, for the Rules of Nomenclature require that the first valid name be kept, regardless of its suitability, and *Triplasia* must therefore be retained for the genus of Foraminifera to which belongs *T. murchisoni,* the genotype species.

Although the first species he mentioned in connection with the name *Rhabdogonium* was *R. murchisoni* (the genotype species of *Triplasia*), Reuss also included in his discussion some triangular calcareous species (*R. globuliferum, R. anomalum,* and *R. acutangulum*), all of which are now considered to belong to the genus *Tristix* Macfadyen. Furthermore, and ironically, the two quadrate species, whose discovery led Reuss to rename his genus, also were calcareous and both are now placed in *Tristix,* as intraspecific variations of triangular species.

Because Reuss had so quickly renamed his genus, he was followed by many workers, and the arenaceous triangular and quadrate species were for nearly a century referred either to *Rhabdogonium* or *Haplophragmium.* The first species referred to *Triplasia* (other than the genotype species) was *T. manderstjeni* Costa, 1894. This species, however, was a calcareous, coiled form, and undoubtedly a *Saracenaria.* The next species to be referred to the genus were *T. reussi* Cushman, also a calcareous form and probably a *Trifarina,* and *T. wilcoxensis* Cushman and Ponton, 1932, *T. temirica* Daïn, 1934, and *T. somaliensis* Macfadyen, 1935, which are all calcareous, uniserial, triangular lagenids, now referable to the genus *Tristix.*

Agglutinated and calcareous species were included in the same genus by many of the earlier workers, including Reuss, who had not considered wall characters to be diagnostic. Apparently the later workers noted the calcareous species referred to *Triplasia* and *Rhabdogonium* by their author and ignored the arenaceous character of the type species.

As late as 1932 Cushman considered *Triplasia* to be a calcareous genus, and Cushman and Ponton described *T. wilcoxensis* in 1932, stating, "It may be referred to Reuss' genus *Triplasia* which was afterward renamed by him *Rhabdogonium* because he later found specimens which had more than three sides . . . It is apparently uniserial throughout and belongs with the Lagenidae." This species now is placed in *Tristix,* as is mentioned above.

The genus *Frankeina* was described by Cushman and Alexander (1929, p. 61) for arenaceous forms with an early coil and triangular uniserial later portion, and was placed in the Lituolidae with the genotype species *F. goodlandensis,* from the Lower Cretaceous (Albian) Goodland formation of Texas (erroneously stated in original publication to be from the "Upper Cretaceous, Upper Middle Goodland formation"). Cushman and Alexander also called attention to the peculiar living South Pacific species, *Verneuilina variabilis* Brady, stating that it might possibly be a living example of *Frankeina,* but further study was necessary to prove this point. It was also pointed out that some Upper Cretacecous triangular forms referred to *Clavulina* might not have an early triserial portion and had their origin in *Frankeina,* by acceleration of development and resultant loss of the early coil.

After a trip to Germany and Austria in 1932 Cushman placed *Triplasia* (and *Rhabdogonium* as a synonym) in the Lituolidae (Foraminifera, 2d ed., 1933), describing it as "triangular or quadrangular in section, early stages in the microspheric form planispirally coiled, in the megalospheric form uniserial throughout; . . . wall rather coarsely arenaceous . . ." He further stated that "Study of type material in Vienna showed that this species is derived from *Frankeina,* by the loss of the coiled stage in the megalospheric form." Later, however, Cushman (1946, p. 26) called attention to this reduction of the coil in the species *Frankeina taylorensis* Cushman and Waters, stating that little more acceleration would eliminate the coil entirely and that it would be difficult to distinguish these forms from *Pseudoclavulina* unless their early portions were sectioned. However, if *Triplasia* represented those species in which the coil is lost in the megalospheric generation, as stated by Cushman in his text, then this species and similar ones should have been referred to *Triplasia.* Had Cushman's reexamination of the European material occurred before the description of the numerous American species of *Frankeina,* it seems very probable that the latter would have been originally placed in *Triplasia.* However, as the genotype species represented opposite ends of the gradational series of species, *Frankeina goodlandensis* with an exceptionally well-developed coil, and *Triplasia murchisoni* lacking or with a very poorly developed coil, both genera were recognized by Cushman in his texts of 1933, 1940, and 1948.

In practice, however, American workers have apparently referred all species to *Frankeina,* and European workers have recently placed their species in *Triplasia,* a duplication in nomenclature which obviously should be discontinued.

While this paper was being prepared with the intention of suppressing *Frankeina, Centenarina,* and *Tetraplasia* all as synonyms of *Triplasia,* the publication of Bartenstein and Brand (1951) appeared, in which for the first time *Frankeina* was suppressed as a synonym of *Triplasia,* although the quadrate forms were separated as species of the genus *Tetraplasia.*

Bartenstein and Brand stated (1951, p. 273, translation from German):

> In the foreign literature *Triplasia*-like tests from the Lower and Upper Cretaceous have been placed as a rule in the genus *Frankeina* Cushman and Alexander, 1929 . . . [quoting Cushman's statement that *Triplasia* is derived from *Frankeina* by the loss of the coil in the megalospheric form]. . . . This distinction we do not consider sufficient as both genera agree fully in all other characters of the test. We therefore believe that *Frankeina* must be suppressed as a synonym of *Triplasia.*

Reuss considered the number of angles in the test to be of specific importance, but not generic. Two later workers, Beissel and Brady, described triangular and quadrate specimens as conspecific as well. As the quadrate forms are much less common, little attention was paid to them by most writers, although a few quadrate species and varieties were described. In the past four years two generic names were proposed independently for these quadrate species (*Centenarina* Majzon, 1948, and *Tetraplasia* Bartenstein and Brand, 1949) and in both publications the quadrate specimens figured by either Beissel or Brady were mentioned.

The present writers have examined numerous species of these rhomboid lituolids, and in every instance, whenever a large suite of specimens was available, each species was found to show gradations from triangular to quadrate sections. This is also true for all geologic horizons, the earliest known species from the Lias, *T. kingakensis,* new species, showing some flattened, some triangular, and some quadrate specimens, and the youngest species, the Recent *T. variabilis* (Brady), showing a similar gradation. The genotype species of *Frankeina, F. goodlandensis,* shows the same gradation, and the type species of *Tetraplasia, T. georgsdorfensis,* is conspecific with triangular forms from the same strata. The type species of *Triplasia* has not been studied by the present writers, and no quadrate topotypes have been figured (those so placed by Beissel later being referred to a distinct species). However, it is most probable that a large suite of specimens would also show the quadrate character in this species. It is probable that all quadrate species described in the past also have triangular counterparts which in some cases have been described as distinct species, although perhaps others have not yet been noted.

The present writers have examined very large suites of specimens of the majority of species referred to both *Triplasia* and *Frankeina* and have found that in most species there is a variation from straight forms lacking the coil to specimens with a well-coiled base, and a gradation from flattened uniserial portions (*Flabellammina*-like) to triangular and quadrate tests. These gradations are more fully discussed under the specific descriptions, and are also illustrated on the plates, but seem sufficient reason to suppress *Centenarina, Tetraplasia,* and *Frankeina* all as synonyms of *Triplasia.*

ACKNOWLEDGMENTS

The writers have been aided immeasurably in this study in having available many of the types of these species through the generosity of Dr. C. I. Alexander, Magnolia Petroleum Corporation, San Antonio, Tex., who presented his entire private collection of types to the U. S. National Museum, including the many types of *Frankeina* described by Alexander and Smith (1932). The large collection of Foraminifera from Arkansas, made by the late Dr. W. H. Deaderick and bequeathed to the National Museum, has supplied abundant specimens of many old and new species.

Dr. Helmut Bartenstein, Deutsche Vacuum Oel, Celle, Germany, generously supplied types of species described by Bartenstein and Brand (1949 and 1951), some of which are here illustrated. Dr. R. W. Harris, University of Oklahoma, lent the writers the types of the Midway species from Arkansas, and Mrs. Billye Jobe, Humble Oil and Refining Co., Tyler, Tex., presented to the National Museum topotype specimens of *T. fundibularis* (Harris and Jobe).

To Cameron D. Ovey, British Museum (Natural History), we are indebted for the fine suite of topotypes of the Recent species *Verneuilina variabilis* Brady.

The remaining Lower Cretaceous specimens here described were obtained by the writers in the course of preparation of a monographic study of American Lower Cretaceous Foraminifera. These collections were financed in part by a grant from the Penrose Bequest of the Geological Society of America.

All illustrations were prepared by Mrs. Sally D. Lee, scientific illustrator, Smithsonian Institution.

SYSTEMATIC DESCRIPTIONS

Family LITUOLIDAE

Genus TRIPLASIA Reuss, 1854

Genotype: *Triplasia murchisoni* Reuss, 1854.
Synonyms: *Rhabdogonium* Reuss, 1860 (part).
Verneuilina (part) Brady, 1884 (not d'Orbigny, 1840).
Haplophragmium (part) Andrae, 1890; Beissel, 1891; De Amicis, 1895; Liebus, 1911; Eichenberg, 1934; Keller, 1946 (not Reuss, 1860).
Ammobaculites (part) Franke, 1928 (not Cushman, 1910).
Frankeina Cushman and Alexander, 1929, and others.
Flabellammina (part) Alexander and Smith, 1932 (not Cushman, 1928).
Centenarina Majzon, 1948.
Tetraplasia Bartenstein and Brand, 1949.

Emended diagnosis.—Test free, early portion may be planispiral, later portion uniserial or may be uniserial throughout, uniserial portion rhomboid in section, most commonly triangular, but occasionally quadrate even in the same species; sutures more or less arched on the faces of the test, recurved at the angles; wall arenaceous; aperture terminal, occasionally on a neck, round to elongate. Range: Lower Jurassic to Recent.

Remarks.—All species of *Triplasia* known to the writers are here described, and figures are given for most of these. The earliest-known species is from the upper Lias, and a few species are found in strata of nearly every age from Lias to Recent. Apparently the genus had two periods of climax, the Albian of America (seven species have been described) and the Senonian (five species described from America and three others from Europe).

Geologic occurrence of Triplasia

Quaternary	Recent	*T. variabilis*
	Pleistocene	
Tertiary	Pliocene	*T. wrighti*
	Miocene	*T. marwicki, T. minutum*
	Oligocene	*T. hungarica, T. trigona*
	Eocene	*T. andraei*
	Paleocene	*T. fundibularis, T.* sp.
Upper Cretaceous	Danian	
	Maestrictian	*T. saratogensis*
	Senonian	*T. abkhasicus, T. beisseli, T. cushmani, T. deadericki, T. plummerae, T. römeri, T. rugosissima, T. taylorensis*
	Turonian	*T. murchisoni*
	Cenomanian	*T. nodosa*
Lower Cretaceous	Albian	*T. acutocarinata, T. glenrosensis, T. goodlandensis, T. incerta, T. insolita, T. rugosa, T. wenoensis*
	Aptian	
	Neocomian	*T. acuta, T. georgsdorfensis, T. grosserugosa, T. pseudoroemeri, T. mexicana*
Jurassic	Malm	*T. commutata, T. elegans, T. jurassica*
	Dogger	*T. bartensteini*
	Lias	*T. kingakensis*

TRIPLASIA KINGAKENSIS Loeblich and Tappan, new species

Plate 1, figures 1-8

Test large, elongate, early portion planispiral, with a comparatively large and well-developed coil of about 6 chambers, followed by 4 or 5 uniserial and triradiate chambers, which increase gradually in size in the megalospheric forms (figs. 3, 5-8) and flare more rapidly in the microspheric form (figs. 1, 4a, b), occasional specimens develop a somewhat weaker fourth angle, so that the test is irregularly quadrate in section (figs. 2a, b), and in addition two specimens were found which never developed the third angle, remaining in the *Flabellammina* stage, whereas other specimens have a poorly developed third angle, showing all gradations between; sutures moderately distinct, depressed, arched on the faces and curving downward at the angles; wall arenaceous, of medium to coarse particles, with considerable cement, smoothly finished; aperture terminal, rounded, on a slight neck.

Length of holotype, 1.53 mm.; greatest breadth, 0.94 mm. Length of paratype of figure 6, 1.74 mm.; greatest breadth, 0.73 mm. Length of paratype of figure 3, 1.64 mm.; greatest breadth 0.52 mm. Other specimens range from 0.91 to 1.69 mm. in length.

Number of specimens examined, 18.

Remarks.—This species resembles *T. acutocarinata* (Alexander and Smith) in the flaring character of the test but differs in being smaller, in having less-excavated sides and broader and more-rounded angles, and in having a larger initial coil. It is quite variable in shape, ranging from narrow to widely flaring and from flattened to triangular to quadrangular in the later portion. The third and fourth angles are less prominent than the two in the plane of the coil.

Occurrence.—Holotype (U.S.N.M. No. P266), figured paratypes (U.S.N.M. Nos. P267a-g), and unfigured paratypes (U.S.N.M. No. P268) all from the Kingak formation (Lower Toarcian) in a core at 2,028-2,048 feet in South Barrow Test Well No. 3, lat. 71° 09′ 40″ N., long. 156°34′45″ W., south of Point Barrow, northern Alaska. This species has a very restricted vertical range, as a complete core sequence throughout the Jurassic of this well showed the specimens to be present only in this 20-foot interval.

TRIPLASIA BARTENSTEINI Loeblich and Tappan, new species

Plate 1, figure 9

Triplasia variabilis (Brady) BARTENSTEIN and BRAND, 1937 (not *Verneuilina variabilis* Brady, 1884), Abh. Senckenberg. naturf. Ges., No. 439, p. 185, pl. 14A, fig. 6.

Description from Bartenstein and Brand (translation from German):

> Test triangular in section, with rounded angles, greatest breadth in the later portion. The early chambers form a small coil that becomes obscured by the rapidly enlarging angles. Sutures but slightly marked, concealed by the coarsely arenaceous surface of the test. Sides excavated. Aperture a slit at the thickened point of intersection of the angles. Length 1.2 mm, breadth 0.9 mm.

Remarks.—This species differs from *T. variabilis* (Brady) in being smaller and more flaring, with more deeply excavated sides and more bluntly rounded angles. It is the only Middle Jurassic species of *Triplasia* yet described.

Types and occurrence.—Holotype, specimen figured by Bartenstein and Brand (Senckenberg Museum XXVII 644 a 2) from the Middle Jurassic Dogger Epsilon (*Wurttembergicus*-Schichten) from the well Bethel 2 at Bielefeld, Teutoberger Wald, in northwestern Germany. This species was also recorded from the *Parkinsoni*-Schichten.

TRIPLASIA COMMUTATA (Loeblich and Tappan)

Plate 1, figures 12a-16

Frankeina sp. WICKENDEN, 1933, Trans. Roy. Soc. Canada, ser. 3, sect. 4, vol. 27, p. 158, pl. 1, fig. 2.

Frankeina commutata LOEBLICH and TAPPAN, 1950, Journ. Washington Acad. Sci., vol. 40, No. 1, p. 6, pl. 1, figs. 3a-4.

Test free, medium-sized, elongate, compressed and planispiral in the early part, later uniserial and triangular in section, periphery rounded; planispiral chambers strongly compressed, comprising a relatively large portion of the test, about one and two-thirds volutions in the coil; later portion uniserial, chambers increasing slowly in diameter, in the holotype the final chamber being less in diameter than the early coil, sides moderately excavated; sutures generally indistinct, in the coiled part straight or with a very slight backward curve, very slightly depressed in the uniserial portion, but generally indistinct except at peripheral angles; wall medium to coarsely arenaceous, surface roughly finished; aperture rounded, on a slight neck.

Length of holotype, 1.77 mm.; greatest diameter of coiled part, 0.75 mm.; greatest width of uniserial portion, 0.68 mm.; width from center of side through opposite angle, 0.39 mm. Other specimens vary from 0.65 mm. to 1.92 mm. in length, and in diameter of early coiled part from 0.39 to 0.75 mm.

Remarks.—This species is closest to *Triplasia incerta* (Alexander and Smith), from the Lower Cretaceous (Albian) of Texas, both in size and in having a comparatively large coil. The Jurassic form differs in having the pronounced coil of diameter equal to the breadth of the later triangular portion, and in lacking the early *Flabellammina* stage characteristic of *T. incerta*. The chambers do not enlarge as rapidly, the sides are more excavated, and the sutures are more distinct in *T. commutata*.

Types and occurrence.—Holotype (U.S.N.M. No. 106017), unfigured paratypes (U.S.N.M. No. 106018), and unfigured hypotypes (U.S.N.M. No. P878) from 94-99 feet above the base of the Rierdon formation; unfigured paratypes (U.S.N.M. No. 106019) and unfigured hypotypes (U.S.N.M. No. P879) from 99-104 feet above the base of the Rierdon formation; unfigured paratypes (U.S.N.M. No. 106020) from 134 feet above the base of the Rierdon formation; figured hypotype (U.S.N.M. No. P880) from 14-19 feet above the base of the Rierdon formation (Callovian); all from the gorge of the Shoshone River, 2.0 miles west of Cody, Park County, Wyo. Collected by Ralph W. Imlay and Alfred R. Loeblich, Jr.

Figured paratype (U.S.N.M. No. 106021), unfigured paratypes (U.S.N.M. No. 106022) and unfigured hypotypes (U.S.N.M. No. P881) from 81 feet above the base of the Rierdon formation; unfigured paratypes (U.S.N.M. No. 106023) and unfigured hypotypes (U.S.N.M. No. P882) from 33 feet above the base of the Rierdon formation; unfigured hypotypes (U.S.N.M. No. P883) from 55 feet above the base of the Rierdon formation; all from the southwest corner of Red Dome, east of Bridger, in the Pryor Mountains, sec. 19, T. 7 S., R. 24 E., Carbon County, Mont. Collected by Ralph W. Imlay and Alfred R. Loeblich, Jr.

Unfigured paratypes (U.S.N.M. No. 106024) and unfigured hypotypes (U.S.N.M. No. P884) from 47-52 feet above the base of the Stockade Beaver shale (Callovian); figured hypotype (U.S.N.M. No. P885) and unfigured paratype (U.S.N.M. No. P886) from 11-21 feet above the base of the Redwater shale (Oxfordian); all from the east side of Red Gulch, about 2.5 miles south of Little Big Horn River, sec. 22, T. 58 N., R. 89 W., Sheridan County, Wyo. Collected by Ralph W. Imlay and Alfred R. Loeblich, Jr.

Unfigured hypotypes (U.S.N.M. No. P887) from 7 feet above the base of the Rierdon formation, in a gulch east of Swift Reservoir, SW¼, sec. 6, T. 28 N., R. 10 W., Pondera County, Mont. Collected by Ralph W. Imlay and Alfred R. Loeblich, Jr.

Unfigured hypotype (U.S.N.M. No. P888) from the Redwater shale, 28-33 feet above the base, on the west side of Stockade Beaver Creek, 5.0 miles northeast of Newcastle, sec. 18, T. 45 N., R. 60 W., Weston County, Wyo. Collected by Ralph W. Imlay and Alfred R. Loeblich, Jr.

Unfigured hypotype (U.S.N.M. No. P889) from the Redwater shale, 59-69 feet above base, 1.0 mile north-northeast of the center of Spearfish, sec. 3, T. 6 N., R. 2 E., Lawrence County, S. Dak. Collected by Ralph W. Imlay and Alfred R. Loeblich, Jr.

Unfigured hypotype (U.S.N.M. No. P890) from 1 foot above the base; unfigured hypotypes (U.S.N.M. No. P891) from 9 feet above the base; unfigured hypotype (U.S.N.M. No. P892) from 13 feet above the base; unfigured hypotypes (U.S.N.M. No. P893) from 19 feet above the base; figured hypotype (U.S.N.M. No. P894) from 22 feet above the base, and unfigured hypotypes (U.S.N.M. No. P895) 25 feet above the base; all from the Swift formation (Oxfordian), 1.0 mile southwest of Landusky, sec. 32, T. 25 N., R. 24 E., Little Rocky Mountains, Phillips County, Mont. Collected by Ralph W. Imlay and Alfred R. Loeblich, Jr.

TRIPLASIA ELEGANS (Mjatliuk)

Plate 1, figure 10

Frankeina elegans Mjatliuk, 1939, Neftianyi Geol. Razved. Inst., Trudy, ser. A, vol. 120, pp. 48 (Russian), 71 (English), pl. 2, fig. 26.

Remarks.—This is a rather narrow species, with comparatively small coil, closest in appearance to *T. glenrosensis,* new species, although with a smaller coil, more excavated sides, and more depressed sutures. The locality description referred to "isolated specimens," but the specific description refers only to the holotype.

Type and occurrence.—Holotype (Geol. Oil Inst. collection, Leningrad) from the Upper Jurassic, Lower Volga series, zone of *Perisphinctes panderi* d'Orbigny at a depth of 9-13 meters in Vostokneft Well No. 1501, near the Station Ozinki on the Ryazan-Uralsk railroad, in the southern part of the Obschiy Syrt, Saratov District, U.S.S.R.

TRIPLASIA JURASSICA (Mjatliuk)

Plate 1, figures 11a, b

Flabellammina (*Frankeina?*) *jurassica* Mjatliuk, 1939, Neftianyi Geol. Razved. Inst., Trudy, ser. A, vol. 120, pp. 47 (Russian), 70 (English), pl. 2, figs. 22 a-b.

Translation from Russian (p. 47), from Ellis and Messina (supplement for 1950), states in part:

> Test rounded-triangular, in the early stages close-coiled, later becoming uniserial. . . . On one of the lateral surfaces of the test there is a slight ridge, extending from the spire to the base of the last chamber. There is a corresponding depression on the opposite side of the test. . . .
>
> . . . the present species differs [from *Flabellammina alexanderi* Cushman] in its less curved sutures and in the presence of a distinct costa, relating it to the genus *Frankeina.* However, its cross-section not being triangular, we refer it to the genus *Flabellammina.*

Length of holotype is given as 1.22 mm., width 0.66 mm., thickness 0.29 mm.

Remarks.—This species is very similar in character to the Lower Cretaceous *T. incerta,* which also shows a close relationship between *Triplasia* and *Flabellammina.* For this reason, and because the test does develop a distinct third angle, we have here placed this species in *Triplasia.*

Type and occurrence.— Holotype (Geol. Oil Inst. collection, Leningrad) from the Upper Jurassic, Lower Volga series, zone of *Perisphinctes panderi* d'Orbigny, dark gray shaly clay interbedded with dark brown and dark gray bituminous shales, with layers of dark gray clay, at a depth of 22-24 meters (given on p. 48 as 22-29 meters), in Vostokneft Well No. 1501, near the station Ozinki, on the Ryazan-Uralsk railroad, southern part of the Obschiy Syrt, Saratov District, U.S.S.R. Isolated specimens.

TRIPLASIA ACUTA Bartenstein and Brand

Plate 2, figure 6a, b

Triplasia emslandensis Bartenstein and Brand subsp. *acuta* BARTENSTEIN and BRAND, 1951, Abh. Senckenberg. naturf. Gesell., No. 485, p. 274, pl. 3, fig. 68.

The original description states (translation from German):

> Diagnosis: A subspecies of *Triplasia emslandensis* with sharp angles, unequal strongly concave sides and almost completely suppressed coil.
>
> Description: Test free, elongate, older chambers planispirally coiled, however the spire more or less imperceptible, triangular with sharp angles and variable strongly concave sides. Sutures somewhat depressed, strongly arched, wall mostly medium-grained to finely arenaceous. Greatest breadth in the younger part of the test due to slight and uniform enlarging. End chamber truncate above, aperture irregularly elongate, situated on a small neck.

Length of holotype, 1.65 mm.

Remarks.—*T. emslandensis* subsp. *emslandensis* is a synonym for *T. georgsdorfensis* (see discussion under that species). Therefore the name *T. emslandensis* is invalid and if considered only a subspecies, the present form would thus be known as *T. georgsdorfensis* subsp. *acuta*. As the present species seems quite distinct, however, the subspecific name *acuta* is here raised to specific rank.

Types and occurrence.—Holotype (Senckenberg Natur Museums, Frankfurt am Main collections) from Grenzbereich, Upper Valendian 3 to 2, in Bohrung Düste (Blatt 1736, neu 3317) K 521.6-526.3 m, northwestern Germany.

TRIPLASIA GEORGSDORFENSIS (Bartenstein and Brand)

Plate 1, figures 17a-21b

Tetraplasia georgsdorfensis BARTENSTEIN and BRAND, 1949, Journ. Paleontol., vol. 23, No. 6, p. 672, text figs. 9a, b; 1951, Abh. Senckenberg. naturf. Gesell., No. 485, p. 275, pl. 11, figs. 70-71.

Triplasia emslandensis emslandensis BARTENSTEIN and BRAND, 1951, ibid., p. 274, pl. 3, figs. 65-67.

not *Haplophragmium murchisoni* Reuss, BEISSEL, 1891, Abh. preuss. geol. Landesanst., Berlin, N.S., No. 3, p. 15, pl. 4, figs. 2, 5, 9.

The following description is from Bartenstein and Brand (1949), the original description of *Tetraplasia georgsdorfensis*:

> Test free, elongate, regularly increasing in size. Earliest chambers rarely recognizable but planispirally coiled (often the coiled part is only suggested by the irregularity of the juvenile chambers), later chambers uncoiled, quadrangular, walls depressed with more or less rounded edges; sutures somewhat depressed. Walls rather coarsely arenaceous. Aperture terminal, central, round or somewhat elongate. . . .

The original description of the triangular form, named *Triplasia emslandensis emslandensis* by Bartenstein and Brand, states (translation from German):

> Diagnosis: A subspecies of the species *Triplasia emslandensis* n. sp. with broad angles, sharply excavated sides, thick-set chambers and a uniform rate of growth of isolated single chambers.
>
> Description: Test free, elongate stout, older chambers spirally enrolled, generally very thick, younger chambers broader, triangular with concave sides and ± broadly rounded angles. Test generally very coarse, straight or weakly curved in growth, greatest breadth reached by the youngest chambers, aperture circular or elongate in the center of the short tubular or produced end chamber. Sutures depressed, walls agglutinated, medium- to fine-grained. Often mature single chambers occur that are caused by especially strong constriction of the sutures and ultimate separation of the chambers and whose membership in this species may be assumed.
>
> Two form groups may be distinguished: one form with thicker, although distinct, spire and truncated end chamber (principal occurrence in upper Valendian), another form with long acuminate end chamber lacking a spire and tendency to separation of single chambers (principal occurrence in Lower Hauterivian).

Length of type of *Tetraplasia georgsdorfensis,* 1.25 mm.; length of type (fig. 17) of *Triplasia emslandensis emslandensis,* 1.5 mm. Length of small quadrate hypotype (fig. 18), 0.75 mm.; length of hypotype of figure 20, 1.33 mm.; breadth, 0.83 mm.; length of hypotype (fig. 21), 1.61 mm., greatest breadth, 0.62 mm.

Number of quadrate specimens examined by the present writers, two. We also have three triangular specimens originally referred to *Triplasia emslandensis emslandensis* by Bartenstein and Brand.

Remarks.—T. georgsdorfensis is the genotype species for the genus *Tetraplasia* Bartenstein and Brand. However, as stated by Bartenstein and Brand, "close relationship to *Triplasia* is indicated by individuals showing transitional characters." As similar transitional forms are found in nearly every species of *Triplasia* the present writers believe the triangular and quadrangular forms to be congeneric and conspecific as well, as gradations are so frequent in the various species. Furthermore, *T. georgsdorfensis* and *T. emslandensis emslandensis* are similar in other respects, as can be seen from the figures and descriptions, and have almost identical geologic ranges, the triangular forms being somewhat more abundant, as is true of all species yet observed by the writers. The name *Tetraplasia* is thus suppressed as a junior synonym of *Triplasia,* but as *Tetraplasia georgsdorfensis* was the first specific name proposed it has priority over *Triplasia emslandensis* and the species thus becomes known as *Triplasia georgsdorfensis* (Bartenstein and Brand).

Bartenstein and Brand included in their synonymy of *Tetraplasia georgsdorfensis* the Upper Cretaceous *Haplophragmium murchisoni* Reuss of Beissel, 1891, as they noted that three quadrate specimens were figured by Beissel with seven triangular forms. Comparison of topotypes of Beissel's form and topotypes of *T. georgsdorfensis* shows these species to be distinct, and in fact the Upper Cretaceous form has been described as *Frankeina beisseli* Marie (1941).

Types and occurrence.—Holotype of *Tetraplasia georgsdorfensis* and types of *Triplasia emslandensis emslandensis* (Senckenburg Museum collections) all from the upper Valendian in a deep well, Georgsdorf 9, at 625 meters in depth, at Emsland, Germany. The quadrate hypotype specimens here figured (U.S.N.M. Nos. P896a, b) are from the upper Valendian in Georgsdorf 7 well, at a depth of 440 meters; the triangular figured hypotype (U.S.N.M. No. P897) and unfigured triangular hypotypes (U.S.N.M. No. P898) from the lower Hauterivian (*Noricus*-Schichten) Zgl. Spiekerberg, Messtischblatt 1950, Germany.

The triangular forms have been recorded from upper Valendian to upper Hauterivian, from rare to common, and sporadically abundant in the lower *Noricus*-Schichten. The quadrate forms are very rare from upper Valendian to lower Hauterivian.

TRIPLASIA GROSSERUGOSA ten Dam

Plate 2, figures 5a-c

Triplasia grosserugosa TEN DAM, 1946, Journ. Paleontol., vol. 20, p. 571, pl. 87, figs. 6a-c.

Original description:

> Test free, elongate, triangular in section. Sides distinctly concave, angles rounded. Initial chamber globular, fairly large, followed by 2 or 3 uniserial chambers, slightly curved backward along the angles. Sutures slightly depressed, faintly curved. Aperture terminal, circular. Wall very coarsely arenaceous, rather roughly finished.
>
> Dimensions.—Length, 1.65 mm.; width, 0.85 mm.; diameter of proloculum, 0.4 mm.

Remarks.—According to ten Dam, "This species is somewhat similar to *Triplasia roemeri* Reuss, but differs in its concave sides and in its smaller number of chambers."

Types and occurrence.—Holotype in Netherlands Geological Survey, Haarlem, from the Hauterivian (Lower Cretaceous), near boundary stone No. 849, in the Glanerheek near the village of Glanerbrug, Overijsel Province, Netherlands.

TRIPLASIA MEXICANA Loeblich and Tappan, new species

Plate 2, figures 21-22b

Test free, flaring, triangular in section, sides excavated, angles subacute; early chambers in a small planispiral coil which may be somewhat obscure, later chambers uniserially arranged, low and broad, up to nine in number, triangular in section; sutures obscured but gently arched on the faces, recurved at the angles; wall moderately coarsely arenaceous, with occasional large grains, rather smoothly finished; aperture terminal, rounded.

Length of holotype, 1.79 mm.; greatest breadth, 0.94 mm. Length of figured paratype, 1.01 mm.; greatest breadth, 0.55 mm. Other paratypes range in length from 0.57 to 2.08 mm.

Remarks.—The writers have examined 55 specimens of this species. It is closest to the Albian species *T. acutocarinata* but is smaller, about one-third to one-half as large, and the sides are less excavated. It is sufficiently similar, however, to suggest that it may be the ancestral form for the Albian species.

Types and occurrence.—Holotype (U.S.N.M. No. P1022), figured paratype (U.S.N.M. No. P1023), and unfigured paratypes (U.S.N.M. No. P1024, and in the Paleontological Laboratory, Gerencia de Exploración of Petroleos Mexicanos, Mexico City, and Instituto de Geología, Mexico City) all from 300 feet below the top of the Lower Cretaceous (Hauterivian) Barril Viejo shale, Potrero Ovallos, in the Sierra Hermanos, lat. 27°27′ N., long. 101°28′ W., Coahuila, Mexico. Collected by R. W. Imlay.

TRIPLASIA PSEUDOROEMERI Bartenstein and Brand

Plate 2, figures 1a-4b

Haplophragmium sp. (? n. sp.) EICHENBERG, 1934, Niedersächs. geol. Ver. Hannover, Jahrb. 26, p. 151, pl. 17, figs. 2a-b.

Triplasia pseudoroemeri BARTENSTEIN and BRAND, 1951, Abh. Senckenberg. naturf. Gessell., No. 485, p. 274, pl. 3, fig. 69, pl. 13, fig. 362.

Tetraplasia quadrata BARTENSTEIN and BRAND, 1951, ibid., p. 275, pl. 3, fig. 72.

According to Bartenstein and Brand (translation from German):

> Test free, uniformly broad, without a coil, with a thickened proloculus, triangular with convex to straight sides (and in the younger part of the test

> occasionally also weakly concave) and bluntly rounded corners, few chambers, broader than high (only the final chamber is higher than broad) and gently curved, slightly depressed sutures. Wall finely agglutinated with less-coarse components. Final chamber weakly acuminate to the elongate aperture, which is somewhat eccentric in position.
>
> Remarks: The older chambers are occasionally somewhat irregularly biserial and indicate therefore the beginning of the spiral coiling. A true coil is apparently not evident.

Eichenberg's specimen (figs. 4a, b) is very similar to the type of this species and was described as follows (translation from German): "Shell coarsely arenaceous, with interspersed dark green irregular grains. Three chambers, the first two inflated, ovate; the third larger, rounded in section, elongated, 3-sided. Aperture an elliptical opening."

Bartenstein and Brand separated the very similar quadrate forms as a distinct species (*T. quadrata*) (figs. 2a, b) referred to their genus *Tetraplasia*. Their description and figures (which are here refigured) seem to make it evident that the two "species" are the same, the triangular specimens being more abundant, and the quadrate form very rare. The description of the quadrate forms given by Bartenstein and Brand follows (translation from German):

> Test free, uniformly broad, without a coil, in its place the older chambers are somewhat irregularly biserial. Sides only very weakly concave, angles broadly rounded, cross section therefore approximately rectangular. Chambers broader than high, only the end chamber increasing in height, sutures slightly depressed and gently curved, test broadly rounded at the base, the top weakly acuminate with the indication of an apertural neck and more or less rounded aperture. Walls agglutinated, of fine to medium coarseness. The cross section of the test shows broader and narrower sides.

The holotype of *T. pseudoroemeri* (fig. 1) is 1.2 mm. in length, the type of "*Tetraplasia quadrata*" Bartenstein and Brand (fig. 2) is 1.1 mm. in length, and the triangular juvenile specimen of Eichenberg (fig. 4) is 0.97 mm. in length and 0.6 mm. in breadth.

Remarks.—The triangular and quadrate specimens referred to above are similar in having an abortive coil of two large, inflated, adjacent chambers at the base, followed by the angular later chambers with nearly flat sides and broadly rounded angles, and a moderately produced, rounded aperture. Both authors recorded their forms as "very rare," although *T. pseudoroemeri* was stated to be locally frequent, and all are from the Neocomian of northern Germany. Eichenberg's specimen was from the Hauterivian, and Bartenstein and Brand recorded the quadrate form only from the upper Valendian, and the triangular one from the upper Valendian to lower Hauterivian.

This species is not so coarsely arenaceous as the Netherlands

Hauterivian species, *Triplasia grosserugosa* ten Dam, and is slightly larger, but it is otherwise similar in shape; abortive coil, nearly flat sides and rounded angles, low early chambers and much elevated pyriform final chamber. The two may be conspecific, but an examination of the types is necessary for confirmation of this.

Types and occurrence.—Holotype from the subsurface upper Valendian from Bohrung Georgsdorf 6 (Blatt 1 799, neu 3408), K 477 m, in northwestern Germany. Holotype of "*Tetraplasia quadrata*" from the subsurface upper Valendian in Bohrung Georgsdorf 7, at K 450 m, in northwestern Germany.

Triangular juvenile specimen of Eichenberg, from the *Tenuis* zone of the Hauterivian of Wenden on the Mittellandkanal, in northwestern Germany.

TRIPLASIA GLENROSENSIS Loeblich and Tappan, new species

Plate 2, figures 7a-13b

Frankeina goodlandensis Cushman and Alexander, STEAD, 1951 (not Cushman and Alexander, 1929), Texas Journ. Sci., vol. 3, No. 4, p. 589, pl. 1, fig. 6.

Test large, early portion planispiral, later uniserial and triangular or quadrangular in section, 5 or 6 inflated planispiral chambers forming a large coil, followed by 2 to 5 uniserial rectilinear chambers which may be triangular in section with nearly flat sides and broadly rounded angles (figs. 7a, b) or quadrangular (14 percent, as fig. 13), or may lose the third angle so that the later portion is flattened and *Flabellammina*-like (fig. 8) or the later chambers may lose the angularity and become rounded (figs. 9, 11); sutures arched at the center of the faces, lower at the angles, rather obscure, but sometimes slightly depressed; wall finely arenaceous, with considerable cement, very smoothly finished; aperture terminal, slitlike.

Length of holotype (fig. 7), 2.08 mm.; breadth, 0.83 mm. Length of paratype of figure 8, 2.13 mm.; breadth, 0.78 mm. Length of quadrate paratype (fig. 13), 1.27 mm.; breadth, 0.44 mm. Other paratypes vary in length from 0.83 to 2.24 mm. and in breadth from 0.42 to 1.04 mm.

Remarks.—This species resembles *Triplasia commutata* (Loeblich and Tappan) in possessing a large coil and in having a nearly parallel-sided later portion. It differs in having more-rounded angles, in the smoother finish of the wall, and in the planispiral chambers being inflated and subglobular instead of compressed and flattened. It is very similar to *T. georgsdorfensis* (Bartenstein and Brand) but has a much finer-textured wall, less-incised sutures and less-excavated faces. Of the 190 specimens examined, 26 are quadrate in section, *Occurrence.*—Holotype (U.S.N.M. No. P899), figured paratypes (U.S.N.M. Nos. P900a-f), and unfigured paratypes (U.S.N.M. No. P901) all from the Glen Rose formation, 520 feet below the top in yellowish-gray *Orbitolina*-bearing marl, in a road cut on the east side of U. S. Highway 281, 2.4 miles north of the junction of U. S. Highway 281 and Texas Highway 46, Comal County, Tex. All specimens collected by Alfred R. Loeblich, Jr.

TRIPLASIA GOODLANDENSIS (Cushman and Alexander)

Plate 2, figures 14a-20

Frankcina goodlandensis Cushman and Alexander, 1929, Contr. Cushman Lab. Foram. Res., vol. 5, p. 62, pl. 10, figs. 1, 2.—Alexander and Smith, 1932, Journ. Paleontol., vol. 6, No. 4, p. 307, pl. 47, fig. 8; Lozo, 1944, Amer. Midl. Nat., vol. 31, No. 3, p. 542, pl. 3, fig. 8.

Test small for the genus, early portion planispiral and compressed, later rectilinear and triangular (figs. 15-20) or quadrangular (fig. 14) in section (about 3 percent of the specimens), sides concave, the test may flare rapidly (fig. 20) or have nearly parallel sides (figs. 15, 16), periphery subacute; chambers numerous, about 5 in the coil, increasing rapidly in size in the uniserial portion, although the first few uniserial chambers may be of slightly less diameter than the coil, chambers curve strongly backward at the angles, and the final chamber may reach half the distance to the coil at the margins, sides moderately excavated; sutures somewhat obscure, but may be slightly depressed in the later portion, straight and radiate in the coil, but strongly recurved at the angles of the triangular portion, in many specimens the position of the sutures suggested by the alignment of shell fragments such as *Inoceramus* prisms, as they are nearly always placed parallel to the sutures; wall arenaceous, of medium-sized grains with considerable cement, surface smoothly finished; aperture rounded, at the end of the somewhat produced final chamber.

Length of holotype, 1.0 mm.; breadth, 0.40 mm. Length of topotype of figure 19, 1.01 mm.; breadth, 0.42 mm. Length of quadrate topotype (fig. 14), 0.68 mm.; breadth, 0.34 mm. Length of flaring topotype of figure 20, 1.14 mm.; breadth of coil, 0.16 mm.; greatest breadth of triangular portion, 0.65 mm. Length of topotype of figure 15, 0.52 mm. Length of topotype of figure 16, 0.62 mm. Length of topotype of figure 18, 0.73 mm. Length of topotype of figure 17, 0.52 mm.

Remarks.—This was the genotype species of *Frankeina,* and of the 862 specimens examined, 25 (about 3 percent) were quadrate. It can be distinguished from other species of the genus by its rather small size, sharp angles, and very strongly arched sutures.

Occurrence.—Holotype (Cushman Coll. No. 12030) and paratypes (Cushman Coll. Nos. 12031 and 12032) collected by C. I. Alexander, and figured topotypes (U.S.N.M. Nos. P902a-g) and unfigured topotypes (U.S.N.M. Nos. P910-P914) collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr., all from the Goodland formation (blue marls and chalky limestones) at the Lake Worth Dam, west of Fort Worth, Tarrant County, Tex.

Plesiotype (U.S.N.M. No. P915) figured by Alexander and Smith and unfigured hypotypes (U.S.N.M. Nos. P916-P920) all from the upper Goodland formation at "Cragin Knobs" on the old Stove Foundry Road, 3.8 miles west of Montgomery Street, in Fort Worth, Tarrant County, Tex. Collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr.

Unfigured hypotypes (U.S.N.M. No. P921) from the Goodland formation in the east bank of North Fork of Mary's Creek on the Fort Worth–Weatherford highway, 11.5 miles west of Fort Worth, Tarrant County, Tex. Collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr.

Unfigured hypotypes (U.S.N.M. No. P922) from the Goodland formation in the south bank of Clear Creek, 0.2 miles west of Farm Road 425 bridge, 4.9 miles west of U. S. Highway 77 junction, Denton County, Tex. Collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr.

Unfigured hypotypes (U.S.N.M. No. P923) from the Goodland formation in a high cliff on the east side of U. S. Highway 77, 3.4 miles north of the main road turning east to Marietta, SE$\frac{1}{4}$ sec. 31, T. 6 S., R. 2 E., Love County, Okla. Collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr.

TRIPLASIA ACUTOCARINATA (Alexander and Smith)

Plate 4, figures 1-9

Frankeina acutocarinata ALEXANDER and SMITH, 1932, Journ. Paleontol., vol. 6, No. 4, p. 307, pl. 47, figs. 1, 6.—TAPPAN, 1943, Journ. Paleontol., vol. 17, No. 5, p. 483, pl. 77, figs. 14a, b.—LOZO, 1944, Amer. Midl. Nat., vol. 31, No. 3, p. 542, pl. 1, fig. 7.

Test free, large, elongate, flaring, the early portion a planispiral coil, later uniserial and triangular in section, occasionally quadrangular, periphery angular in the early stages, later the angles are bluntly rounded; chambers recurved at the angles, strongly arched on the center of each face; sutures radial and indistinct in the coil, but may be reflected by the slightly lobulate periphery, strongly arched on the faces of the polygonal rectilinear portion and slightly depressed; wall medium to coarsely arenaceous, but may be smoothly finished, frequently a number of *Inoceramus* prisms are incorporated into the wall; aperture rounded to elongate, at the end of the slightly produced final chamber.

Length of holotype, figure 6, 3.3 mm.; breadth, 1.4 mm. Length of topotype of figure 5, 2.67 mm.; breadth, 1.14 mm. Length of hypotype of figure 2, 2.94 mm.; breadth, 2.16 mm.

Remarks.—Of the 4,913 specimens examined, 30 specimens (0.6 percent) were found to be quadrate in section. This species is characterized by its large size, extremely excavated sides, and narrow keel-like angles.

Types and occurrence.—This extremely large species is quite abundant in the Lower Cretaceous (Albian) of Texas and Oklahoma. It ranges from the Kiamichi formation (Fredericksburg group) through the Duck Creek, Fort Worth, Denton, and Weno formations (Washita group). Holotype, shown in figures 6a, b (U.S.N.M. No. P903), and unfigured paratype (Cushman coll. 17842) collected by C. I. Alexander; topotype of figures 5a, b (U.S.N.M. No. P904) and unfigured topotypes (U.S.N.M. No. P905) collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr.; all from the Duck Creek formation, in the south bank of a small stream, about 15 feet north of the road, 0.1 mile east of the bridge, 0.9 mile east of Fink, Grayson County, Tex.

Hypotype (U.S.N.M. No. P906) of figure 1 from the Kiamichi formation, a 1.3-foot zone of yellow-gray clay marl, 4 feet below the top of the formation, in a road cut 2.6 miles northeast of Mosheim schoolhouse, on the northerly route from Mosheim to Valley Mills, just west of the bridge over Hogg Creek, in the southern part of Bosque County, Tex. Collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr.

Hypotype of figure 3 (U.S.N.M. No. P907) from the basal 4.5 feet of the Duck Creek formation, alternating yellow marls and yellow-white limestone beds, in a low, east-facing cliff of a small tributary creek which flows north into Oliver Creek, just within the eastern edge of Wise County, Tex. Collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr.

Hypotype of figure 9 (U.S.N.M. No. P908) from the basal 3 feet of the exposure of the upper Denton formation, a dark blue and black fissile clay in an exposure along the steep west bank of the north fork of Noland's River, about 100 feet south of the bridge on the Godley-Joshua road, 1.4 miles northeast of Godley, Johnson County, Tex. Collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr.

Hypotypes (U.S.N.M. Nos. 909a-c) of figures 4, 7, and 8 from the upper part of the Weno formation exposed in a road cut on the Fort Worth–Mansfield road, 0.3 mile south of the bridge across Sycamore Creek, southeast of Fort Worth, Tarrant County, Tex. Collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr.

Hypotype of figure 2 (U.S.N.M. No. P1025) from the Fort Worth formation, in a low road cut near the bend of the road, in the northeastern corner of sec. 28, T. 8 S., R. 2 E., in Love County, Okla. Collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr.

TRIPLASIA INCERTA (Alexander and Smith)

Plate 3, figures 1-13

Frankeina incerta Alexander and Smith, 1932, Journ. Paleontol., vol. 6, No. 4, p. 308, pl. 47, fig. 4.—Tappan, 1943, Journ. Paleontol., vol. 17, No. 5, p. 483, pl. 77, figs. 15, 16.

Test free, large, early portion planispirally coiled, flattened, later portion uniserial and *Flabellammina*-like with arched flattened chambers for a variable portion of the test (figs. 2, 11), later portion develops a third angle, usually lower than the two in the plane of coiling, and occasionally a fourth, so that in the later portion the test is triangular (figs. 1-7, 9-13) or quadrangular (fig. 8) sides moderately excavated, periphery subangular; chambers numerous, about four in the coil, later portion with about 8 uniserial chambers, increasing very slowly in size so that sides are nearly parallel, chambers arched at the center of the sides, bending downward at the angles; sutures may be slightly depressed, but usually indistinct; wall coarsely arenaceous, containing numerous shell fragments in a ground mass of finer material, surface somewhat rough; aperture terminal, rounded to elongate, at the end of a short blunt necklike extension of the final chamber.

Length of holotype (fig. 7), 1.7 mm.; breadth, 0.95 mm. Length of hypotype of figure 1, 4.08 mm. Length of hypotype of figure 2, 2.49 mm.; breadth, 0.77 mm.; thickness through *Flabellammina* stage, 0.28 mm.; thickness through triangular portion, 0.34 mm. Length of hypotype of figure 3, 2.78 mm. Length of hypotype of figure 4, 3.07 mm.; length of *Flabellammina* stage, 0.83 mm.; breadth, 0.68 mm. Length of hypotype of figure 5, 4.24 mm. Length of hypotype of figure 6, 2.55 mm. Length of quadrangular hypotype of figure 8, 1.61 mm.; breadth, 0.83 mm. Length of hypotype of figure 9, 2.70 mm.; length of *Flabellammina* stage, 1.38 mm.; breadth, 1.07 mm. Length of hypotype of figure 10, 1.09 mm. Length of hypotype of figure 11, 1.14 mm.; breadth, 0.70 mm. Length of hypotype of figure 12, 1.51 mm. Length of hypotype of figure 13, 1.82 mm.

Number of specimens examined, 882, of which 30 (3.4 percent) are quadrate.

Remarks.—This is an extremely variable species with a *Flabellammina* portion of variable length (figs. 3, 11), the third angle developing late and somewhat lower than the other two angles. Occasional specimens develop a fourth angle (fig. 8), and some with a triangular test lose this third angle, and revert to a *Flabellammina* form (fig. 6).

Occurrence.—This species was first described from the Fort Worth and Denton formations (Alexander and Smith, 1932) and later recorded from the Duck Creek formation (Tappan, 1943). The range is here extended downward into the Kiamichi formation and upward to the Weno formation.

Holotype, figure 7 (U.S.N.M. No. P924), and paratypes (Cushman coll. No. 17850) collected by C. I. Alexander, from the upper Fort Worth formation, in an exposure in the east bank of Denton Creek, 1.4 miles east of Justin, Denton County, Tex.

Hypotypes of figures 2 and 11 (U.S.N.M. Nos. P925a, b) from the Duck Creek formation, from a 5.5-foot section of blue-gray shale, about 30 feet above the base of the exposure, in the west bank of the Red River, in SW¼ sec. 22, T. 8 S., R. 2 E., on the southwest side of Horseshoe Bend, Love County, Okla. Collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr.

Hypotype of figure 8 (U.S.N.M. No. P926) from the Weno formation, in a road cut exposing about 10 feet of interbedded limestones and yellow-gray marls, on the Fort Worth–Mansfield road, 0.3 mile south of the bridge over Sycamore Creek, southeast of Fort Worth, in Tarrant County, Tex. Collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr.

Hypotype of figure 10 (U.S.N.M. No. P927) from a 3-foot section of the dark gray and yellow shales of the Fort Worth formation, about 10 feet above the base and 4 feet below the top of the exposure in a deep road cut on the west side of U. S. Highway 75 (the Denison-Durant road), 1,000 feet north of the Calvary Cemetery, 1.6 miles north of the intersection with Main Street in Denison, Grayson

County, Tex. Collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr.

Hypotypes of figures 6, 12, 13 (U.S.N.M. Nos. P928a-c) from the upper Denton formation, about 7.5 feet of yellowish and reddish clay, 3 feet above the base and 5 feet below the top of the exposure, along the steep west bank of the north fork of Nolands River, about 100 feet south of the bridge on the Godley-Joshua road, 1.4 miles northeast of Godley, Johnson County, Tex. Collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr.

Hypotype of figure 9 (U.S.N.M. No. P929) from the Kiamichi formation in a 3-foot exposure of bluish-gray clay and nodular limestones, just above the Edwards limestone and immediately below the Georgetown limestone (Duck Creek member) in the eastern bank of Hogg Creek just north of the bridge at Patton, McLennan County, Tex. Collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr.

Hypotype of figure 3 (U.S.N.M. No. P930) from the uppermost 2 feet of the Kiamichi formation, just below the Duck Creek formation in thin shaly layers between ledges of *Gryphea* shell agglomerate, in a high, north-facing slope on the south bank of the Red River, cleared by excavation at the site of the Denison Dam, north of Denison, Grayson County, Tex. This slope is now covered and grassed over. Collected in July 1940 by Helen Tappan Loeblich and Alfred R. Loeblich, Jr.

Hypotype of figure 1 (U.S.N.M. No. P931) from the Fort Worth formation, in a 6-foot exposure of yellowish-gray marls in a road cut on the east side of U. S. Highway 77, 1.4 miles south of the south end of the bridge across the Red River, in Cooke County, Tex. Collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr.

Hypotype of figure 5 (U.S.N.M. No. P932) from the upper 4.5 feet of alternating yellow-gray limes and marly clays of the Fort Worth formation, in a west-facing creek bank, just north of U. S. Highway 70, and across the railroad tracks, in SW$\frac{1}{4}$NE$\frac{1}{4}$ sec. 20, T. 6 S., R. 7 E., about 0.9 mile east of Aylesworth, Marshall County, Okla. Collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr.

Hypotype of figure 4 (U.S.N.M. No. P933) from the Fort Worth formation, from a 3-foot marl zone between heavy limestone beds, 10 feet above the base of a road cut in the 1700 block of East Lancaster Street, just west of the corner of Riverside Drive and Lancaster Street, in the Fort Worth–Dallas highway, in eastern Fort Worth, Tarrant County, Tex. Collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr.

TRIPLASIA INSOLITA (Alexander and Smith)

Plate 5, figures 1a-7

Frankeina insolita ALEXANDER and SMITH, 1932, Journ. Paleontol., vol. 6, No. 4, p. 308, pl. 47, figs. 2, 3.—TAPPAN, 1943, Journ. Paleontol., vol. 17, No. 5, p. 483, pl. 77, figs. 17a-18b.

Test free, large, early portion planispiral and compressed, then becoming *Flabellammina*-like for a short distance (figs. 2a, b), or abruptly triangular (figs. 1a, b), or quadrangular (figs. 3a, b), sides of test somewhat excavated, angles bluntly rounded, chambers numerous, at first increasing rapidly in size from the four or five of the tiny planispiral coil, later chambers increase more slowly in size, so that sides of test are nearly parallel; sutures obscure, somewhat more distinct in the planispiral portion; wall coarsely arenaceous, incorporating many shell fragments, such as *Inoceramus* prisms; aperture terminal, rounded.

Length of holotype (fig. 1), 2.7 mm.; breadth, 0.9 mm. Length of topotype of figure 2, 2.60 mm.; breadth, 1.07 mm.; thickness in early portion of test, 0.28 mm.; thickness near aperture, 0.62 mm. Length of topotype of figure 3, 2.00 mm.; breadth, 1.20 mm.; thickness, 1.01 mm.

Number of specimens examined, 328.

Remarks.—This is a large and extremely variable species and shows all gradations between the flattened forms, the triangular and the quadrangular ones.

Types and occurrence.—Although Alexander and Smith state (1932, p. 308) that "*F. insolita* has been found in samples from the Duck Creek formation only, and is thus an excellent marker of basal Washita," the writers have found specimens in the Fort Worth, Weno, and Main Street formations which appear identical in all respects to typical *T. insolita.* It seems probable that this species is characteristic of a limy lithologic facies, and is found where these formations are of similar facies as the Duck Creek limes and marls.

Holotype, figure 1 (U.S.N.M. No. P934), and paratypes (U.S.N.M. No. P935 and Cushman Coll. 17849) collected by C. I. Alexander; and topotypes of figures 2 and 3 (U.S.N.M. Nos. P936a-b) and unfigured topotypes (U.S.N.M. No. P937) collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr.; all from the Duck Creek formation, in a low north-facing cliff on the south bank of a small stream north of the road, 0.1 mile east of the bridge, 0.9 mile east of Fink, Grayson County, Tex.

Hypotype of figures 5 and 7 (U.S.N.M. Nos. P938a, b) from the

Main Street formation, in 5.5 feet of section of alternating limes and marls (*Exogyra arietina* zone), 4 feet below the top of the section exposed in a road cut on the road leading eastward to Grayson Bluff, about 1 mile east of the Fort Worth–Denton highway, 3.5 miles northeast of Roanoke, Denton County, Tex. Collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr.

Hypotype of figure 6 (U.S.N.M. No. P939) from the Fort Worth formation, in the lowest 5.5 feet of alternating limestones and light gray marls exposed in a road cut on the east side of U. S. Highway 77, 1 mile west-southwest of the Gainesville courthouse square, just south of a small bridge, in Cooke County, Tex. Collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr.

Hypotype of figure 4 (U.S.N.M. No. P940) from the alternating thin limestones and thicker marl beds of the upper Weno formation, in the upper one-half of the lower 5.5 feet exposed, and just under a 1-foot limestone bed, 7 feet below the top of the formation, in a road cut on the west side of the Fort Worth–Burleson highway, where it swings southward near the top of the hill, 0.25 mile southeast of the fork of the Fort Worth-Everman road from the Fort Worth-Burleson highway, southeast of Fort Worth, Tarrant County, Tex. Collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr.

TRIPLASIA NODOSA Loeblich and Tappan, new species

Plate 5, figures 8-15

Test free, narrow, elongate, base rounded and bulbous, chambers uniserially arranged, varying from somewhat flattened to distinctly triangular or quadrangular in section, or even biformed, flattened at first (fig. 11) and developing the third angle late in its growth, or triangular at first and losing the third angle in the later development (fig. 10), the later chambers sometimes inflated and nodular in appearance and separated by definite constrictions (figs. 13, 14); sutures obscure to strongly constricted; wall coarsely arenaceous, incorporating grains and shell fragments of varying sizes, surface very rough and irregular; aperture rounded at the end of a narrow, much-produced neck.

Length of holotype (fig. 12), 1.27 mm.; breadth, 0.60 mm. Length of paratype of figure 8, 0.96 mm.; breadth, 0.49 mm. Length of paratype of figure 10, 1.53 mm.; breadth, 0.70 mm. Length of paratype of figure 11, 1.51 mm.; breadth, 0.60 mm. Length of paratype of figure 13, 1.22 mm.; breadth, 0.44 mm.

Remarks.—This extremely variable species is closest in appearance to the early Washita *Triplasia rugosa* (Alexander and Smith), but differs in the much more elongate neck, absence of a distinct coil, more nodular appearance of the chambers and greater constriction of the sutures. The later chambers are generally widest at their base and taper sharply toward the aperture.

Types and occurrence.—Holotype (fig. 12, U.S.N.M. No. P941), paratypes of figure 9 and 10 (U.S.N.M. Nos. P942a-b), and unfigured paratypes (U.S.N.M. No. P943) all from the Grayson formation, basal 3 feet, just above the Main Street formation, in a road cut on the south bank of Chuckwa Creek, 1.0 mile north of Durant, on U. S. Highway 75, in NE$\frac{1}{4}$ sec. 29, T. 6 S., R. 9 E., Bryan County, Okla. Collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr., 1937.

Paratypes of figures 8, 14, 15 (U.S.N.M. Nos. P944a-c) and unfigured paratypes (U.S.N.M. No. P945) all from the Grayson formation, at Grayson Bluff, a high southwest-facing bluff on Denton Creek, 3.5 miles northeast of Roanoke, Denton County, Tex. Collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr., 1937.

Unfigured paratypes (U.S.N.M. No. P946) from the Del Rio clay, 15.5 to 21 feet above the base exposed, on the west bank of Shoal Creek, just south of the bridge at 34th Street and just north of a fault, in Austin, Travis County, Tex. Collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr., July 1940.

Paratypes of figure 13 (U.S.N.M. No. P947) and unfigured paratypes (U.S.N.M. No. P948) from thin marl beds between limestone ledges of the Main Street formation, basal 5.5 feet of section exposed at an underpass of the Atchison, Topeka and Santa Fe Railroad, on the Cleburne-Hillsboro road, just south of the city of Cleburne, in Johnson County, Tex. Collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr., July 1940.

Paratype of figure 11 (U.S.N.M. No. P949) and unfigured paratype (U.S.N.M. No. P950) from the thin marl seams between projecting limestone ledges of the Main Street formation, in an 8-foot, west-facing bank of a small stream, east of the road leading south one block east of the eastern edge of the campus (Fort Worth–Crowley road), 3.9 miles south of the southeastern edge of the Baptist Seminary Campus, south of Fort Worth, Tarrant County, Tex. Collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr., July 1940.

Unfigured paratypes (U.S.N.M. No. P951) from the lower Main Street formation, in thin marl seams between heavy beds of limestone, in a road cut on the north side of the road, at the western edge of the Federal Narcotic Farm, southeast of Fort Worth, Tarrant County, Tex. Collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr., June 1939.

TRIPLASIA RUGOSA (Alexander and Smith)

Plate 3, figures 14-20c

Flabellammina rugosa ALEXANDER and SMITH, 1932, Journ. Paleontol., vol. 6, No. 4, p. 302, pl. 45, figs. 6-7 (not 8-9), text figs. 1, 2c (not 2b).—TAPPAN, 1943, Journ. Paleontol., vol. 17, No. 5, p. 482, pl. 77, figs. 11a-13.

not *Flabellammina rugosa* Alexander and Smith, CUSHMAN, 1946, U. S. Geol. Surv. Prof. Pap. 206, p. 24, pl. 4, figs. 9-10.

Test free, of medium size, elongate, either with a bulbous base (fig. 18) or an obscure coil (figs. 19, 20), later compressed (fig. 20) to subtriangular (fig. 19) or quadrangular (fig. 16) in section; chambers of the early coil usually somewhat obscure (fig. 19), those of the early uncoiled portion slightly arched, later chambers irregular in appearance, of somewhat greater breadth than height, final chamber may be somewhat pyriform in outline (figs. 16, 18, 19); sutures generally indistinct, slightly arched, later ones somewhat constricted and nearly straight; wall coarsely arenaceous, incorporating various-sized grains and *Inoceramus* prisms, surface roughly finished; aperture at the end of a short neck, rounded to somewhat elongate.

Length of holotype, 1.61 mm.; breadth, 0.78 mm.; thickness, 0.34 mm. Length of hypotype of figure 16, 1.82 mm.; breadth, 0.55 mm. Length of hypotype of figure 15, 1.46 mm.; breadth, 0.57 mm. Length of topotype of figure 17, 1.38 mm.; breadth, 0.64 mm.; thickness, 0.37 mm. Length of topotype of figure 18, 1.53 mm.; breadth, 0.62 mm. Length of topotype of figure 19, 1.16 mm.; breadth, 0.38 mm.

Remarks.—This species was originally described as a species of *Flabellammina* and the holotype is somewhat flattened. Nevertheless, because the majority of specimens are much less noticeably flattened, but are triangular to quadrate, the species is here considered to belong to *Triplasia*. It is similar in some respects to *T. incerta* in that there may be an elongate flattened portion before the test becomes triangular or quadrangular.

Alexander and Smith, and later Cushman, also referred Upper Cretaceous specimens to this species. However, their specimens from the Austin chalk are typical *Flabellammina* and may possibly belong to *Flabellammina clava* Alexander and Smith, which was also described from the Austin chalk, and is of similar size, shape, and appearance. The Austin chalk specimens are much more compressed than the present species, with broader and lower chambers and with strongly arched sutures. They also lack the apertural neck of *T. rugosa.*

Types and occurrence.—Holotype (fig. 20, U.S.N.M. No. P952) and unfigured paratype (U.S.N.M. No. P953) collected by C. I. Alexander, from the lower Duck Creek limestone and marl; and topotypes of figures 17-19 (U.S.N.M. No. P954a-c) collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr., June 1939, from the basal 1-foot of alternating limestones and marls of the Duck Creek formation (Lower Cretaceous, Albian), all from the south bank of a small creek, about 15 feet north of the road leading eastward from Fink, 1 mile east of town, in Grayson County, Tex.

Hypotype of figure 14 (U.S.N.M. No. P955) from the blue-gray shales of the Duck Creek formation, from 19 to 24 feet above the base, and hypotypes of figures 15 and 16 (U.S.N.M. Nos. P956a-b) from 24 to 30 feet above the base, on the west bank of the Red River, in SW¼ sec. 22, T. 8 S., R. 2 E., on the southwest side of Horseshoe Bend, Love County, Okla. Collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr., August 1939.

We have recorded this species from many Duck Creek outcrops in Texas and Oklahoma, as well as from the lower Fort Worth limestone of Oklahoma.

TRIPLASIA WENOENSIS (Alexander and Smith)

Plate 4, figures 10-15b

Frankeina wenoensis ALEXANDER and SMITH, 1932, Journ. Paleontol., vol. 6, No. 4, p. 309, pl. 47, fig. 5.

Test free, small for the genus, flaring, early portion planispiral, later uniserial and triangular or very rarely quadrate (fig. 15), sides moderately excavated, angles bluntly rounded; chambers few in number with only 3 or 4 comprising the uniserial portion, rather broad and low; sutures indistinct, occasionally marked by slight indentations at the angles of the test, arched across the center of each side; wall arenaceous, of medium-sized grains in a finer ground mass, very roughly finished; aperture terminal, rounded, on a short blunt neck.

Length of holotype (fig. 14), 1.30 mm.; breadth, 0.78 mm. Length of hypotype of figure 10, 0.91 mm.; breadth, 0.57 mm. Length of hypotype of figure 12, 0.81 mm.; breadth, 0.62 mm. Length of hypotype of figure 13, 1.51 mm.; breadth, 0.99 mm. Length of quadrate hypotype of figure 15, 1.64 mm.; breadth, 0.78 mm. Other hypotypes range from 0.83 to 1.14 mm. in length.

Remarks.—Alexander and Smith stated that "This species is restricted to the Weno formation, but the fact that it is a rather rare form detracts from its value as an horizon marker. The writers' collections have failed to disclose a locality where individuals occur in abundance." Actually, the species was based on a single specimen, the holotype, which was the only specimen in the Alexander collection (now in the U. S. National Museum). In the large number of Washita samples examined by the present writers, this species is very rare, being represented by a total of eight hypotype specimens. However, it has been found in the Main Street and Georgetown formations, as well as the Weno formation, and its range within the middle Washita was apparently governed by the environment, as all specimens occur in the marly limestone facies of the respective formations. In spite of its rarity, this species is represented by two quadrate specimens, which are otherwise similar to the more typical triangular forms.

This species resembles *T. acutocarinata* (Alexander and Smith) in the somewhat flaring character but is smaller and has less-excavated sides, more-rounded angles, and more-obscure sutures.

Types and occurrence.—Holotype (U.S.N.M. No. P957) from the Weno formation (Lower Cretaceous, Albian) in a roadside ditch on the Fort Worth-Mansfield road, 0.25 mile south of the bridge over Sycamore Creek, Tarrant County, Tex. C. I. Alexander collection.

Hypotype of figure 13 (U.S.N.M. No. P958) from the upper 10 feet exposed of the interbedded light yellow-gray marls and limestones of the Weno formation in a road cut on U. S. Highway 287 (Fort Worth–Mansfield road), 0.3 mile south of the bridge over Sycamore Creek, southeast of Fort Worth, in Tarrant County, Tex. Collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr., August 1941.

Hypotypes of figures 10-12 and 15 (U.S.N.M. Nos. P959a-d), from the lower 1-foot marl bed of the Weno formation, exposed beneath a heavy limestone and about 15-20 feet stratigraphically below the Paw Paw formation, in a road cut on the east side of the old Mansfield road, downhill and to the north of the Paw Paw exposure, 0.25 mile south of the bridge over Sycamore Creek, west of the Glen Garden Country Club, 3 miles southeast of Fort Worth, Tarrant County, Tex. Collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr., October 1943.

Because of the many changes in the highways over the past 20 years, it is uncertain which of the two preceding localities of the present writers represents the actual type locality of Alexander and Smith. They are only a fraction of a mile distant, however.

Unfigured hypotype (U.S.N.M. No. P960) from the upper 3 feet exposed of the alternating limestones and light gray marls and yellowish and brownish clays of the lower Weno formation, about 8 feet above the contact with the Denton formation, on the south bank of a tributary to Sycamore Creek, which was dammed to form Katy Lake, 0.25 mile east of and below the dam, southeast of Fort Worth, Tarrant County, Tex. Collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr., September 1938.

Unfigured hypotype (U.S.N.M. No. P961) from the upper 5 feet exposed of the Main Street formation (Lower Cretaceous, Albian) consisting of marl beds between limestone ledges, at an underpass under the Atchison, Topeka and Santa Fe railroad just south of Cleburne, on the Cleburne-Hillsboro road, in Johnson County, Tex. Collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr., July 1940.

Unfigured hypotype (U.S.N.M. No. P962) from the Georgetown formation (Lower Cretaceous, Albian), in marls between large fucoid-bearing limestone ledges, containing *Macraster elegans* (Shumard), along Smith Branch, the first main creek east of the town of Georgetown, approximately one-half mile northeast (downstream) from Texas State Highway 104, Williamson County, Tex. Collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr., 1940.

TRIPLASIA MURCHISONI Reuss

Plate 5, figures 16-17c

Triplasia murchisoni Reuss, 1854, Denkschr. Akad. Wiss. Wien, math.-naturw. Kl., vol. 7, p. 65, pl. 25, figs. 1a-2.

Ammobaculites variabilis (Brady) Franke, 1928 (not Brady, 1884), Abh. preuss. geol. Landesanst., Berlin, N.S., No. 111, p. 166, pl. 15, figs. 6a-b.

not *Triplasia murchisoni* Reuss, Egger, 1899, Abh. bayer. Akad. Wiss., München, Kl. 2, vol. 21, pt. 1, p. 42, pl. 15, fig. 24.

Original description (translation from German):

> Up to 3.2 mm. high, inverted ovate, more or less elongate, base bluntly pointed, quite sharply triangular, the lateral sides indented along the direction of the long axis, so that the cross section presents an equilateral, quite sharply angled triangle, with concave sides.
>
> Chambers up to 10, increasing gradually in size from base to top, triradiate, attached across their entire breadth with no separating constrictions; each somewhat overlapping the preceding. The sutures only slightly depressed and

descending somewhat obliquely from the middle of each side to the angles of the test. The last chamber elongated in a short, somewhat thickened, central tubular neck, which carries on the apex the round bare aperture. The outer surface of the shell rough.

Remarks.—All attempts by the writers to obtain specimens of this species have been futile. However, Cushman stated (1948, p. 106) that a study of type material in Vienna showed that the microspheric generation possessed a coil, which was not present in the megalospheric form.

This specimen figured by Egger is quite distinct, being much longer and narrower, with higher chambers and horizontal and constricted sutures. It does not even appear to belong to *Triplasia,* but only an examination of the types could prove this.

Franke referred to *Ammobaculites variabilis* (Brady) some rapidly flaring specimens with a triangular section and low, broad chambers. They seem closer in appearance to *T. murchisoni* Reuss which is also from the Senonian (or Turonian) in this general region. Typical *T. variabilis* is larger, has a less flaring test which becomes nearly parallel-sided in the later portion, and has a more slitlike aperture.

Occurrence.—Described from the Turonian, or lower Senonian, Gosaugebilde, Mergel, present at Edelbachgraben, and very rare at Wegschiedgraben in Gosau, Ostalpen (Salzburg), Austria.

TRIPLASIA ABKHASICUS (Keller)

Plate 7, figure 15

Haplophragmium abkhasicus KELLER, 1946, Bull. Soc. Natur. Moscow, N.S., vol. 51 (Sect. Géol., vol. 21), No. 3, pp. 89 (Russian), 106 (English), pl. 1, fig. 17, pl. 3, fig. 19.

Translation from the Russian, p. 89 (Ellis and Messina, supplement for 1950):

Test very large, tightly coiled in the initial portion, later becoming uniserial. Width of the test in the initial portion about the same as in the final portion. In transverse section the uniserial portion of the test is angular, almost triangular, with a rounded dorsal and a somewhat tapering ventral side. In the spiral portion of the test there are 4 or 5 chambers, forming a single volution. Chambers of the uniserial portion number 2-4, sutures linear, slightly depressed. Aperture poorly defined, apparently complex, terminal. Wall agglutinated, containing prisms of *Inoceramus, Pythonellas* and calcareous fragments.

The type specimens measured 2.0 mm. in length, 0.72 mm. in width, and 1.32 mm. in length and 0.70 mm. in width.

Remarks.—According to Keller, the species is related to *Haplo-*

phragmium aequale Roemer, but differs in having slightly depressed sutures and narrower uniserial chambers. It also seems close to *Rhabdogonium römeri* Reuss, from the German upper Senonian, but has a better-developed coil. Possibly Reuss's type is megalospheric and Keller's microspheric. Both species are "very rare."

Types and occurrence.—Types in the State Institute of Sciences, Moscow, from the lower Senonian (Campanian), Upper Cretaceous, on the southern flank of the Dzykhrin anticline on the River Mzymta, environs of Sotchi, western Caucasus, Krasnodar, U.S.S.R.

TRIPLASIA BEISSELI (Marie)

Plate 5, figures 18-20b; text figures 1-10

Haplophragmium murchisoni (Reuss) BEISSEL, 1891 (not Reuss, 1854), Abh. preuss. geol. Landesanst., Berlin, N.S., No. 3, p. 15, pl. 4, figs. 1-10.

Ammobaculites murchisoni Beissel (not Reuss) FRANKE, 1928, Abh. preuss. geol. Landesanst., Berlin, N.S., No. 111, p. 165, pl. 15, fig. 5.

Frankeina beisseli MARIE, 1941, Mém. Mus. Nat. Hist. Natur., Paris, N.S., vol. 12, No. 1, p. 23, pl. 2, fig. 12a-c.

not *Frankeina cushmani* ALEXANDER and SMITH, 1932, Journ. Paleontol. vol. 6, No. 4, p. 309, pl. 47, figs. 10, 11.

not *Tetraplasia georgsdorfensis* BARTENSTEIN and BRAND, 1949, Journ. Paleontol. vol. 23, No. 6, p. 672, text figs. 9a, b.

Test free, large, flaring, with a well-developed planispiral coil, followed by a few triangular or quadrate uniserial chambers, sides moderately excavated, angles broadly rounded; sutures distinct, slightly depressed, gently arched on the faces, recurved at the angles; wall coarsely arenaceous, but grains of nearly uniform size, little cement, so that the surface is rough in appearance; aperture a terminal slit, sometimes slightly produced.

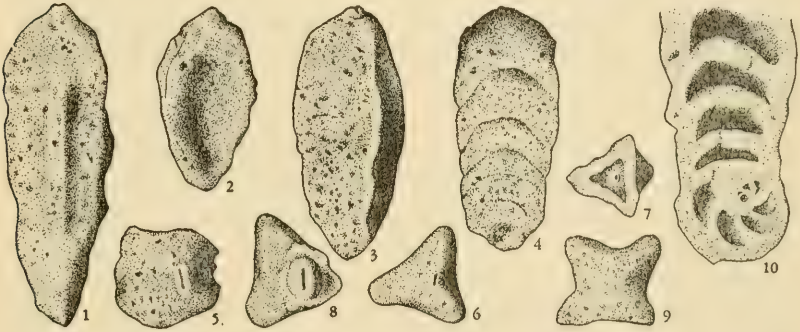
Length of hypotype (fig. 18), 2.70 mm.; breadth, 1.30 mm. Length of hypotype of figure 19, 3.17 mm.; breadth, 1.48 mm. Length of hypotype of figure 20, 1.61 mm.; breadth, 0.62 mm. Other hypotypes range from 1.30 to 2.68 mm. in length.

Remarks.—Although referred to *Haplophragmium murchisoni* (Reuss) by Beissel, it differs from Reuss's species in being less flaring, in having a more-prominent coil and less-acute angles, in lacking the neck and in having a slitlike rather than a rounded aperture.

Beissel's reference was also placed in synonymy of *Frankeina cushmani* Alexander and Smith by the authors of that species, but the European species is larger and more flaring and has better-defined and slightly excavated sutures and a less coarsely arenaceous and more smoothly finished wall.

Bartenstein and Brand (1949, p. 672) considered the quadrate specimens figured by Beissel to belong to their new genus and species *Tetraplasia georgsdorfensis.* The latter does not have as prominent a coil, has less highly arched sutures and more excavated sides, and is a much smaller species.

Types and occurrence.—Holotype in the Marie collection, from the Campanian (Upper Cretaceous), *Belemnitella mucronata* chalk at Montereau, Seine-et-Marne, Paris Basin, France. Paratypes (d'Orbigny collections, Muséum Nationale d'Histoire Naturelle, Paris) from Meudon, Seine-et-Oise, France.



FIGS. 1-10.—*Triplasia beisseli* (Marie): 1, A biformed individual, which is flattened in part and develops a third angle in the central portion of the test. 2, Face view of a quadrate specimen. 3, Side view of a triangular specimen. 4, Face view showing arched sutures. 5, Apertural view of a quadrate specimen. 6. Apertural view of a triangular specimen. 7, Opening of the penultimate chamber. 8, Opening of one of the earliest uncoiled chambers. 9, A more excavated quadrate specimen. 10, Sectional view. (After Beissel.)

Hypotype of figure 18 (U.S.N.M. No. P963), hypotype of figure 19 (U.S.N.M. No. P964), and unfigured hypotype (U.S.N.M. No. P965) all from the *Mucronaten*-Kreide, Friedrichsberg bei Aachen, Germany (topotypes of *Haplophragmium murchisoni* of Beissel, and identified as such by A. Franke), in the Alexander collection deposited in the U. S. National Museum.

Hypotypes (U.S.N.M. No. P966) from the lower Senonian, of Westphalia, Germany. Collected by A. Franke and donated to the U. S. National Museum by C. I. Alexander.

Quadrate hypotype of figure 20 (U.S.N.M. No. P967) and unfigured hypotypes (U.S.N.M. No. P968) from the lower Senonian, between Hannover and Hildesheim, Germany. Collected by A. Franke and donated to the U. S. National Museum by C. I. Alexander.

TRIPLASIA CUSHMANI (Alexander and Smith)

Plate 7, figures 1a-5

Frankeina cushmani ALEXANDER and SMITH, 1932, Journ. Paleontol., vol. 6, No. 4, p. 309, pl. 47, figs. 10-11.—CUSHMAN, 1946, U. S. Geol. Surv. Prof. Pap. 206, p. 25, pl. 4, figs. 11, 12.

Test free, of medium size for the genus, flaring in the early portion, later with nearly parallel margins, planispiral coil large, later uniserial portion triangular to quadrate with moderately excavated sides and acute angles; chambers low and broad, moderately arched on the sides; sutures obscure, discernible largely by the alignment of the larger grains and calcite prisms in the wall, rarely slightly depressed; wall coarsely arenaceous, with large grains and shell fragments in a finer ground mass, roughly finished; aperture a terminal slit, not produced.

Length of holotype (fig. 2), 1.51 mm.; breadth, 0.86 mm. Length of hypotype of figure 1, 1.43 mm.; breadth, 0.81 mm.; thickness, 0.52 mm. Length of quadrate hypotype of figure 3, 2.24 mm. Length of hypotype of figure 4, 0.86 mm. Length of hypotype of figure 5, 0.99 mm.

Remarks.—Of the 232 specimens examined, 4 are quadrate, and the remainder are triangular in section, a percentage of 1.72 quadrate forms.

This species is characterized by the comparatively large coil, parallel sides, and obscure sutures, and the coarsely arenaceous and roughly textured wall. Alexander and Smith placed in the synonymy of this species *Haplophragmium murchisoni* (Reuss) of Beissel, 1891 (not *Triplasia murchisoni* Reuss, 1854). Topotypes of Beissel's form, identified by A. Franke, show that this is a distinct species (described elsewhere in this paper as *T. beisseli* (Marie)). *T. beisseli* is a larger and more flaring species, with better-defined sutures and less coarsely arenaceous and more smoothly finished wall.

Types and occurrence.—Holotype (fig. 2, U.S.N.M. No. P989), paratype figured by Alexander and Smith (U.S.N.M. No. P990), and unfigured paratype (Cushman coll. No. 17852) all from the Pecan Gap (Upper Cretaceous), in an abandoned clay pit, 1.0 mile east of Farmersville, on the Farmersville-Greenville road, Collin County, Tex. Collected by C. I. Alexander.

Hypotype of figure 3 (U.S.N.M. No. P991) and unfigured hypotypes (U.S.N.M. No. P992) from the Upper Cretaceous Annona chalk, about 1 mile north of the quarry of the Arkansas Lime Products Co., on Little River, Ark. Collected by W. H. Deaderick.

Hypotype of figure 1 (U.S.N.M. No. P969) and unfigured hypotypes (U.S.N.M. No. P970) from the Annona chalk about 0.5 mile north of the White Cliffs Post Office, Ark. Collected by W. H. Deaderick.

Hypotypes of figures 4 and 5 (U.S.N.M. Nos. P971a-b) and unfigured hypotypes (U.S.N.M. No. P972) from the Ozan sand (Upper Cretaceous), in natural erosion on the east side of the Arkinda road, 5.0 miles northwest of Foreman, Little River County, Ark. Collected by W. H. Deaderick.

Unfigured hypotypes (U.S.N.M. No. P973) from the Annona chalk, about 0.5 mile west of the Brownstown–White Cliffs road, 1.7 miles south of Brownstown, Ark. Collected by W. H. Deaderick.

Unfigured hypotypes (U.S.N.M. No. P974) from the Annona chalk (at the Ozan contact) on the east side of the road to White Cliffs, 2.8 miles south of the Brownstown crossroads, Ark. Collected by W. H. Deaderick.

Unfigured hypotypes (U.S.N.M. No. P975) from the Annona chalk, on the east side of the road to Columbus, 1.0 mile south of Yancey, Hempstead County, Ark. Collected by W. H. Deaderick.

Unfigured hypotypes (U.S.N.M. No. P976) from the Saratoga chalk, on the south side of the road to Columbus, 2.0 miles east of Saratoga, Howard County, Ark. Collected by W. H. Deaderick.

Unfigured hypotypes (U.S.N.M. No. P977) from the Upper Cretaceous Nacatoch sand, on the north side of Highway 26, 0.5 mile east of Big Decipher Creek, 5.0 miles west of the corner of 10th and Pine Streets in Arkadelphia, in SW$\frac{1}{4}$ sec. 27, T. 7 S., R. 20 W., Clark County, Ark. Collected by W. H. Deaderick.

TRIPLASIA DEADERICKI Loeblich and Tappan, new species

Plate 6, figures 1-5

Test free, of medium size, elongate margins nearly parallel, early portion planispirally coiled, later chambers uniserial and generally triangular in section with somewhat rounded angles and slightly concave sides, occasionally quadrate (fig. 4), and one specimen (fig. 1) was found to have only two angles, and thus *Flabellammina*-like. Occasional additional specimens are flattened in the early uniserial portion, developing the third angle about one-half the distance from the base, chambers numerous, low and broad in the early portion, later ones higher, and final one or two chambers generally of smaller diameter and rounded in section (figs. 1-3), and of approximately equal height and breadth; sutures obscure in the early portion, becoming well marked and constricted in the later portion of the test, radial in the coil, slightly arched in the rhomboid uniserial chambers and horizontal between the later rounded chambers; wall finely arenaceous, with occasional coarser grains, usually rather smoothly finished; aperture terminal, ovate to slitlike, slightly produced.

Length of holotype (fig. 3), 2.18 mm.; breadth, 0.78 mm. Length of paratype of figure 1, 1.77 mm.; breadth, 0.75 mm.; thickness 0.47 mm. Length of paratype of figure 2, 1.90 mm.; breadth, 0.60 mm. Length of paratype of figure 4, 1.01 mm.; breadth, 0.60 mm.

Remarks.—This species resembles *T. glenrosensis,* new species, in the rounded later chambers, large coil, and nearly parallel margins. It differs in being narrower with sharper angles, more coarsely arenaceous, and with a roughened finish.

The species is named in honor of the late Dr. W. H. Deaderick, in recognition of this work in assembling a superb collection of Foraminifera from the Cretaceous strata of Arkansas.

Types and occurrence.—Holotype (fig. 3, U.S.N.M. No. P978), paratypes of figures 2, 4, 5 (U.S.N.M. Nos. P979a-c), and unfigured paratypes (U.S.N.M. No. P980) from the Upper Cretaceous Annona chalk, at the Ozan contact, on the east side of the road to White Cliffs, 2.8 miles south of the Brownstown crossroads, Ark. Collected by W. H. Deaderick.

Paratype of figure 1 (U.S.N.M. No. P981) and unfigured paratypes (U.S.N.M. No. P982) from the Annona chalk, about 0.25 mile north of the White Cliffs Post Office, Ark. Collected by W. H. Deaderick.

TRIPLASIA PLUMMERAE Loeblich and Tappan, new species

Plate 6, figures 14-19b

Test free, large, elongate, triangular or occasionally quadrate in section, angles rounded, sides moderately excavated, slightly flaring to subparallel-sided, uniserial throughout, base occasionally slightly curved; chambers numerous, low, increasing very gradually in height as added, each succeeding chamber overlapping the preceding, final chamber nearly as high as broad, chambers extending sharply downward at the angles; sutures fairly distinct, slightly depressed, especially in the later portion of the test, strongly arched on the faces of the test, recurved at the angles; wall arenaceous, with grains of medium size in a ground mass of finer material and occasionally incorporating tests of smaller species of Foraminifera; aperture terminal, a narrow slit, occasionally slightly produced on a short neck.

Length of holotype (fig. 19), 5.46 mm.; breadth, 1.74 mm. Length of quadrate paratype of figure 17, 4.34 mm.; breadth, 1.46 mm. Other paratypes range from 2.21 to 5.41 mm. in length and from 0.86 to 2.29 mm. in breadth.

Remarks.—This species is somewhat variable in character, two specimens from the Saratoga chalk of Arkansas showing a compressed *Flabellammina*-like early portion, although no distinct coil is present, and the third angle is only developed in the latter half of the test. The majority of specimens are regularly triangular in section, but four of the paratypes are quadrate, two of these from the Taylor marl of Texas being figured, the other two occurring in the Saratoga chalk of Arkansas. As 156 specimens of this species were examined, approximately 2.6 percent of the specimens are quadrate and about 1.3 percent are flattened, lacking the third angle in the early stage.

Although a few specimens show a slight curve at the base (fig. 14) there is no definite coil.

The present species differs from *Triplasia murchisoni* Reuss in being less flaring, with less-excavated sides and more-rounded final chambers. *T. murchisoni* Reuss is approximately three-fifths as large as the present species and has a rounded rather than elongate aperture.

Triplasia taylorensis (Cushman and Waters), which occurs with this species, has a more flaring test with a definite coil at the base and more deeply excavated sides, and tends to be more coarsely arenaceous, incorporating larger fragments in the wall.

Types and occurrence.—Holotype (fig. 19, U.S.N.M. No. P983), paratypes of figures 14-18 (U.S.N.M. Nos. P984a-e), and unfigured paratypes (U.S.N.M. No. P985) all from the greenish-gray marls of the upper Taylor, on the right bank of Onion Creek, just downstream from the bridge at Moore and Berry's Crossing, 8.5 miles southeast of the State Capitol building in Austin, Travis County, Tex. Collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr.

Paratype (U.S.N.M. No. P986) from the Saratoga chalk, on U. S. Highway 51, 10.5 miles southwest of Wright's store at the junction of highways 26 and 51, 3.1 miles northeast of Okalona, on the northeast side of the road, Clark County, Ark. W. H. Deaderick collection in the U. S. National Museum.

Paratypes (U.S.N.M. No. P987) from the Saratoga chalk, 2.0 miles east of Saratoga, on the south side of the road to Columbus, Howard County, Ark. W. H. Deaderick collection in the U. S. National Museum.

TRIPLASIA RÖMERI (Reuss)

Plate 5, figures 21a-22b

Rhabdogonium römeri Reuss, 1860, Sitzb. Akad. Wiss. Wien, math.-naturw. Kl., vol. 40, p. 201, pl. 6, figs. 7a-c.

Ammobaculites roemeri (Reuss) Franke, 1928, Abh. preuss. geol. Landesanst., Berlin, n.s., No. 111, p. 166, pl. 15, fig. 8.

Original description (translated from German):

> Test elongate, 1.97 mm. in length by 0.643 mm. in breadth, occasionally somewhat curved, of almost equal breadth for the entire length, at the upper end short and bluntly acuminate, sharply rounded below or tapering to a blunt end, sharply triangular, with nearly equal sides. Three to six 3-sided chambers, uniform, with shallow, very weakly curved sutures and sharp angles; only the last chamber shows somewhat convex faces and rounded angles. They have the form of a 3-sided pyramid, whose rounded apex bears the round simple aperture. Surface of the test rough. Very rare.

Remarks.—This species somewhat resembles *T. deadericki,* new species, from the Annona chalk of Arkansas, in general shape and the relatively high and somewhat rounded later chambers. It differs in having more distinct angles and somewhat convex sides instead of the slightly concave sides and broadly rounded angles of the American species.

Types and occurrence.—Originally described from the upper Senonian (Mucronatenkreide) marl at Hilgenberg bei Hamm, Westphalia, Germany. It was also recorded from the upper Senonian of Westphalia by Franke.

Hypotype of figure 22 (U.S.N.M. No. P988) from the upper Senonian, Dasbeck bei Hamm, Germany. Collected by A. Franke and given to the U. S. National Museum by C. I. Alexander.

TRIPLASIA RUGOSISSIMA (Alexander and Smith)

Plate 7, figures 6a-9

Frankeina rugosissima Alexander and Smith, 1932, Journ. Paleontol., vol. 6, No. 4, p. 311, pl. 47, figs. 12-13.—Cushman, 1946, U. S. Geol. Surv. Prof. Pap. 206, p. 25, pl. 4, figs. 13-14.

Test free, large, flaring from the base, later with nearly parallel sides, with a small planispiral coil at the base which is apparently obsolete in some specimens (fig. 9), the major portion of the test uniserial and triangular in section, occasionally quadrate (fig. 6), angles sharp, sides moderately excavated; chambers broad, gently arched; sutures obscure, but discernible on some specimens; wall coarsely arenaceous, surface rough with many fragments of shells, fish bones, occasional ostracod carapaces, glauconite and other dark mineral grains mixed with the large quartz grains, in a ground mass of finer material; aperture terminal, elongate.

Length of holotype (fig. 7), 3.75 mm.; breadth, 1.85 mm. Length of quadrate hypotype of figure 6, 2.47 mm.; breadth, 1.12 mm. Length of hypotype of figure 9, 3.59 mm.; breadth, 1.61 mm. Other hypotypes range in length from 0.96 to 3.85 mm.

Remarks.—Alexander and Smith stated that this species occurred only in the lower middle Taylor and was geographically restricted to southern Texas. We have specimens that are identical in all characteristics from the Saratoga and Annona chalks of Arkansas. This is one of the largest and most coarsely agglutinated species of this genus.

Types and occurrence.—Holotype (fig. 7, U.S.N.M. No. P993), paratypes figured by Alexander and Smith (1932, pl. 47, fig. 12; U.S.N.M. No. P994), and unfigured paratypes (Cushman coll. No. 17851) all from about 150 feet above the base of the Upper Cretaceous Taylor clay, in a gully north of the Austin-Manor highway, near the east end of the long bridge over Walnut Creek, 6.0 miles northeast of Austin, Travis County, Tex. Collected by C. I. Alexander.

Unfigured hypotypes (U.S.N.M. No. P995) from the Upper Cretaceous Saratoga chalk from the top of Devil's Backbone, Howard County, Ark. Collected by W. H. Deaderick.

Unfigured hypotypes (U.S.N.M. No. P996) from the Annona chalk at the Ozan contact, 2.8 miles south of the Brownstown crossroads on the east side of the road to White Cliffs, Ark. Collected by W. H. Deaderick.

Hypotypes of figures 6, 8, 9 (U.S.N.M. Nos. P997a-c) and unfigured hypotypes (U.S.N.M. No. P998) from a natural erosion of the Annona chalk about 0.5 mile north of the White Cliffs Post Office, Ark. Collected by W. H. Deaderick.

TRIPLASIA TAYLORENSIS (Cushman and Waters)

Plate 6, figures 6-13

Frankeina taylorensis Cushman and Waters, 1929, Contr. Cushman Lab. Foram. Res., vol. 5, p. 63, pl. 10, figs. 3a-b.—Alexander and Smith, 1932, Journ. Paleontol., vol. 6, No. 4, p. 310, pl. 47, figs. 7, 9.—Cushman, 1946, U.S. Geol. Surv. Prof. Pap. 206, p. 25, pl. 5, figs. 1-2.

Test free, large, elongate, somewhat flaring, planispiral coil very small or obsolete, uniserial portion generally triangular, occasionally quadrate (about 0.9 percent of the specimens observed), sides moderately excavated, angles acute; chambers numerous, low and broad, increasing very little in height but increasing somewhat in breadth in the early portion so that the test is flaring at first, but later has nearly parallel sides, final chamber somewhat higher than the preceding; sutures distinct, slightly depressed, gently arched on the sides, recurved at the angles; wall arenaceous, of uniformly sized, moderately coarse grains of quartz with a scattering of dark mineral grains, surface even, but very granular in appearance; aperture terminal, slitlike, not produced.

Length of holotype (fig. 8), 2.13 mm.; breadth, 0.96 mm. Length of hypotype of figure 6, 3.61 mm.; breadth, 1.56 mm.; thickness, 1.51 mm. Length of hypotype of figure 7, 3.46 mm.; breadth, 1.40 mm. Length of hypotype of figure 9, 1.51 mm.; breadth, 0.62 mm. Length of hypotype of figure 10, 3.17 mm. Length of hypotype of figure 11, 3.77 mm.

Remarks.—Among the holotype, three paratypes, and 437 hypotypes, there are four quadrate specimens, the remainder being triangular. The species is characterized by its large size, acute angles, excavated faces, low chambers and reduced early coil.

Types and occurrence.—Holotype (fig. 8, Cushman coll. No. 12033) and paratype (Cushman coll. No. 12034) from the Upper Cretaceous Taylor marl at 360 feet depth, and paratypes (Cushman coll. No. 12035) from the Taylor marl at a depth of 365 feet, all from the Sun Oil Company, Martindale D 10, in Caldwell County, Tex.

Hypotypes figured by Alexander and Smith, 1932 (U.S.N.M. No. P999) from the upper Taylor marls, in the bank of a small stream 200 yards south of the bridge on Pierce's Lane, 1.5 miles southeast of Del Valle, in Travis County, Tex. Collected by C. I. Alexander.

Hypotypes of figures 6, 7, 9-13 (U.S.N.M. Nos. P1000a-g) and unfigured hypotypes (U.S.N.M. No. P1001) from the upper Taylor marl, in the right bank of Onion Creek, just downstream from the bridge at Moore and Berry's Crossing, 8.5 miles southeast of the State Capitol building, in Austin, Travis County, Tex. Collected by Helen Tappan Loeblich and Alfred R. Loeblich, Jr.

Hypotypes (U.S.N.M. No. P1002) from the Upper Cretaceous Annona chalk, about 0.5 mile north of the White Cliffs Post Office, Ark. Collected by W. H. Deaderick.

Hypotypes (U.S.N.M. No. P1003) from the Annona chalk, about 0.5 mile west of the road between Brownstown and White Cliffs, and about 1.7 miles south of Brownstown, Ark. Collected by W. H. Deaderick.

Hypotypes (U.S.N.M. No. P1004) from the Annona chalk, 1.0 mile south of Yancey, on the east side of the road to Columbus, in Hempstead County, Ark. Collected by W. H. Deaderick.

TRIPLASIA SARATOGENSIS Loeblich and Tappan, new species

Plate 7, figures 10a-11b

Test free, narrow and elongate, of nearly uniform breadth for most of its length, triangular to quadrate in section, sides nearly flat to slightly concave, angles broadly rounded; chambers usually indistinct, with a coil of about three chambers at the base, followed by uniserial chambers, final chamber slightly produced to the aperture; sutures indistinct, occasionally visible and gently arched on the faces of the test; wall arenaceous, of medium to coarse grains in a finer ground mass, surface moderately rough in appearance; aperture terminal, ovate.

Length of holotype, 2.47 mm.; breadth, 0.91 mm. Length of quadrate paratype, 2.76 mm.; breadth, 0.75 mm. Other paratypes range from 1.01 to 3.25 mm. in length.

Remarks.—This species differs from *Triplasia cushmani* (Alexander and Smith) in being longer and comparatively more narrow, and in having a less well-defined coil and less-depressed sutures. The sides are also flat, while those of *T. cushmani* are excavated and the angles sharper. *Triplasia rugosissima* (Alexander and Smith) has a larger, much broader and more flaring test. *T. deadericki,* new species, has a smaller test, with higher chambers and much more constricted sutures.

Types and occurrence.—Holotype, figure 10 (U.S.N.M. No. P1005), quadrate paratype of figure 11 (U.S.N.M. No. P1006), and unfigured paratypes (U.S.N.M. No. P1007) from the Saratoga chalk, at the top of Devil's Backbone, in Howard County, Ark. Collected by W. H. Deaderick.

Unfigured paratypes (U.S.N.M. No. P1008) from the Saratoga chalk, in natural erosion just west of Saratoga, Howard County, Ark. Collected by W. H. Deaderick.

Unfigured paratypes (U.S.N.M. No. P1009) from the Saratoga chalk, on the north side of the road, at the top of a high hill, 2.0 miles east of the junction of Highways 73 and 55 in Saratoga, Howard County, Ark. Collected by W. H. Deaderick.

Unfigured paratypes (U.S.N.M. No. P1010) from the Saratoga chalk, on the east side of the road, just north of Saratoga, Howard County, Ark. Collected by W. H. Deaderick.

Unfigured paratypes (U.S.N.M. No. P1011) from the Saratoga chalk, on the south side of the road to Columbus, 2.0 miles east of Saratoga, Howard County, Ark. Collected by W. H. Deaderick.

Unfigured paratypes (U.S.N.M. No. P1012) from the Saratoga chalk, on the east side of Highway 29, 1.8 miles south of Blevins, 13.5 miles north of Hope, Hempstead County, Ark. Collected by W. H. Deaderick.

Unfigured paratypes (U.S.N.M. No. P1013) from the Saratoga chalk, on the east side of Highway 4, on the road to Ozan, 3.1 miles north of Washington, Hempstead County, Ark. Collected by W. H. Deaderick.

TRIPLASIA species

Plate 7, figures 12a, b

Frankeina sp. ISRAELSKY, 1951, U. S. Geol. Surv. Prof. Pap. 240-A, p. 12, pl. 3, figs. 5-8.

Test free, of medium size, with a large planispiral coil of about five chambers, followed by a few uniserial chambers with nearly parallel margins and triangular in section, the two angles in the plane of coiling more prominent and the third angle less elevated, sides flat, angles rounded; chambers low and broad; sutures radiate in the coil, slightly arched on the faces of the triangular portion, distinct and slightly depressed; wall coarsely arenaceous, with occasional dark mineral grains, surface rough in appearance; aperture terminal, elongate.

Length of figured specimen, 1.69 mm.; breadth of coil, 0.73 mm.; greatest breadth of triserial portion, 0.68 mm.

Remarks.—This species resembles *T. glenrosensis,* new species, in the large coil and less prominent third angle. It differs in having lower chambers, more acute angles and more coarsely arenaceous and more roughly finished wall. The species is represented by a single specimen, and because a single specimen often is not representative of the complete species of this variable genus, this form has not been named.

Types and occurrence.—Figured specimen (U.S.N.M. No. 560500) from the Lodo formation (Paleocene and Eocene in age), greenish-gray, silty calcareous claystone, 960 feet below the Middle Eocene Domengine formation, sec. 29, T. 15 S., R. 12 E., northwest Tumey Hills, Fresno County, Calif. Collected by M. C. Israelsky.

TRIPLASIA FUNDIBULARIS (Harris and Jobe)

Plate 7, figures 13a-14b

Frankeina fundibularis HARRIS and JOBE, 1951, Microfauna of basal Midway outcrops near Hope, Arkansas, p. 7, pl. 1, figs. 8a-c.

Test free, of medium size for the genus, elongate, with a large early planispiral portion and later triangular portion, sides moderately to deeply excavated, angles acute; chambers increasing in size as added, low and broad, slightly arched on the faces, extending downward at the angles; sutures distinct, slightly depressed; wall very coarsely arenaceous, incorporating smaller Foraminifera and organic fragments with the sand and other mineral grains, surface rough; aperture terminal, rounded.

Length of hypotype of figure 13, 1.87 mm.; breadth, 0.99 mm. Length of hypotype of figure 14, 1.27 mm.; breadth, 0.62 mm. Other hypotypes range from 1.09 to 1.98 mm. in length.

Remarks.—Only a few specimens (seven in all) were available to the writers, and all of these were triangular. It is probable that a very large suite of specimens would show the quadrate or flattened modifications. This species differs from *Triplasia* species, here figured from the Paleocene Lodo formation of California, in being more flaring and more sharply angled, and in having a somewhat smaller planispiral portion and more highly arched sutures.

Types and occurrence.—The holotype (deposited in the University of Oklahoma collection), figured hypotypes (U.S.N.M. Nos. P1014a, b) and unfigured hypotypes (U.S.N.M. No. P1015) are all from the Paleocene Midway formation, 1.25 miles south of Terre Rouge Creek on State Highway 29, 5 miles north of Hope, sec. 9, T. 12 S., R. 24 W., Hempstead County, Ark. Collected by Mrs. Billye Jobe.

TRIPLASIA ANDRAEI (Liebus)

Text figure 11

Haplophragmium andraei LIEBUS, 1911, Sitzb. Akad. Wiss. Wien, math.-naturw. Kl., vol. 120, pt. 1, p. 940, text figs. 5a-c.

Original description (translation from German):

The test is over 1.5 mm. long, and very coarsely agglutinated, so that the chamber arrangement is almost completely obscured from the exterior. The center of the test's breadth is very highly elevated, in certain places so strongly inflated that it has the appearance of padding, extending from about one-eighth of the distance from the base of the test almost six-eighths of the entire length. The ends of this swelling slope very sharply down to the remaining upper surface of the test. At the end of the test is found a short projection, bearing a somewhat broad and distended aperture.

First in the development one observes 5 chambers spirally arranged in the older portion of the test, to which the remaining uniserial ones are then joined; concerning the relationship to *Haplophragmium* there can be no doubt. None of the previously known forms of this genus show a 4-sided cross section caused by the inflated swelling and the flattening of the surrounding area.

The form also varies somewhat, however, and these variations do not show the inflated elevation of the broad side to such a height as the example here figured. These specimens tend toward the form that Andrae recorded under the name *Haplophragmium humboldti* Reuss var. *latum,* n. var. A comparison with the former occurrence of *H. humboldti* Reuss shows that an eventual gradation of Andrae's form into the true *H. humboldti* Reuss does not exist. The typical *H. humboldti* Reuss is somewhat compressed in its older portion but has, however, without exception, a round cross section in the younger uniserial portion, whereas in the present form the younger part still earlier demonstrates a strong beveling of the test.

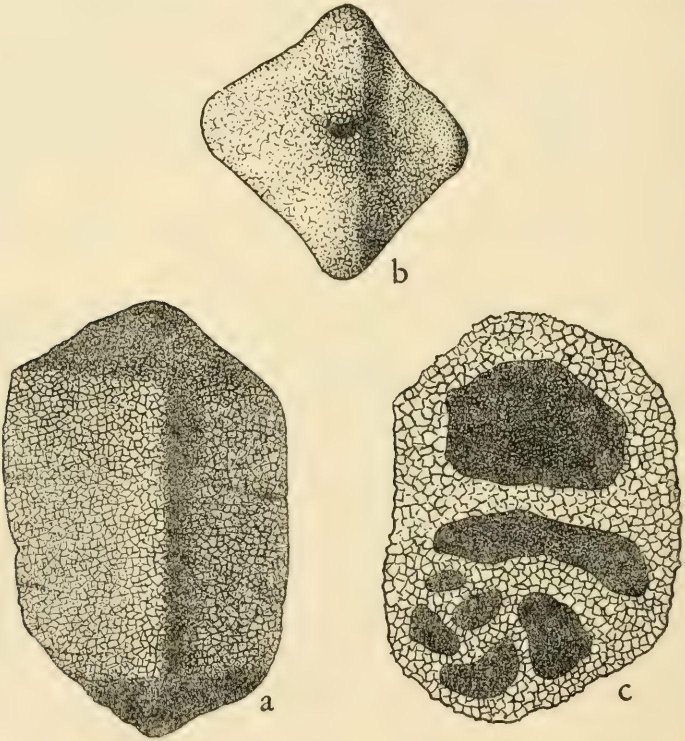


FIG. 11.—*Triplasia andraei* (Liebus): a, Side view of holotype. b, Top view, showing aperture and quadrate section. c, Sectional view, showing early coil followed by uniserial chambers. (After Liebus.)

For the present, as long as the material is still rare—there are 4 specimens observed—I consider this species as identical with the form that Andrae described as *H. humboldti* Reuss var. *latum* although differing from the true *H. humboldti* Reuss and propose as a new designation *Haplophragmium andraci.*

For these *Haplophragmiums* that at the end are composed of uniserially arranged chambers, Cushman has recently proposed the name *Ammobaculites,* whereas he placed the completely enrolled forms in *Haplophragmoides.* According to this definition the preceding would be known as *Ammobaculites andraei* n. sp.

Remarks.—The nomenclature of this species is quite complicated. As quoted above, Liebus proposed this specific name, figuring a definite quadrate *Triplasia,* but in his description stating that it was identical to *H. humboldti* Reuss var. *latum* Andrae.

On this basis, Ellis and Messina (Catalogue of Foraminifera) refer to the present species as *Haplophragmium andraei* Liebus, 1911, nom. nov. If the species had been so described, the type of Andrae's species would have thus become the type for the new name and Liebus would have had no basis for proposing a new specific name, but should have elevated Andrae's variety *latum* to specific rank. Liebus's name thus would be a synonym for *Haplophragmium latum* (Andrae).

However, Liebus erroneously considered Andrae's variety to be conspecific, as the latter is not angular in section, but ovate, and as it has horizontal sutures in this compressed uniserial portion it should thus be placed in *Ammobaculites.*

Furthermore, Liebus described his species under the heading *n. sp.* and not *nom. nov.,* and his specific description referred to the quadrate specimen he figured (shown here in text figure 11) and not to the specimens of Andrae. Therefore, it was apparently his intent to describe a new species for his quadrate specimen, and in fact in the last paragraph of his discussion he stated that it might belong to *Ammobaculites* and would be known then as *Ammobaculites andraei,* new species. Therefore his name is here recognized as a valid specific name for this quadrate *Triplasia.*

Occurrence.—Middle Eocene beds in a well at the village of Kolarine, northern Dalmatia.

TRIPLASIA HUNGARICA (Majzon)

Plate 8, figures 1a-c

Centenarina hungarica MAJZON, 1948, Földtani Közlöny, vol. 78, p. 24, figs. 1, 1a, 1b.

The following is a free translation from the Hungarian:

In the first stage of development appears a flat planispiral portion of four to five chambers and later there is a uniserial development of arched chambers which are rectangular in cross section. Their number cannot be determined exactly because of the rough sandy material of the test. They form approximately four concave rectangular prisms that are somewhat produced terminally where the aperture is slit-shaped. The sutures in the coiled portion are radial and in the 4-sided prismatic portion they are somewhat arched.

Length, 1.6 mm.; width, 0.65 mm.

Remarks.—This species was described as the type species of the genus *Centenarina* Majzon, but the latter name is a junior synonym of *Triplasia* and is here suppressed. *T. hungarica* resembles quadrangular forms of *T. variabilis* (see pl. 8, figs. 5, 9) in shape, excavation of sides, and slitlike aperture, but is only one-half as large and has a more inflated early portion.

Occurrence.—(Translation) "It is found in the Farkasreti cemetery in Budapest, in the fourth foraminiferal horizon of the Rupelian (Oligocene) strata."

TRIPLASIA TRIGONA (Andrae)

Haplophragmium humboldti (Reuss) var. *trigona* ANDRAE, 1890, Mitt. geol. Landesanst., Alsace-Lorraine, vol. 3, No. 1, p. 116.

The original description (translation from German) states, "This variety differs from the typical form in that the last chambers become triangular, as are many *Clavulinas* and *Tritaxias*."

Remarks.—As *Spirolina humboldti* Reuss is an *Ammobaculites,* and the triangular section of this "variety" places the present form in *Triplasia,* Andrae's varietal name is here raised to specific rank. Unfortunately this species has never been figured, and no specimens were available to the writers.

Types and occurrence.—Middle Oligocene, Septarienthon, Lobsann and Sulz unterm Wald, Unter-Elsass. The types are deposited in the collection of the Geologische Landesanstalt of Alsace-Lorraine, Strassbourg, France.

TRIPLASIA MARWICKI Loeblich and Tappan, new species

Plate 8, figures 2-4b

Test free, large, elongate, planispiral coil not evident, early portion flaring, later triangular to quadrate in section, sides flat to slightly excavated, angles rounded; chambers low in the early portion, increasing somewhat in height as added; sutures obscure, gently arched at the center of the faces, recurved at the angles; wall arenaceous, with occasional very large grains incorporated in the main body of finer-grained material, surface rather smoothly finished; aperture a terminal slit.

Length of holotype (fig. 4), 3.59 mm.; breadth, 1.53 mm. Length of small paratype of figure 2, 1.69 mm.; breadth, 1.33 mm. Length of paratype of figure 3, 3.04 mm.; breadth, 1.51 mm.

Remarks.—This species is named in honor of Dr. J. Marwick, Director of the New Zealand Geological Survey, in recognition of his work on the Upper Cretaceous and Tertiary of New Zealand.

It differs from *T. rugosissima* (Alexander and Smith) in being broader with less concave sides and lower chambers, and in lacking the slight neck of the Cretaceous species.

Types and occurrence.—Holotype (U.S.N.M. No. P1016) and unfigured paratype (U.S.N.M. No. P1017) from the Miocene of Kawhia, New Zealand. Paratypes of figures 2 and 3 (U.S.N.M. Nos. P1018a, b) and unfigured paratype (U.S.N.M. No. P1019) from the Miocene of Motatura, New Zealand.

TRIPLASIA MINUTA (Reuss)

Plate 7, figures 16a-17b

Rhabdogonium minutum Reuss, 1867, Sitzb. Akad. Wiss. Wien, math.-naturw. Kl., vol. 55, pt. 1, p. 85, pl. 5, figs. 4a-5b.

not *Rhabdogonium minutum* Reuss, Brady, 1884, Rep. Voy. *Challenger*, Zool., vol. 9, p. 526, pl. 67, figs. 4-6.

Original description (translation from German):

> In this species with very fragile margins two very different principal forms may be distinguished. One is larger as a rule, inverted-ovate in side view, wider above than below, quite often considerably elongated, often irregularly twisted. The surface of the shell is rougher above.
>
> Other tests are, on the other hand, often more regularly oval, tapering at both ends, generally regularly formed and with even margins. In all cases, however, the three lateral angles are thin, flangelike, the sides concave. The development of the uniserial chambers lying in a straight line one on another is only sporadically indicated by the very slight, transverse, gently curved furrows. The terminal round aperture is small, often indistinct. From this, in the individuals which are broader above, extend three fine, short furrows which lie upon the upper thicker portion of the angles.
>
> In appearance this species, which is found to be common in Salzthone, is very close to *Tritaxia tricarinata* Reuss from the Upper Cretaceous.

Remarks.—This species has not been seen by the writers, but is here considered to belong to *Triplasia,* on the basis of Reuss's figures and descriptions and because he referred it to *Rhabdogonium* (of which he was the author, proposing it to supersede *Triplasia* when he found some specimens to be quadrate). It is the only Miocene species of this genus previously described.

Occurrence.—Miocene, Salzthone, at Wieliczka, Galizien, Poland.

TRIPLASIA WRIGHTI (De Amicis)

Plate 7, figures 18a-b

Haplophragmium wrighti De Amicis, 1895, Natur. Siciliano, Palermo, Ann. 14 (1894-95), Nos. 4-5, p. 58, pl. 1, figs. 12a-b.

This species was described as having an initial spire, followed by uniserial triangular chambers. The coil is comparatively large, the sides of the triangular portion flat to slightly convex, and the angles unusually sharp, the uniserial portion has parallel margins and strongly constricted sutures. The aperture is terminal and rounded. The type is 2.8 mm. in length and only a single specimen was found.

Remarks.—This is the only Pliocene species recorded. It somewhat resembles *T. römeri* in the large coil, and rather high, slightly inflated uniserial chambers, with parallel margins. It differs in having much sharper angles, and is about one-third larger.

Type and occurrence.—Type specimen from the Lower Pliocene of Bonfornello, presso Termini-Imerese, Sicilia, Italy.

TRIPLASIA VARIABILIS (Brady)

Plate 8, figures 5-9b

Verneuilina variabilis Brady, 1884, Rep. Voy. *Challenger,* Zool., vol. 9, p. 385, pl. 47, figs. 21-24.

not *Ammobaculites variabilis* Brady, Franke, 1928, Abh. preuss. geol. Landesanst., Berlin, n.s., No. 111, p. 166, pl. 15, figs. 6a-b.

Test large, small specimens or early portion of larger ones flaring, later portion nearly parallel-sided, triangular to quadrangular in section, and a few specimens may lack the third angle and be flattened, angles acute, sides moderately excavated, chambers numerous, broad and low, gently arched; sutures obscure to well marked and slightly depressed; wall coarsely arenaceous, surface rough; aperture a terminal slit, only very slightly produced, if at all.

Brady gave the length as 3 mm. The hypotype here shown in figure 5 is 2.86 mm. in length and 1.43 mm. in breadth. Length of hypotype of figure 7, 3.80 mm., and breadth, 1.85 mm. Length of hypotype of figure 9, 3.77 mm.; breadth, 2.11 mm.

Remarks.—Brady described this species as typically triangular, but stated that it was polymorphic: "Of the numberless modifications of the typical structure, the most common are . . . those . . . in which the test is more or less quadrate and . . . in which it loses to some extent its ternate character in the other direction and presents during part of its growth only two marginal edges. No specific or even varietal distinction can be drawn between these forms; and . . . every intermediate condition is common." Brady thus figured triangular and quadrate specimens as well as the flattened forms resembling *Flabellammina.* A parallel development is shown in the Lower Cretaceous *Triplasia incerta* (Alexander and Smith), some of which show a *Flabellammina* stage of varying length before the third angle appears, and in the Lower Jurassic *Triplasia kingakensis* which also has flattened, triangular, and quadrate forms.

Franke (1928, p. 166) referred to this species Upper Cretaceous specimens (Senonian) but placed the species in the genus *Ammobaculites.* His specimens seem closer to *Triplasia murchisoni* Reuss, however.

Majzon (1948, p. 24) in describing a 4-sided species as the type for his genus *Centenarina,* stated in footnotes (free translation from the Hungarian), "In my opinion, Brady's *Verneuilina variabilis* is *Frankeina,*" and "One of Brady's figures of the above mentioned *V. variabilis* may possibly belong to *Centenarina.*"

Thus these specimens figured by Brady have been variously referred to the genera *Verneuilina* (by Brady), *Ammobaculites* (Franke, 1928, p. 166), *Triplasia* (Bartenstein and Brand, 1937, p. 185), *Frankeina* (Majzon, 1948, p. 24), and *Centenarina* (Majzon, 1948, p. 24).

Types and occurrence.—Brady's types from the coral sands of Kandavu, Fiji Islands, at 210 fathoms, are in the British Museum at South Kensington and in the Brady collection in the Museum of Comparative Anatomy at Cambridge, England. Figured hypotypes (U.S.N.M. Nos. P1020a-e) and unfigured hypotypes (U.S.N.M. No. P1021) from *Challenger* station 174-D, from coral sands at 210 fathoms, off Kandavu, Fiji Islands, at lat. 19°6′ S., long. 178°14′ 20″ E., collected March 8, 1874.

REFERENCES

Alexander, C. I., and Smith, J. P.
1932. Foraminifera of the genera *Flabellammina* and *Frankeina* from the Cretaceous of Texas. Journ. Paleontol., vol. 6, No. 4, pp. 299-311, pls. 45-47.

Andrae, A.
1890. Weitere Beiträge zur Kenntniss des Oligocäns im Elsass. Mitt. geol. Landesanst., Alsace-Lorraine, Strassbourg, vol. 3, No. 1, pp. 105-122, pls. 5-6.

Bartenstein, H., and Brand, E.

1937. Mikro-paläontologische Untersuchungen zur Stratigraphie des nordwestdeutschen Lias und Doggers. Abh. Senckenberg. naturf. Ges., No. 439, pp. 1-224, pls. 1-20.

1949. New genera of Foraminifera from the Lower Cretaceous of Germany and England. Journ. Paleontol., vol. 23, No. 6, pp. 669-672, 10 figs.

1951. Mikropaläontologische Untersuchungen zur Stratigraphie des nordwestdeutschen Valendis. Abh. Senckenberg. naturf. Ges., No. 485, Festschrift Rudolf Richter, pp. 239-336, pls. 1-25.

Beissel, I.

1891. Die Foraminiferen der Aachener Kreide. Abh. preuss. geol. Landesanst., Berlin, n.s., No. 3, pp. 1-78, pls. 1-16.

Brady, H. B.

1884. Report on the Foraminifera dredged by H. M. S. *Challenger* during the years 1873-1876. Rep. Voy. *Challenger,* Zool., vol. 9, pp. 1-814, pls. 1-115.

Cushman, J. A.

1933. Foraminifera, their classification and economic use. 2d ed. Cushman Lab. Foram. Res. Spec. Publ. No. 4, pp. 1-349.

1946. Upper Cretaceous Foraminifera of the Gulf coastal region of the United States and adjacent areas. U. S. Geol. Surv. Prof. Pap. 206, pp. 1-241, pls. 1-66.

1948. Foraminifera, their classification and economic use. 4th ed., pp. 1-605, pls. 1-55. Harvard Univ. Press.

Cushman, J. A., and Alexander, C. I.

1929. *Frankeina,* a new genus of arenaceous Foraminifera. Contr. Cushman Lab. Foram. Res., vol. 5, pp. 61-62, pl. 10.

Cushman, J. A., and Ponton, G. M.

1932. An Eocene foraminiferal fauna of Wilcox age from Alabama. Contr. Cushman Lab. Foram. Res., vol. 8, pp. 51-72, pls. 7-9.

Cushman, J. A., and Waters, J. A.

1929. Some arenaceous Foraminifera from the Taylor marl of Texas. Contr. Cushman Lab. Foram. Res., vol. 5, pp. 63-66, pl. 10.

De Amicis, G. A.

1895. I Foraminiferi del pliocene inferiore di Bonfornello. Natur. Siciliano, Palermo, Ann. 14, Nos. 4-5, pp. 51-74, 1 pl.

Egger, J. G.

1899. Foraminiferen und Ostrakoden aus den Kreidemergel der Oberbayerischen Alpen. Abh. bayer. Akad. Wiss., München, Kl. 2, vol. 21, pt. 1, pp. 1-230, pls. 1-27.

Eichenberg, W.

1934. Die Erforschung der Mikro-organismen, insbesondere der Foraminiferen der norddeutschen Erdölfelder. Teil 1. Die Foraminiferen der Unterkreide. Folge 3. Foraminiferen aus dem Hauterive von Wenden am Mittellandkanal. Niedersächs. geol. Ver. Hannover, Jahrb. 26, pp. 150-196, pls. 10-17.

Franke, A.

1928. Die Foraminiferen der Oberen Kreide Nord—und Mitteldeutschlands. Abh. preuss. geol. Landesanst., Berlin, n.s., No. 111, pp. 1-207, pls. 1-18.

HARRIS, R. W., and JOBE, B. I.
1951. Microfauna of basal Midway outcrops near Hope, Arkansas, pp. 1-113, pls. 1-14. Norman, Okla.
ISRAELSKY, M. C.
1951. Foraminifera of the Lodo formation, central California. U. S. Geol. Surv. Prof. Pap. 240-A, pp. 1-29, pls. 1-11.
KELLER, B. M.
1946. The Foraminifera of the Upper Cretaceous deposits in the Sotchi region. Bull. Soc. Natur., Moscow, N.S., vol. 51 (Sect. Géol., vol. 21), No. 3, pp. 83-108.
LIEBUS, A.
1911. Die Foraminiferenfauna der mitteleocänen Mergel von Norddalmatien. Sitzb. Akad. Wiss. Wien, math.-naturw. Kl., vol. 120, pt. 1, pp. 865-956, 3 pls.
LOEBLICH, A. R., JR., and TAPPAN, HELEN.
1950. North American Jurassic Foraminifera II: Characteristic western interior Callovian species. Journ. Washington Acad. Sci., vol. 40, No. 1, pp. 5-19, 1 pl.
LOZO, F. E., Jr.
1944. Biostratigraphic relations of some north Texas Trinity and Fredericksburg (Comanchean) Foraminifera. Amer. Midl. Nat., vol. 31, No. 3, pp. 513-582, 5 pls.
MAJZON, L.
1948. *Centenarina,* n. gen., and *Cassidulina vitálisi,* n. sp., from the Lower Rupelian strata at Budai. Földtani Közlöny, vol. 78, pp. 22-25.
MARIE, P.
1941. Les foraminifères de la Craie à *Belemnitella mucronata* du Bassin de Paris. Mém. Mus. Nat. Hist. Natur., Paris, N.S., vol. 12, No. 1, pp. 1-296, pls. 1-37.
MJATLIUK, E.
1939. The Foraminifera from the Upper Jurassic and Lower Cretaceous deposits of the middle Volga region and Obschiy Syrt. Neftianyi Geol. Razved. Inst. (Trans. Geol. Oil Inst.), Trudy, ser. A, vol. 120, pp. 3-76, pls. 1-4.
REUSS, A. E.
1854. Beiträge zur Charakteristik der Kreideschichten in den Ostalpen, besonders im Gosauthale und am Wolfgangsee. Denkschr. Akad. Wiss. Wien, math.-naturw. Kl., vol. 7, pp. 1-156, pls. 1-31.
1860. Die Foraminiferen der Westphalischen Kreideformation. Sitzb. Akad. Wiss. Wien, math.-naturw. Kl., vol. 40, pp. 147-238.
1867. Die fossil Fauna der Steinsalzablagerung von Wieliczka in Galizien. Sitzb. Akad. Wiss. Wien, math.-naturw. Kl., vol. 55, pt. 1, pp. 17-182, pls. 1-8.
STEAD, F. L.
1951. Foraminifera of the Glen Rose formation (Lower Cretaceous) of central Texas. Texas Journ. Sci., vol. 3, No. 4, pp. 577-605, pls. 1-3.
TAPPAN, H.
1943. Foraminifera from the Duck Creek formation of Oklahoma and Texas. Journ. Paleontol., vol. 17, No. 5, pp. 476-517, pls. 77-83.

TEN DAM, A. ,

1946. Arenaceous Foraminifera and Lagenidae from the Neocomian (Lower Cretaceous) of the Netherlands. Journ. Paleontol., vol. 20, pp. 570-577, pls. 87-88.

WICKENDEN, R. T. D.

1933. Jurassic Foraminifera from wells in Alberta and Saskatchewan. Trans. Roy. Soc. Canada, ser. 3, sect. 4, vol. 27, pp. 157-170, pls. 1-2.

EXPLANATION OF PLATES

Plate 1. Jurassic, Neocomian *Triplasia*

Page

Figs. 1-8. *Triplasia kingakensis* Loeblich and Tappan, new species...... 7
1, Side view of flattened paratype (U.S.N.M. No. P267a) showing *Flabellammina*-like character. 2a, Side view of quadrate megalospheric paratype (U.S.N.M. No. P267b) showing large planispiral coil, and the less-prominent fourth angle. 2b, Top view of quadrate specimen showing rounded aperture and less-prominent fourth angle. 3, Side view of elongate and narrow paratype (U.S.N.M. No. P267c). 4a, Side view of holotype (U.S.N.M. No. P266), showing rapidly flaring test, and small coil of the microspheric generation. 4b, Top view of holotype showing moderately excavated sides, slightly lower third angle, and rounded aperture. 5, Side view of smaller paratype (U.S.N.M. No. P267d) showing large megalospheric coil. 6, Side view of paratype (U.S.N.M. No. P267e) showing loss of third angle in the final chamber with reversion to the *Flabellammina* type of development. 7, Side view of paratype (U.S.N.M. No. P267f) showing *Flabellammina*-like form, with a third angle suggested in the terminal chamber. 8, Side view of paratype (U.S.N.M. No. P267g) with well-developed coil and later triangular portion. All × 27. From the Lower Jurassic Kingak formation, northern Alaska.

Fig. 9. *Triplasia bartensteini* Loeblich and Tappan, new species.......... 8
Side view of holotype, showing deeply excavated sides and flaring test (after Bartenstein and Brand), × 30. Middle Jurassic (Dogger Epsilon) of northwestern Germany.

Fig. 10. *Triplasia elegans* (Mjatliuk).................................. 11
Side view of holotype, showing narrow, elongate test, slight excavation of sides, and broadly rounded angles (after Mjatliuk), × 30. Upper Jurassic of Saratov District, U.S.S.R.

Figs. 11a, b. *Triplasia jurassica* (Mjatliuk)............................ 11
11a, Side view of holotype, showing flattened character, with the third angle developed only in the early portion of the test. 11b, Edge view (after Mjatliuk), × 30. Upper Jurassic of Saratov District, U.S.S.R.

Figs. 12a-16. *Triplasia commutata* (Loeblich and Tappan)............... 9
12a, Side view of holotype (U.S.N.M. No. 106017) showing large planispiral coil and more narrow triangular uniserial portion. 12b, Top view, showing rounded aperture, × 27, from the Rierdon formation (Upper Jurassic, Callovian) of Wyoming. 13, Side view of young paratype (U.S.N.M. No. 106021) showing coil and first triangular chamber, × 27, from the Rierdon formation of Montana. 14, Side view of hypotype (U.S.N.M. No. P885), × 22, from the Redwater formation (Upper Jurassic, Oxfordian) of Wyoming. 15, Side view of narrow microspheric paratype

Page

(U.S.N.M. No. P880), × 22, from the Rierdon formation of Wyoming. 16, Side view of hypotype (U.S.N.M. No. P894), × 22, from the Swift formation (Upper Jurassic, Oxfordian) of Montana.

Figs. 17a-21b. *Triplasia georgsdorfensis* (Bartenstein and Brand)........ 12

17a, Side view of "holotype" of *T. emslandensis emslandensis* showing large irregular coil, and triangular later portion. 17b, View of side showing regularly arched sutures. 17c, Cross section (after Bartenstein and Brand), × 25, Upper Valendian of Germany. 18, Side view of small hypotype of *"Tetraplasia georgsdorfensis"* (U.S.N.M. No. P896a) with almost obsolete coil, quadrate section, and slightly tapering final chamber, × 22, from the upper Valendian of Germany. 19a, Side view of paratype of *"Triplasia emslandensis emslandensis,"* showing more elongate form, with final chamber tapered as in the preceding quadrate form. 19b, Top view (after Bartenstein and Brand), × 35, from the lower Hauterivian of Germany. 20a, Side view of hypotype of *"Triplasia emslandensis emslandensis"* (U.S.N.M. P897) showing the distinct similiarity of the triangular and quadrate specimens. 20b, Top view, × 22, from the lower Hauterivian of Germany. 21a, Side view of quadrate hypotype (U.S.N.M. No. P896b) showing early planispiral coil and quadrate later chambers, gently arched sutures, nearly parallel sides and distinct similarity of shape of chambers to those of the preceding triangular figured specimen. 21b, Top view, showing somewhat less excavation of the sides than figure in 20, but approximately the same as in figure 19, × 22, from the upper Valendian (Lower Cretaceous) of Germany.

PLATE 2. Neocomian, Albian *Triplasia*

Figs. 1a-4b. *Triplasia pseudoroemeri* Bartenstein and Brand.............. 15

1a, Side view of holotype, showing straight sides, high chambers, and rounded angles. 1b, Top view, showing nearly flat sides (after Bartenstein and Brand), × 30, from the upper Valendian of Germany. 2a, Side view of quadrate form, the holotype of *"Tetraplasia quadrata,"* showing similarity to the triangular form in the much-reduced coil, parallel sides, very slightly arched sutures, broad rounded angles, and nearly flat sides. 2b, Top view, showing ovate aperture (after Bartenstein and Brand), × 25, upper Valendian of Germany. 3a, Side view of paratype of *T. pseudoroemeri.* 3b, Cross section of early portion showing nearly flat to slightly convex sides. 3c, Top view, showing slightly concave sides of the later portion, and ovate aperture (after Bartenstein and Brand), × 30, upper Valendian-lower Hauterivian of Germany. 4a, Side view of juvenile form figured by Eichenberg, showing similarity to the types of this species. 4b, Top view (after Eichenberg), × 25, Hauterivian of Germany.

Page

Figs. 5a-c. *Triplasia grosserugosa* ten Dam............................ 14
5a, Side view of holotype, showing coarsely arenaceous test. 5b, Face view showing very slightly arched sutures and elevated final chamber. 5c, Top view, showing nearly flat sides and ovate aperture (after ten Dam), × 30, Hauterivian of the Netherlands.

Figs. 6a, b. *Triplasia acuta* Bartenstein and Brand....................... 12
6a, Side view of holotype, showing sharp angles, slightly flaring test, and moderately arched sutures. 6b, Top view, showing flangelike angles, excavated sides, and slitlike aperture (after Bartenstein and Brand), × 30, upper Valendian of Germany.

Figs. 7a-13b. *Triplasia glenrosensis* Loeblich and Tappan, new species.... 17
7a, Side view of holotype (U.S.N.M. No. P899), a large triangular specimen. 7b, Top view, showing slitlike aperture. 8, Side view of paratype (U.S.N.M. No. P900a) showing triangular early development of the uniserial chambers and loss of the third angle in the later stages, with reversion to a *Flabellammina*-type of growth. 9, Side view of paratype (U.S.N.M. No. P900b) showing planispiral coil, triangular development, and rounded terminal chamber which has lost the angularity, showing a tendency toward the *Ammobaculites* type of growth. 10, Side view of quadrate paratype (U.S.N.M. No. P900c) showing one side somewhat narrower than the opposite. 11, Side view of paratype (U.S.N.M. No. P900d) which has lost the angularity in the final chamber. 12, Side view of small triangular paratype (U.S.N.M. No. P900e). 13a, Side view of quadrate paratype (U.S.N.M. No. P900f). 13b, Top view, showing quadrate section and rounded aperture. All × 22. From the Glen Rose formation (Lower Cretaceous, Albian) of Texas.

Figs. 14a-20. *Triplasia goodlandensis* (Cushman and Alexander)........ 18
14a, Side view of quadrate topotype (U.S.N.M. No. P902a). 14b, Top view, showing moderate excavation of the sides. 15, Side view of small megalospheric topotype (U.S.N.M. No. P902b). 16, Side view of small, narrow, megalospheric topotype (U.S.N.M. No. P902c). 17, Side view of small megalospheric topotype (U.S.N.M. No. P902d) showing large coil. 18, Side view of small microspheric topotype (U.S.N.M. No. P902e) showing more flaring test. 19, Side view of larger microspheric topotype (U.S.N.M. No. P902f) showing early coil, flaring test and very strongly recurved sutures. 20a, Side view of large microspheric topotype (U.S.N.M. No. P902g) showing planispiral coil, with a few flattened *Flabellammina* chambers before the triangular development and the rapid flaring of the triangular portion. 20b, Top view, showing acute angles and rounded aperture. All × 48. From the Goodland formation (Lower Cretaceous, Albian) of Texas.

Figs. 21-22b. *Triplasia mexicana* Loeblich and Tappan, new species...... 15
21, Side view of small paratype (U.S.N.M. No. P1023) showing small coil and gently arched sutures. 22a, Side view of holotype (U.S.N.M. No. P1022) showing flared test. 22b, Top view,

Page

showing moderately excavated sides and ovate aperture. × 22. From the Barrill Viejo shale (Lower Cretaceous, Hauterivian) of Coahuila, Mexico.

PLATE 3. Albian *Triplasia*

Figs. 1-13. *Triplasia incerta* (Alexander and Smith) 21

1, Side view of hypotype (U.S.N.M. No. P931), showing typical *Flabellammina*-like early portion, with third angle developed in the last one-third of the test, × 10. From the Fort Worth formation (Lower Cretaceous, Albian) of Texas. 2, Side view of hypotype (U.S.N.M. No. P925a) from the Duck Creek formation (Lower Cretaceous, Albian) of Oklahoma, showing elongate *Flabellammina* stage, × 22. 3, Side view of broad and elongate hypotype (U.S.N.M. No. P930) from the Kiamichi formation (Lower Cretaceous, Albian) of Texas, with very short triangular portion, × 22. 4, Side view of hypotype (U.S.N.M. No. P933) showing an unusually long triangular portion and narrow test, from the Fort Worth formation of Texas, × 22. 5, Side view of hypotype (U.S.N.M. No. P932) from the Fort Worth formation of Oklahoma, × 10. 6, Side view of hypotype (U.S.N.M. No. P928a) from the Denton formation (Lower Cretaceous, Albian) of Texas, × 22. 7a, Side view of holotype (U.S.N.M. No. P924) from the Fort Worth formation of Texas. 7b, Edge view, showing compressed test and low ridgelike third angle. 7c, View of rounded aperture. × 22. 8a, Side view of quadrate hypotype (U.S.N.M. No. P926) from the Weno formation (Lower Cretaceous, Albian) of Texas, showing coil and early development of third angle. 8b, Edge view, showing insertion of fourth angle approximately halfway up the test. 8c, Top view, showing elongate aperture. × 22. 9, Side view of elongate hypotype (U.S.N.M. No. P929) from the Kiamichi formation of Texas, × 22. 10, Side view of small hypotype (U.S.N.M. No. P927) from the Fort Worth formation of Texas, × 22. 11, Side view of small hypotype (U.S.N.M. No. P925b) from the Duck Creek formation of Oklahoma showing more rapid development of third angle, × 22. 12, 13, Side views of hypotypes (U.S.N.M. Nos. P928b, c) from the Denton formation of Texas, × 22.

Figs. 14-20c. *Triplasia rugosa* (Alexander and Smith) 27

14, Side view of hypotype (U.S.N.M. No. P955) showing well-developed planispiral coil, later triangular uniserial portion with final chamber tending to become rounded. 15a, Side view of triangular hypotype (U.S.N.M. No. P956a). 15b, Top view. 16a, Side view of quadrate hypotype (U.S.N.M. No. P956b). 16b, Top view. Figures 14-16 × 22. From the Duck Creek formation of Oklahoma. 17a, Side view of compressed topotype (U.S.N.M. No. P954a), showing *Flabellammina*-like character also found in the holotype. 17b, Top view. 18a, Side view of topotype (U.S.N.M. No. P954b) showing triangular development of the final chamber.

Page

18b, Edge view. 19, Side view of topotype (U.S.N.M. No. P954c) with well-defined planispiral coil, followed by a flattened uniserial portion which becomes triangular in the last two chambers. Figures 17-19 × 27. 20a, Side view of holotype (U.S.N.M. No. P952) showing flattened development which led to its original description as a *Flabellammina*. 20b, Edge view showing degree of compression. 20c, Top view, showing slightly elongate aperture. × 22. Figures 17-20 from the Duck Creek formation of Texas.

PLATE 4. Albian *Triplasia*

Figs. 1-9. *Triplasia acutocarinata* (Alexander and Smith).............. 19
1, Side view of hypotype (U.S.N.M. No. P906) from the Kiamichi formation of Texas. 2, Side view of unusually broad hypotype (U.S.N.M. No. P1025) from the Fort Worth formation of Oklahoma. 3, Side view of large flaring hypotype (U.S.N.M. No. P907) from the Duck Creek formation of Texas. 4, 7, Side view of hypotypes (U.S.N.M. Nos. P909a, b), from the Weno formation of Texas. 5a, Side view of topotype (U.S.N.M. No. P904), showing early planispiral coil and produced final chamber. 5b, Top view, showing a more elongate aperture than is typical. 6a, Side view of holotype (U.S.N.M. No. P903). 6b, Top view, showing flangelike angles and rounded aperture. Figures 5 and 6 from the Duck Creek formation of Texas. 8a, Side view of quadrate hypotype (U.S.N.M. No. P909c). 8b, Top view, showing the narrow angles typical of the species, and the rounded aperture. From the Weno formation of Texas. 9, Side view of long and narrow hypotype (U.S.N.M. No. P908) from the Denton formation of Texas. All figures × 22.

Figs. 10-15b. *Triplasia wenoensis* (Alexander and Smith)............. 28
10-12, Side views of hypotypes (U.S.N.M. Nos. P959 a-c), showing small size, flaring test, and roughly finished wall. 13, Side view of larger hypotype (U.S.N.M. No. P958). 14a, Side view of holotype (U.S.N.M. No. P957), showing small size, rounded angles, and moderately excavated sides. 14b, Top view, showing rounded aperture. 15a, Side view of quadrate hypotype (U.S.N.M. No. P959d). 15b, Top view, showing moderately excavated sides. All figures × 22. From the Weno formation of Texas.

PLATE 5. Albian to Senonian *Triplasia*

Figs. 1a-7. *Triplasia insolita* (Alexander and Smith).................... 24
1a, Side view of holotype (U.S.N.M. No. P934), showing triangular character of early portion grading into a quadrate later portion. 1b, Top view, showing rounded aperture. 2a, Side view of topotype (U.S.N.M. No. P936a), showing early planispiral coil and later *Flabellammina*-stage before development of the third angle. 2b, Edge view, showing flattened character of coil and early arched chambers with abrupt thickening in the later development. 3a, Side view of topotype (U.S.N.M. No. P936b), showing quadrate de-

Page

velopment immediately after the planispiral stage. 3b, Edge view, showing compressed early portion and abrupt thickening. Figures 1-3 from the Duck Creek formation (Lower Cretaceous, Albian) of Texas. 4, Side view of small hypotype (U.S.N.M. No. P940) from the Weno formation (Lower Cretaceous, Albian) of Texas. 5, Side view of hypotype (U.S.N.M. No. P938a) from the Main Street formation (Lower Cretaceous, Albian) of Texas. 6, Side view of hypotype (U.S.N.M. No. P939) from the Fort Worth formation (Lower Cretaceous, Albian) of Texas. 7, Side view of hypotype (U.S.N.M. No. P938b) from the Main Street formation of Texas. All figures × 22.

Figs. 8-15. *Triplasia nodosa* Loeblich and Tappan, new species........... 25

8, Small triangular paratype (U.S.N.M. No. P944a) showing early coil and produced final chamber, from the Grayson formation (mid-Cretaceous, Cenomanian) of Texas. 9, 10, Larger triangular paratypes (U.S.N.M. Nos. P942a-b) from the Grayson formation of Oklahoma, with the latter specimen losing the third angle in the later chambers. 11, Paratype (U.S.N.M. No. P949), showing early coil followed by a flattened uniserial portion, the triangular development appearing only in the last half of the test. From the Main Street formation (Lower Cretaceous, Albian) of Texas. 12a, Side view of holotype (U.S.N.M. No. P941), showing typical triangular development and extended neck. 12b, Top view, showing triangular section. From the Grayson formation of Oklahoma. 13a, Quadrate paratype (U.S.N.M. No. P947) showing constricted sutures and nodose appearance of the pyriform later chambers. 13b, Top view, showing quadrate section. From the Main Street formation of Texas. 14, 15, Triangular paratypes (U.S.N.M. Nos. P944b-c), showing angular nodose tests and much-produced neck. From the Grayson formation of Texas. All figures × 22.

Figs. 16-17c. *Triplasia murchisoni* Reuss................................ 30

16, Face view of narrow paratype, showing gently arched sutures. 17a, Side view of holotype, a flared specimen. 17b, Face view. 17c, Top view, showing slightly excavated sides, subacute angles, and rounded aperture (after Reuss). Approximately × 10. Lower Senonian or Turonian of Austria.

Figs. 18-20b. *Triplasia beisseli* (Marie)................................ 32

18, 19a, Side views of typical triangular hypotypes (topotypes of *Haplophragmium murchisoni* of Beissel (U.S.N.M. Nos. P963, P964), showing regular planispiral coil and gradually enlarging test. 19b, Top view, showing slight excavation of sides, rounded angles, and slit aperture. Both × 10. From the Mucronaten-Kreide (upper Senonian) of Germany. 20a, Side view of quadrate hypotype (U.S.N.M. No. P967), showing basal coil, very slightly enlarging test, and gently arched sutures. 20b, Top view, showing quadrate section, excavated sides, and slit aperture. × 22. From the lower Senonian of Germany.

Figs. 21a-22b. *Triplasia römeri* (Reuss)................................ 38

21a, Side view of holotype, showing rounded base, nearly parallel

Page

margins and sharp angles. 21b, Face view, showing weakly curved sutures, and comparatively high chambers. 21c, Top view, showing somewhat convex sides of the later portion and the rounded aperture (after Reuss), approximately × 16. Mucronaten-Kreide (upper Senonian) of Germany. 22a, Side view of hypotype (U.S.N.M. No. P988), showing basal coil, slightly curved test with nearly parallel margins, and high narrow chambers. 22b, Top view. × 22. From the upper Senonian of Germany.

Plate 6. Senonian *Triplasia*

Figs. 1-5. *Triplasia deadericki* Loeblich and Tappan, new species........ 35
1, Side view of compressed paratype (U.S.N.M. No. P981), which is *Flabellammina* in character, showing low early chambers and the higher and rounded final chamber. 2, Side view of paratype (U.S.N.M. No. P979a) with planispiral early portion, followed by triangular uniserial portion, and last chambers becoming higher and rounded in section. 3a, Side view of holotype (U.S.N.M. No. P978), showing typical triangular form with moderately excavated sides and higher rounded final chamber. 3b, Top view, showing ovate aperture, and excavated sides of triangular portion. 4a, Side view of small quadrate paratype (U.S.N.M. No. P979b), showing early coil and comparatively low early quadrate chambers. 4b, Top view, showing quadrate section. 5, Side view of small paratype (U.S.N.M. No. P979c) with rounded final chamber. All × 22. From the Annona chalk of Arkansas.

Figs. 6-13. *Triplasia taylorensis* (Cushman and Waters)................. 39
6, Side view of hypotype (U.S.N.M. No. P1000a) showing a typical large flaring specimen, with broad low chambers. 7a, Side view of hypotype (U.S.N.M. No. P1000b) which is coiled at the base, then triangular in section, and becomes quadrangular in the last half of the test. 7b, Top view, showing quadrate section. Figures 6-7 × 10. From the upper Taylor marl of Texas. 8, Holotype (Cushman coll. No. 12033), a smaller form, which is otherwise typical of the species, × 22. From the Taylor marl of Texas. 9a, Side view of small quadrate hypotype (U.S.N.M. No. 1000c), showing typical flaring test. 9b, Top view showing sharp angles, excavated sides, and slit aperture. 10a, 11, 12, Side view of regularly flaring triangular hypotypes (U.S.N.M. Nos. P1000d-f). 10b, Top view, showing excavated sides and slit aperture. Figures 9-12, × 10. 13, Side view of small quadrate hypotype (U.S.N.M. No. P1000g), × 22. Figures 9-13 from the upper Taylor marl of Texas.

Figs. 14-19b. *Triplasia plummerae* Loeblich and Tappan, new species...... 36
14, Side view of paratype (U.S.N.M. No. P984a), showing flaring triangular test, broad and low early chambers, and higher and somewhat rounded final chamber. 15a, Side view of quadrate paratype (U.S.N.M. No. P984b), showing gently arched sutures. 15b, Top view, showing flat to moderately excavated sides. 16, Side view of triangular paratype (U.S.N.M. No. P984c). 17a, Side view of quad-

Page

rate paratype (U.S.N.M. No. P984d). 17b, Top view, showing nearly flat sides and slit aperture. 18, Side view of paratype (U.S.N.M. No. P984e). 19a, Side view of holotype (U.S.N.M. No. P983), showing broad and low early chambers, and higher, rounded final chamber with slight neck. 19b, Top view, showing nearly flat sides and slit aperture. All × 10. From the upper Taylor marl of Texas.

PLATE 7. Senonian to Pliocene *Triplasia*

Figs. 1a-5. *Triplasia cushmani* (Alexander and Smith) 34
1a, Hypotype (U.S.N.M. No. P969) showing early planispiral coil and triangular later portion. 1b, Top view, showing acute angles and excavated sides and slit aperture. From the Annona chalk (Upper Cretaceous, Senonian) of Arkansas. 2, Side view of coarsely arenaceous holotype (U.S.N.M. No. P989), showing early coil and broad low triangular chambers, from the Pecan Gap (Upper Cretaceous, Senonian) of Texas. 3a, Side view of large quadrate hypotype (U.S.N.M. No. P991), 3b, Top view, showing excavated sides and slit aperture. From the Annona chalk of Arkansas. 4, 5, Small hypotypes (U.S.N.M. Nos. P971a-b) from the Ozan sand (Upper Cretaceous, Senonian) of Arkansas. All × 22.

Figs. 6a-9. *Triplasia rugosissima* (Alexander and Smith) 38
6a, Side view of quadrate hypotype (U.S.N.M. No. P997a). 6b, Top view, showing nearly flat sides and slit aperture. From the Annona chalk of Arkansas. 7a, Side view of holotype (U.S.N.M. No. P993), showing coarsely arenaceous test, triangular uniserial portion, and somewhat flattened final chamber. 7b, Top view, showing slit aperture. From the Taylor clay of Texas. 8, 9, Side view of hypotypes (U.S.N.M. Nos. P997b-c) from the Annona chalk of Arkansas. All × 10.

Figs. 10a-11b. *Triplasia saratogensis* Loeblich and Tappan, new species.... 41
10a, Holotype (U.S.N.M. No. P1005), showing typical triangular form, and subparallel margins. 10b, Top view, showing slightly convex sides and broadly rounded angles, and ovate aperture. 11a, Side view of quadrate paratype (U.S.N.M. No. P1006), showing moderately excavated sides in the early portion and nearly flat sides in the later portion. 11b, Top view, showing flattened sides, quadrate section, and ovate aperture. From the Saratoga chalk (Upper Cretaceous, Maestrichtian) of Arkansas. × 22.

Figs. 12a, b. *Triplasia* species 42
12a, Side view of specimen (U.S.N.M. No. 560500), showing early coil and later triangular portion. 12b, Top view, showing slit aperture. × 22. From the Lodo formation (Paleocene and Eocene) of California.

Figs. 13a-14b. *Triplasia fundibularis* (Harris and Jobe) 43
13a, Side view of large hypotype (U.S.N.M No. P1014a), showing broad, low chambers, flaring test, and excavated sides. 13b, Top view. 14a, Side view of smaller hypotype (U.S.N.M. No. P1014b),

Page

showing broadly rounded base and gently arched sutures. 14b, Top view. × 27. Topotypes from the Midway formation (Paleocene) of Arkansas.

Fig. 15. *Triplasia abkhasicus* (Keller) 31
Holotype, showing early planispiral coil and triangular uniserial portion, with rounded angles (after Keller). Approximately × 27. From the lower Senonian (Campanian) of the western Caucasus, U.S.S.R.

Figs. 16a-17b. *Triplasia minuta* (Reuss) 47
16a, Face view of holotype, showing absence of a distinct coil and gently arched uniserial chambers. 16b, Side view, showing grooved angles described by Reuss, but which may be due to breakage of the fragile, very acute angles. 16c, Top view, showing very sharply angled test and deeply excavated sides. 17a, Face view of more flared paratype. 17b, Side view (after Reuss). From the Miocene of Poland.

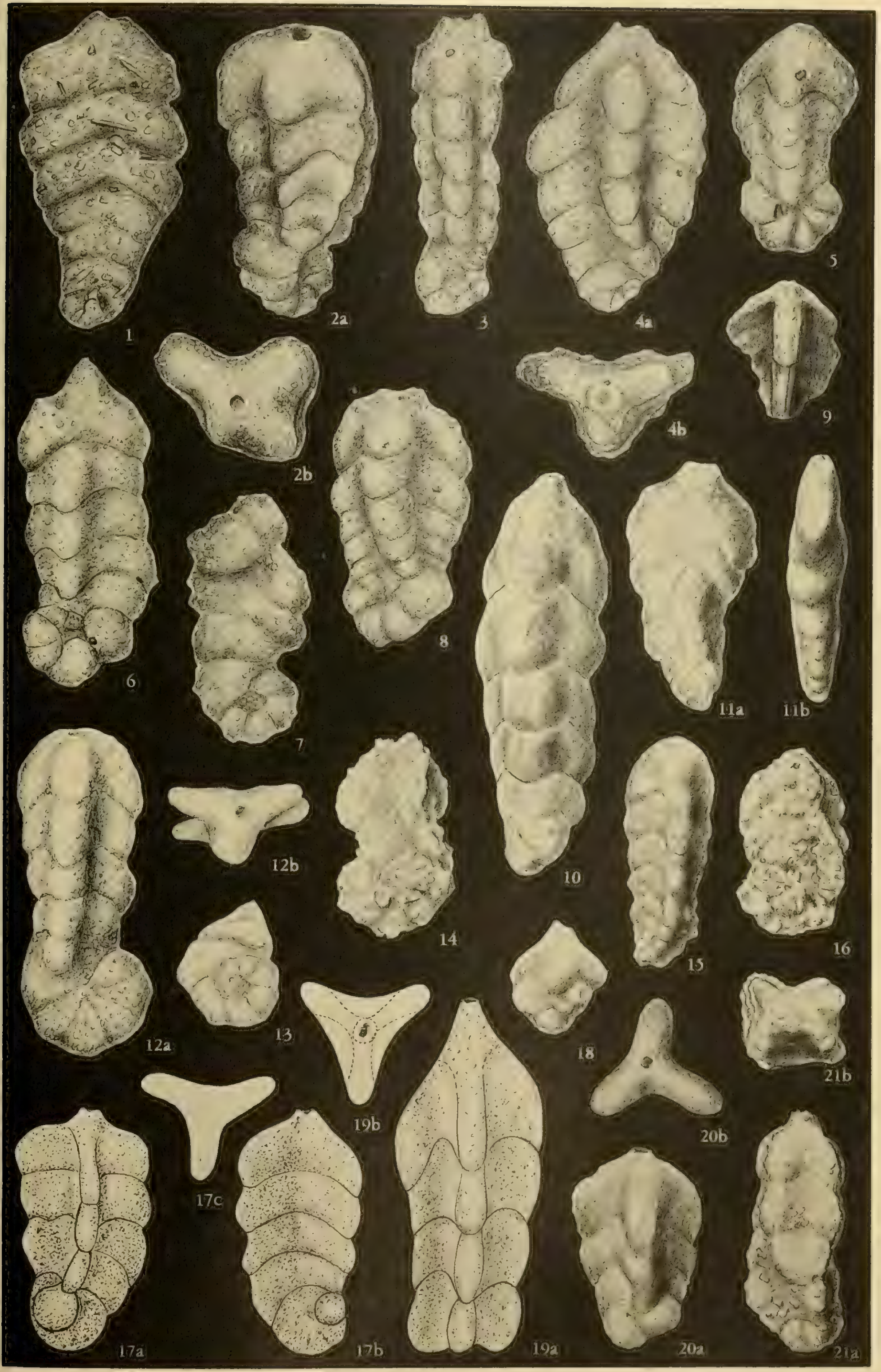
Figs. 18a-b. *Triplasia wrighti* (De Amicis) 48
18a, Side view of holotype, showing large coil and comparatively narrow triangular uniserial portion with nearly parallel margins and broad, low, slightly arched chambers. 18b, Top view, showing slightly convex sides and ovate aperture (after De Amicis), × 16. From the lower Pliocene of Italy.

PLATE 8. Oligocene to Recent *Triplasia*

Figs. 1a-c. *Triplasia hungarica* (Majzon) 45
1a, Side view of quadrate holotype, showing large planispiral coil and broad, low, quadrate uniserial chambers. 1b, Face view, showing compression of the planispiral coil and arched sutures of the uniserial portion. 1c, Top view, showing excavated sides and ovate aperture (after Majzon). × 28. From the Oligocene of Hungary.

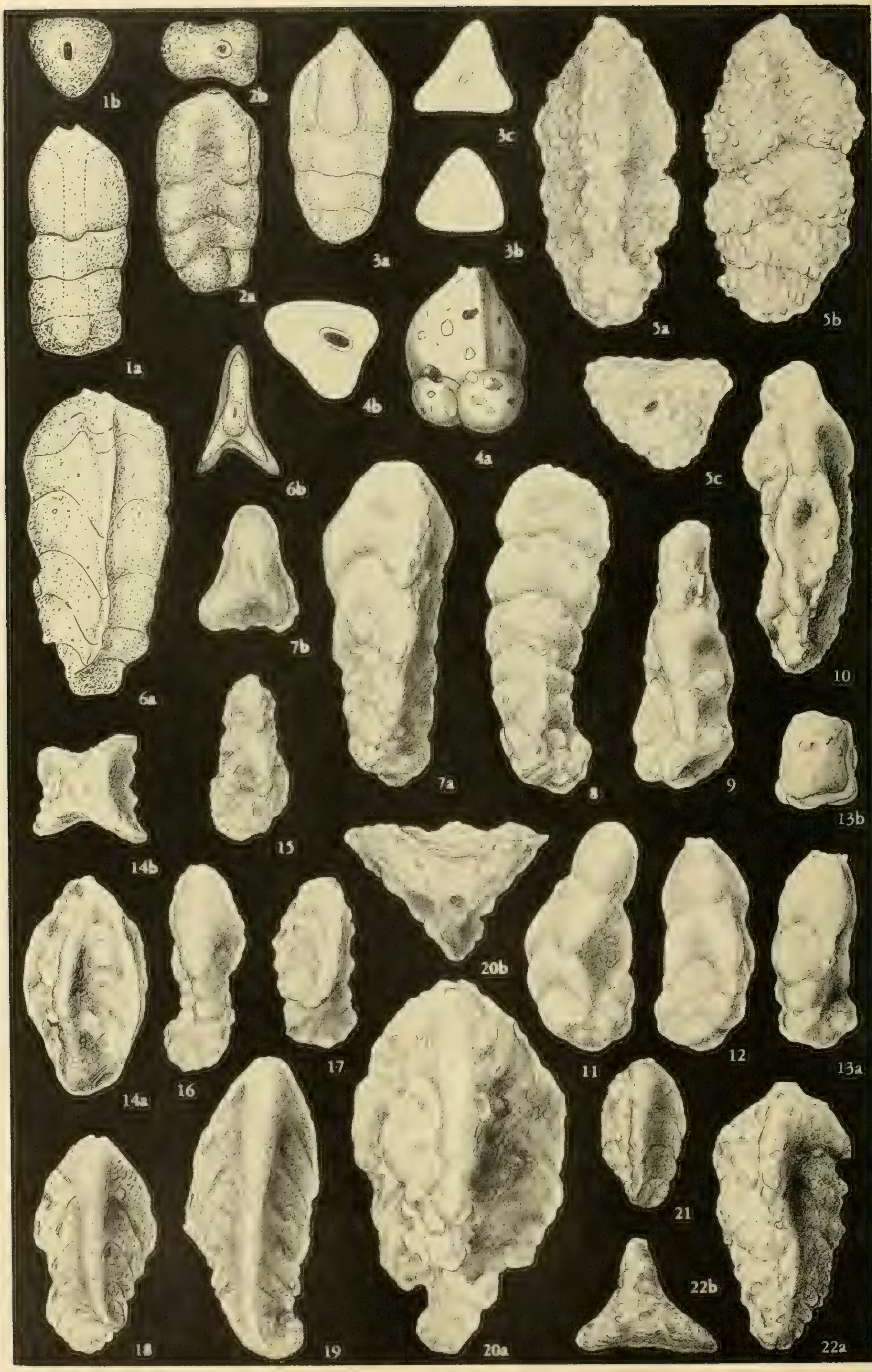
Figs. 2-4b. *Triplasia marwicki* Loeblich and Tappan, new species...... 46
2, Side view of small paratype (U.S.N.M. No. 1018a), showing flared test and arched sutures. 3a, Side view of larger paratype (U.S.N.M. No. P1018b). 3b, Top view. Both from the Miocene of Motatura, New Zealand. 4a, Side view of holotype (U.S.N.M. No. P1016). 4b, Top view. From the Miocene of Kawhia, New Zealand. All × 15.

Figs. 5-9b. *Triplasia variabilis* (Brady) 48
5, Side view of small quadrate hypotype (U.S.N.M. No. P1029a). 6, Side view of small triangular hypotype (U.S.N.M. No. P1029b). 7a, Side view of large triangular hypotype (U.S.N.M. No. P1029c). 7b, Top view showing sharp angles, concave sides, and slit aperture. 8, Side view of small hypotype (U.S.N.M. No. P1029d), 9a, Side view of large quadrate hypotype (U.S.N.M. No. P1029e), showing arched sutures. 9b, Top view, showing quadrate section and slit aperture. All × 15. From coral sands at 210 fathoms, off Kandavu, Fiji Islands.



FORAMINIFERAL GENUS TRIPLASIA

(SEE EXPLANATION OF PLATES AT END OF TEXT.)

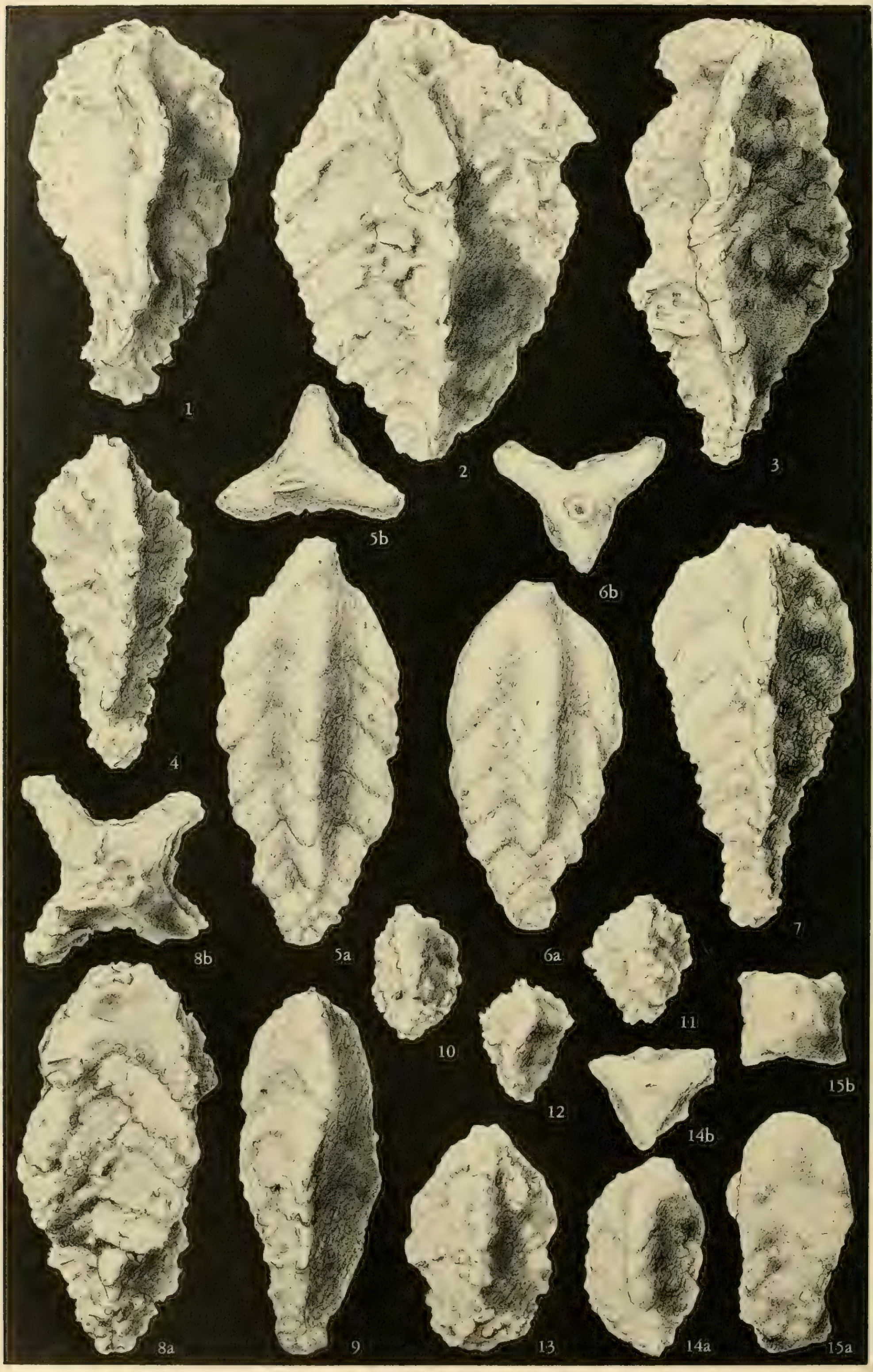


FORAMINIFERAL GENUS TRIPLASIA

(SEE EXPLANATION OF PLATES AT END OF TEXT.)

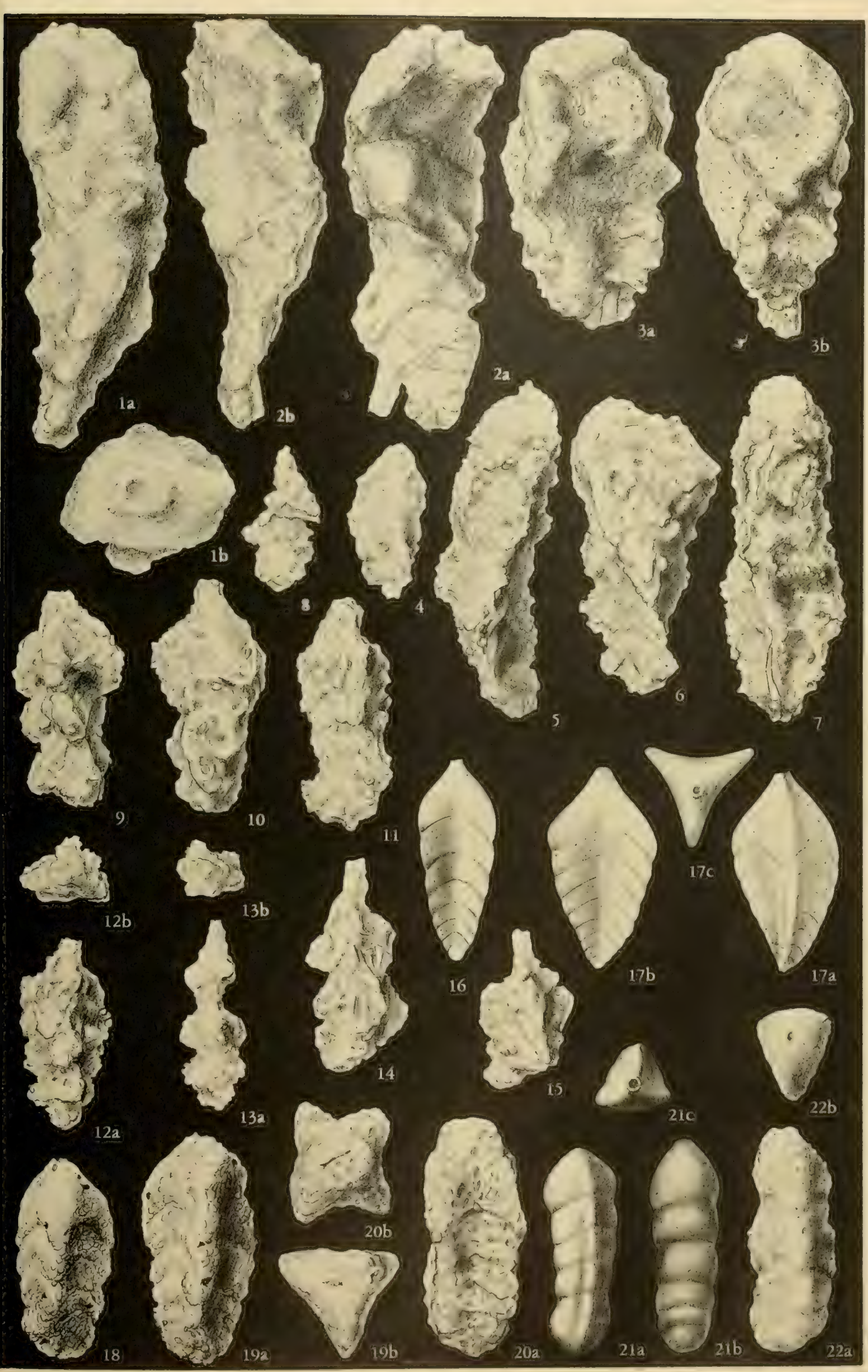
FORAMINIFERAL GENUS TRIPLASIA

(SEE EXPLANATION OF PLATES AT END OF TEXT.)



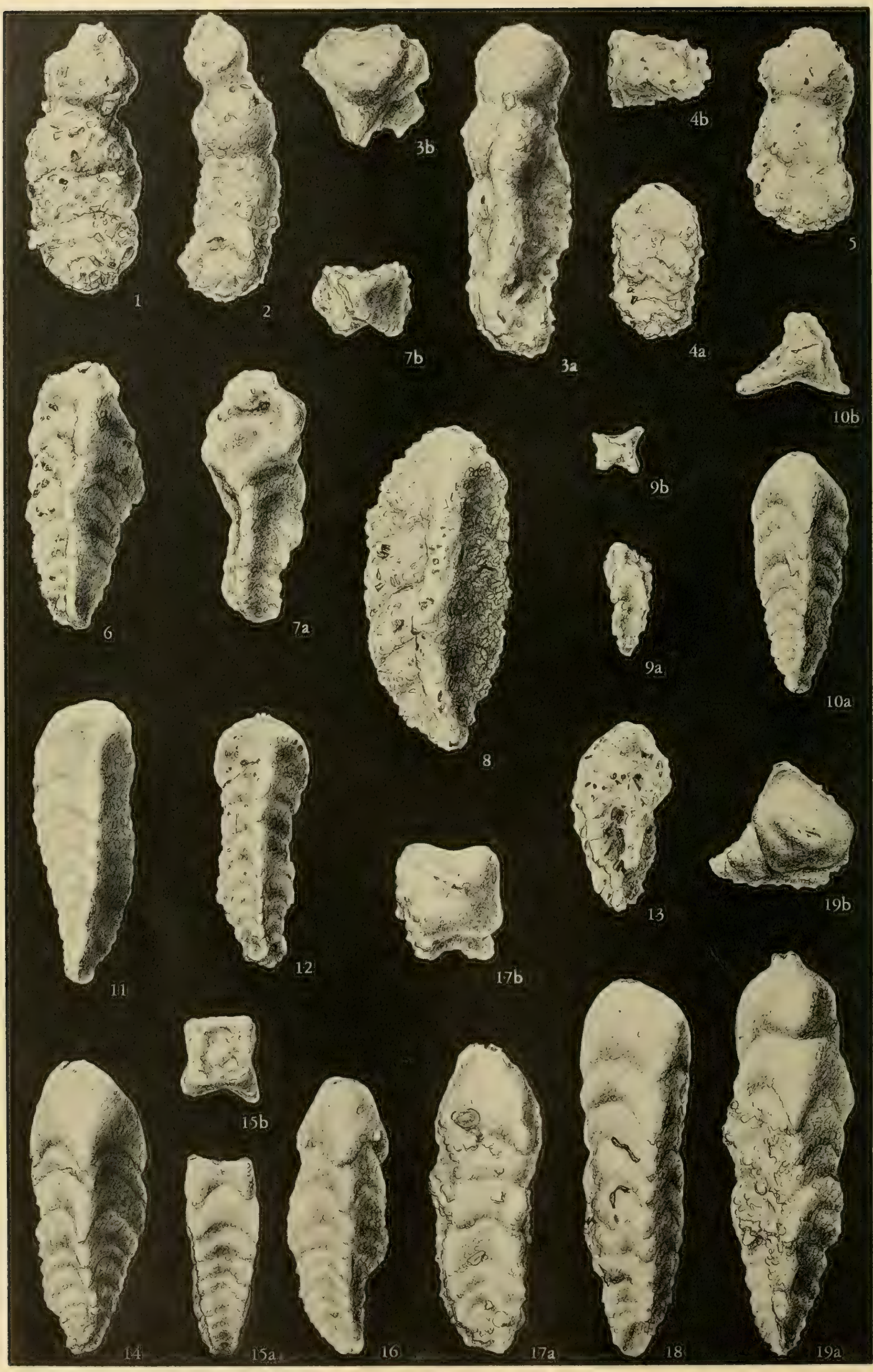
FORAMINIFERAL GENUS TRIPLASIA

(SEE EXPLANATION OF PLATES AT END OF TEXT.)



FORAMINIFERAL GENUS TRIPLASIA

(SEE EXPLANATION OF PLATES AT END OF TEXT.)

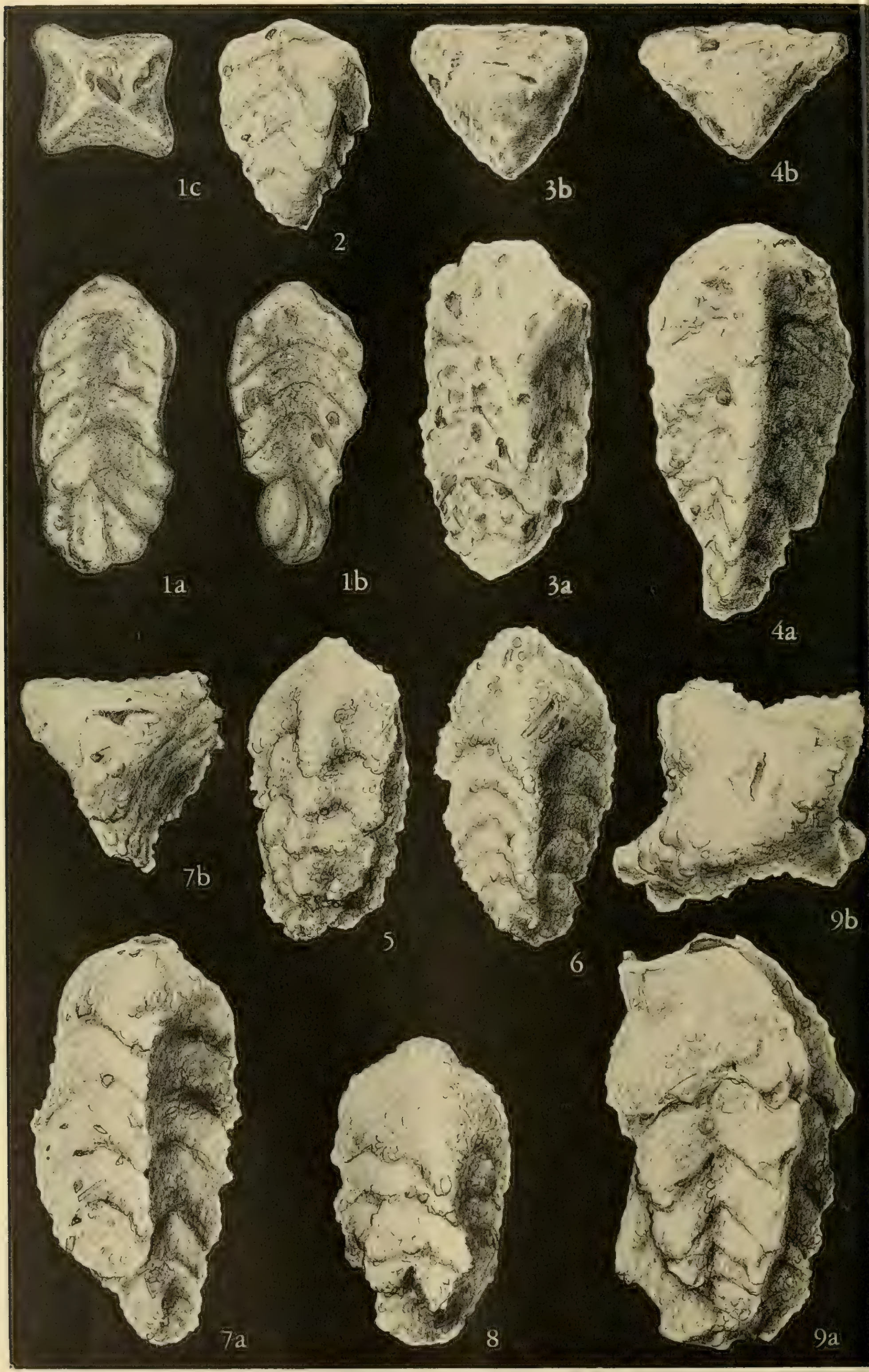


Foraminiferal genus Triplasia

(See explanation of plates at end of text.)

Foraminiferal genus Triplasia

(See explanation of plates at end of text.)



Foraminiferal genus Triplasia

(SEE EXPLANATION OF PLATES AT END OF TEXT.)

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 117, NUMBER 16

Roebling Fund

SOLAR VARIATION AND PRECIPITATION AT PEORIA, ILLINOIS

BY
C. G. ABBOT
Research Associate, Smithsonian Institution

(Publication 4095)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
SEPTEMBER 3, 1952

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

Roebling Fund

SOLAR VARIATION AND PRECIPITATION AT PEORIA, ILLINOIS

By C. G. ABBOT
Research Associate, Smithsonian Institution

In a recent paper [1] it was shown that the intensity of the sun's radiation, as it is outside the earth's atmosphere, varies simultaneously in 23 regular periods, all aliquot parts of approximately 272 months. It would naturally follow that details of variation in observed values of the solar constant of radiation would tend to repeat at intervals of about 23 years. Figure 4A of the paper cited shows that this is indeed the case.

Many years ago it was shown that the precipitation at Peoria, Ill., also tended very strongly to exhibit repetitions of features at intervals of 23 years. I reproduce here as figure 1, the figure 33 of an earlier paper.[2]

Intending to trace the effect of the solar variations above noted on weather, it seemed well to study first the records of precipitation at Peoria, as these were already known to exhibit influences of the master cycle of about 23 years. I have been engaged over 3 years in this investigation, for unexpected complexities kept cropping up, which made it necessary again and again to scrap all results and begin at the beginning. Without being tedious, it may be said that I have tabulated over 1,000 months of precipitation records, of the years between 1856 and 1939, separately in 20 to 30 supposed periods, and repeated the whole tabulation no less than 14 times.

Futility of determining periods from weather records.—Knowing that the sun's radiation varies in regular periods, which are integral submultiples of about 23 years, but being restricted by available solar-constant observations to little more than 20 years with many gaps and inaccuracies in these records, I hoped at first to use the continuous series of Peoria precipitation records from 1856 to 1939 to establish which submultiples of 23 years are active, and to fix their exact lengths.

---

[1] Smithsonian Misc. Coll., vol. 117, No. 10, 1952.
[2] Smithsonian Misc. Coll., vol. 94, No. 10, 1935.

It was soon disclosed that the phases of periodicities, though invariable in solar variation, shifted in Peoria precipitation records, depending on the time of the year. I suppose the cause to be associated with considerations of lag in response to solar impulses. It is patent that though the sun's heating potential reaches a maximum daily at noon, maximum temperatures do not come until several hours after noon, and their arrival displays different lags in different localities, and in the same locality at different times and seasons. Similar it must be with regard to all weather responses to all solar periodicities.

Subdivision of the year.—Accordingly, one of my first modifications of procedure was to prepare separate tabulations for each periodicity in three fractions of the year, namely: January to April, May to August, September to December. Doubtless a finer subdivision of the year would theoretically be better, but for periodicities of 10 to 20 months in length the number of columns in a tabulation becomes few.

Interference between periodic effects.—It is plain that the determination of every periodic fluctuation in precipitation must be affected by the presence, implicitly in the data, of above 20 other periods of different lengths. Theoretically these disturbing influences can only be completely sifted out of the result for one period, if the mean values are computed from an infinite number of repetitions of the chosen period. When, instead of infinity, one becomes limited to a few repetitions, the computed march of the investigated periodicity must evidently be very imperfectly determined. Hence, on account of paucity of data, it was impracticable to divide the years beyond the triple division mentioned above.

Sunspot frequency affects phases.—But still another limitation of freedom in tabulation soon appeared. The phases of features in the periodicities computed were found different in different years. This was found to be associated with sunspot frequency. As said above, the cause of the phenomena of phase changes is probably to be assigned to variable lag of response in weather to solar impulses, depending on the condition of the atmosphere. Such changes in lag are evidently attributable to the varying character of the atmosphere at different seasons of the year as regards transparency, cloudiness, and other conditions. But sunspots continually bombard the atmosphere with multitudes of electric ions. These act as centers of condensation for the constituents of haze. Hence it was only to be expected that phase changes would be associated with Wolf sunspot numbers. Here, again, a compromise had to be made. It was decided to subdivide the precipitation data in two groups, for Wolf numbers $\gtrless 20$.

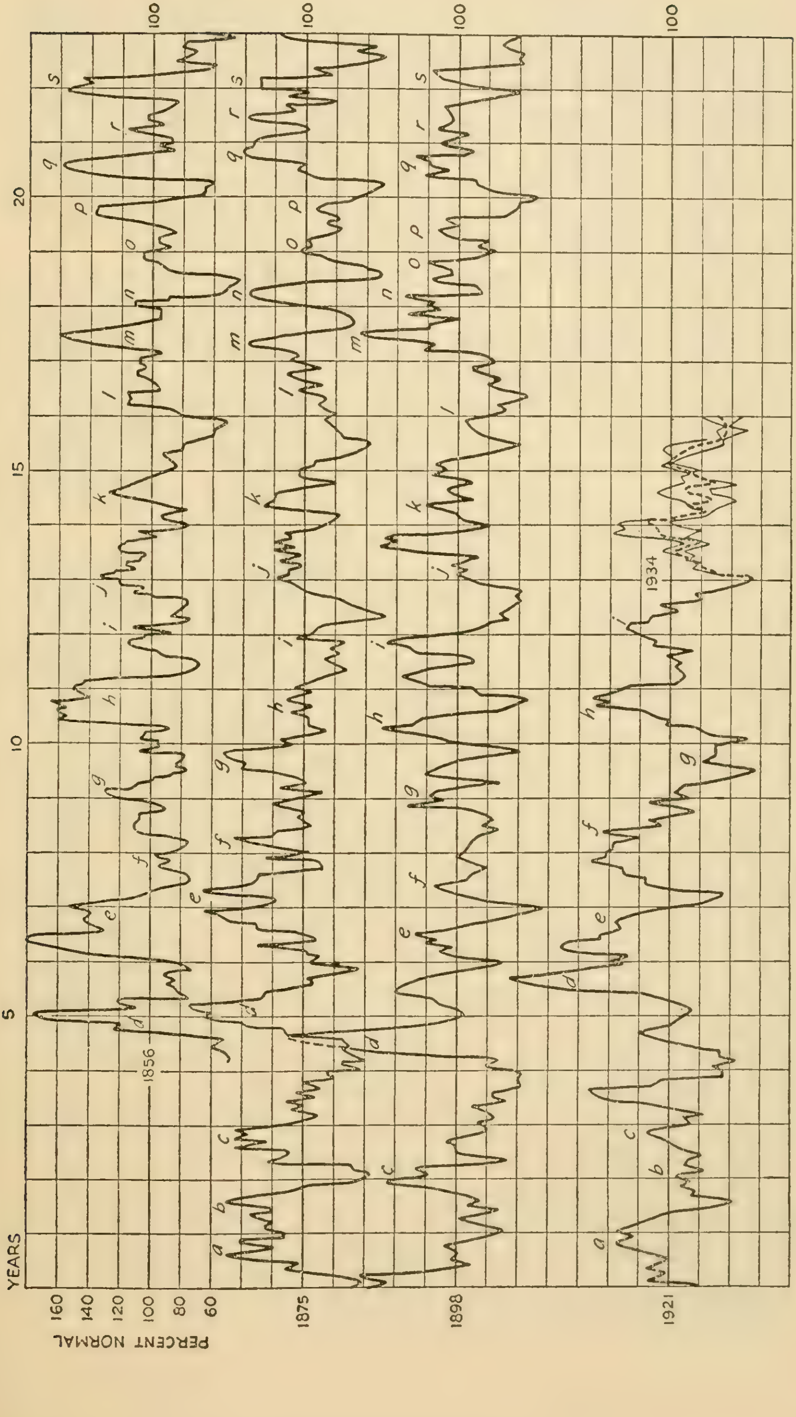


FIG. 1.—Twenty-three-year periodicity in Peoria precipitation.

Necessary roughness of determinations.—Between the accidental influences associated with rainfall, cloudiness, haziness, etc., the undeterminable interferences of some 20 periodic solar variations on the periodicity being considered, and the necessary subdivision of the data for seasonal and sunspot alterations of atmospheric quality, the determinations of periodicities in precipitation became too rough to warrant conclusions that such and such submultiples of 23 years were real, effective periods in solar variations.

Length and number of periods necessarily determined from solar observations.—Thrust back on the solar-constant observations as the only sound source of knowledge of the solar periods, I laid aside the investigation of Peoria precipitation to prepare the paper above cited (footnote 1). In that paper are listed 23 periods that appear to be real in solar variation, and 15 others that were tried and found wanting. In the latter part of the Peoria tabulations the investigation was limited to the confirmed 23 periods. However, for convenience in tabulating, the lengths of some periods were slightly altered.

Faulty normals.—Still another unsuspected hitch occurred in the investigation, which caused several weeks delay and a completely new tabulation of the precipitation data. This is explained in another recent paper.[3] In substance it amounts to this: The monthly normal values printed at the bottom of the pages in World Weather Records [4] make no distinction between times of sunspot maximum and times of sunspot minimum. Two consequences result. First, the average of the monthly data computed as percentages of the published normals of precipitation at Peoria is about 9 percent higher for times when Wolf sunspot numbers exceed 20 than for times when these Wolf numbers are below 20. Second, far more serious, and indeed fatal to success in my investigations made theretofore, is the fact that when averages of data timed for sunspots $\gtreqless 20$ are separated, there is found a large discrepancy, month by month, between these averages for Wolf numbers <20 and for Wolf numbers >20. This plays havoc with tabulations of periodicity. The published normals, in fact, combine two contradicting sets of data as foreign to each other in attitude as dogs are from cats, and tabulations including both sorts in the same periodicity are worthless.

Final preparation of the data.—The recorded monthly values of precipitation at Peoria for the years 1856 to 1950, found in World Weather Records and later publications, were segregated in two

---

[3] Smithsonian Misc. Coll., vol. 117, No. 11, 1952.

[4] Smithsonian Misc. Coll., vols. 79, 90, and 105.

groups, for Wolf numbers $\gtreqless 20$. Monthly normal values were computed separately, 52 years in the high-sunspot group, 30 years in the other. Two years were omitted, when the months were about evenly divided between the two classes.

The new normals for Peoria precipitation, as expressed in inches, are as follows:

Sunspots	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
>20	1.84	1.87	2.80	3.62	3.90	4.04	3.70	3.06	3.56	2.22	2.36	1.91
<20	1.58	1.71	2.82	2.79	3.88	3.24	3.40	2.66	3.85	2.56	2.22	1.88

From these new normals percentages of normal precipitation were computed for every month, 1856 to 1950. There are such large and suddenly changing jumps from month to month in these percentages of normals that the data were then smoothed by 5-month consecutive means. Thus, for March compute

$$\frac{\text{Jan.}+\text{Feb.}+\text{Mar.}+\text{Apr.}+\text{May}}{5}.$$

For April drop January and add June, and so on. Even then, as some exceptionally rainy months occurred, the smoothed data would soar above 200 percent for a brief interval. With the necessarily few columns in a tabulation, such an exceptional case might quite vitiate the determination of a periodicity. Hence for some 20 exceptional months out of over 1,000, the original values were scaled down to 200 before the smoothing process was done.

Division of the interval.—While the number and lengths of the periodicities to be sought in Peoria precipitation had been fixed by study of solar-constant observations, and nothing was to be learned as to the reality or the exact length of these periodicities in solar radiation from the precipitation data, it still was desirable to tabulate Peoria precipitation in several parts independently. Certain of the solar periodicities might produce such weak responses in precipitation that the several groups might give no agreeing results distinguishable from accidental error. Such weak periodic effects could be neglected. Such indeed proved to be the case with periods of $2\frac{1}{7}$ and $3\frac{1}{15}$ months, and with the periodicity of 68 months. There were strong features in the separate determinations of the periodicity of 68 months, but they were so confused by overriding interference from various shorter periods as to be uncertain. Hence that period was dropped.

More important, however, just as the changing atmospheric conditions were found to alter phases with the seasons, and with the prevalence of sunspots, it proved that, apart from these already noted phase alterations, there were secular changes of phases. One group of years, though yielding the same forms of periodicities as another, yielded them in different phases. Such effects were found to vary in character for periods of different lengths.

In the tabulations, therefore, the years 1856 to 1900 were tabulated separately from the years 1900 to 1939. Discordant phases appearing in the earlier interval were shifted to accord with the phases for the years 1900 to 1939. Then the two determinations were averaged together. So the full strength of the data from 1856 to 1939 was concentrated in the phases prevailing from 1900 to 1939.

Fractional months in periods.—In order to preserve the exact period in such cases as $9\frac{1}{6}$, $11\frac{1}{5}$, and $15\frac{1}{6}$ months, and others not exactly even months in length, some columns in tabulating were made a month longer or a month shorter than others. In case of long periods, months were interpolated or cut out of the columns from place to place as required to make the average length of the columns equal to the period. Such additions to columns may be noted in tables 1 and 2 for the $9\frac{1}{6}$-month periodicity, and in tables 3 and 4 for $15\frac{1}{6}$ months.

Examples of tabulation.—In order to fix ideas, I now give two actual tabulations and corresponding plots, to bring out the process employed, and to clarify the explanations above. I select the periods of $9\frac{1}{6}$ and $15\frac{1}{6}$ months. Table 1 gives the tabulation for $9\frac{1}{6}$ months suited to Wolf numbers >20, and table 2 that for Wolf numbers <20. In each table the segregation of the year by 4-month intervals is preserved. Also, two separate tables for each 4-month interval are made, one for the first half, the other for the last half of the 84-year interval. As stated above, there is often found a discrepancy in phase between results of the first and second halves of the 84-year interval. In table 1, sections A_1 and B_1, the symbol $A_1\uparrow_1$ means that to bring the phase of the first half, A_1, to that of the second half, B_1, the mean values for A_1 are moved one month backward. The symbol $A_2\uparrow_2$ obtains in sections A_2 and B_2, and $A_3\downarrow_3$ was required for sections A_3 and B_3. Similar symbols for shifts appear in the tabulation of the data suited to Wolf numbers <20. The final columns, marked Δ, give the departures from the average percentage of results in the general means. The use of these columns of departures will be explained below.

Tables 3 and 4, relating to the periodicity of $15\frac{1}{6}$ months, will be understood from the preceding description of tables 1 and 2 for $9\frac{1}{6}$ months. As before, symbols involving $\uparrow$ mean that the means of the first half of the data were shifted backward by one or more months, and symbols involving $\downarrow$ indicate the contrary.

TABLE I.—*Peoria precipitation. The* $9\frac{1}{6}$*-month period*

Sunspots > 20

A₁

Jan. ’59	Feb. ’62	Mar. ’65	Jan. ’69	Apr. ’71	Jan. ’72	Mar. ’81	Apr. ’84	Jan. ’85	Feb. ’91	Mar. ’68	Mean
149	103	105	108	82	67	96	111	106	82	113	102.0
124	101	112	90	86	67	126	97	112	88	111	101.3
102	80	101	102	95	56	101	109	87	86	111	93.9
96	113	99	127	118	90	85	127	79	91	91	105.0
84	135	118	139	139	124	99	140	90	99	98	115.0
72	135	121	149	139	135	122	139	91	90	71	114.9
74	142	115	133	139	142	122	153	96	86	102	118.5
77	139	95	116	109	137	146	154	108	105	113	118.5
87	142	109	106	79	118	151	131	97	115	106	112.9
96									91	109	

B₁

Mar. ’94	Feb. ’04	Mar. ’07	Feb. ’17	Apr. ’26	Jan. ’27	Mar. ’36	Apr. ’39	Mean	$A_1{\uparrow}_1$	Mean	Δ
96	93	84	83	96	133	67	153	98.1	101.3	99.7	− 5.9
89	106	64	77	103	121	50	128	92.3	93.9	93.1	−12.5
79	98	89	93	126	149	39	121	99.2	105.0	102.1	− 3.5
73	94	113	100	155	158	41	97	103.9	115.0	109.4	+ 3.8
86	89	114	106	167	155	75	108	112.5	114.9	113.7	+ 8.1
80	107	106	98	178	132	97	90	111.0	118.5	114.7	+ 9.1
84	87	101	106	158	137	104	71	106.0	118.5	112.2	+ 6.2
95	76	92	70	136	135	132	64	100.0	112.7	106.4	+ 0.8
93	80	58	68	124	135	148	69	96.9	102.0	99.5	− 6.1
									Mean	105.6	

A₂

Aug. ’60	May ’61	Aug. ’63	June ’64	July ’70	Aug. ’73	May ’74	July ’83	June ’93	July ’96	Mean
99	91	92	75	57	87	54	95	84	136	87.0
101	81	96	55	87	84	83	93	66	109	85.5
93	74	113	79	93	104	76	107	49	116	90.4
91	84	114	98	102	129	79	102	58	83	94.0
105	82	104	115	107	124	88	106	63	91	98.5
127	76	85	107	104	111	80	124	89	77	98.0
128	100	105	122	89	115	47	107	87	108	100.0
107	87	72	114	93	85	65	86	103	105	91.5
105	85	69	125	91	62	70	100	96	108	91.1
		80								

B₂

June ’06	June ’09	Aug. ’15	May ’16	Aug. ’18	June ’19	July ’25	Aug. ’28	May ’29	June ’35	July ’38	Mean	$A_2{\uparrow}_2$	Mean	Δ
70	101	111	63	117	100	101	131	137	109	129	106.3	90.4	98.3	+0.1
82	87	120	86	120	106	116	132	124	112	107	108.4	94.0	101.2	+3.0
77	109	100	98	131	106	123	135	104	86	87	105.1	98.5	101.8	+3.6
82	131	108	106	93	111	112	150	113	88	68	105.6	98.0	101.8	+3.6
85	132	84	109	109	98	99	138	106	88	85	103.0	100.0	101.5	+3.3
114	152	95	121	114	78	96	138	86	101	104	109.0	91.5	100.2	+2.0
88	149	85	102	100	61	92	130	97	100	120	102.6	91.1	96.8	−1.4
95	107	86	84	90	81	84	129	114	98	135	100.3	87.0	93.6	−4.6
90	93	60	73	109	89	83	112	90	73	143	92.3	85.5	88.9	−9.3
	90			101								Mean	98.2	

A₃

Nov. ’59	Nov. ’62	Oct. ’69	Oct. ’72	Dec. ’81	Oct. ’82	Oct. ’85	Dec. ’91	Sept. ’92	Dec. ’94	Mean
89	132	94	88	162	88	102	99	69	72	99.5
98	137	94	96	143	91	91	110	70	67	99.7
87	142	94	87	121	92	81	100	78	58	94.0
76	135	111	89	116	126	77	115	96	57	99.8
73	107	87	98	139	98	83	131	107	45	96.8
77	79	68	112	120	114	72	129	119	82	97.2
92	70	49	89	110	129	84	116	124	89	95.2
100	66	49	98	105	136	67	104	120	101	95.6
103	72	39	97	106	114	72	75	103	98	87.9
			91	88						

B₃

Sept. ’95	Nov. ’04	Sept. ’05	Dec. ’07	Sept. ’08	Nov. ’14	Nov. ’17	Oct. ’24	Oct. ’27	Dec. ’36	Oct. ’37	Mean	$A_3{\downarrow}_3$	Mean	Δ
125	66	88	83	67	88	62	106	140	132	73	93.6	95.2	94.4	−1.4
127	44	81	98	54	88	63	65	134	109	102	87.7	95.6	91.7	−4.1
126	57	91	106	53	76	50	67	120	123	119	89.8	87.9	88.8	−7.0
119	78	101	129	67	83	69	67	99	106	127	95.0	99.5	97.2	+1.4
121	87	94	142	74	103	77	72	76	99	137	98.4	99.7	99.0	+3.2
110	100	88	122	93	93	83	54	62	85	145	94.1	94.0	94.0	−1.8
96	108	86	122	103	102	84	64	90	88	139	98.4	99.8	99.1	+3.3
93	102	84	104	104	128	116	65	95	70	150	101.0	96.8	98.9	+3.1
111	90	78	71	109	146	105	82	112	78	138	101.8	97.2	99.5	+3.7
134	92							114				Mean	95.8	

TABLE 2.—*Peoria precipitation. The 9⅙-month period*

Sunspots < 20

A_1

Apr. '58	Feb. '75	Mar. '78	Feb. '88	Apr. '97	Jan. '98	Apr. '00	Feb. '01	Mar. '65	Mean
148	65	97	119	79	157	101	80	105	105.7
159	80	115	115	92	159	58	84	112	108.2
156	95	104	102	65	165	88	85	101	106.8
139	113	123	121	54	140	96	94	99	108.8
127	106	101	110	48	113	90	73	118	98.4
137	132	109	126	67	98	98	81	121	107.4
144	137	93	109	54	108	100	81	115	104.6
138	125	100	122	93	103	84	61	95	102.3
138	106	80	110	118	100	85	62	109	100.9
						93			

B_1

Jan. '11	Apr. '13	Jan. '14	Mar. '20	Mar. '23	Jan. '24	Feb. '30	Mar. '33	Apr. '10	Mean	$A_4 \downarrow_4$	Mean	Δ
97	110	85	102	93	92	86	132	70	96.3	107.4	101.3	+4.4
109	77	75	102	92	95	87	118	76	92.3	104.6	98.4	+1.5
101	74	79	108	91	81	71	114	78	88.6	102.3	95.4	−1.5
112	62	69	81	83	105	54	101	68	81.8	100.9	91.3	−5.6
99	77	58	57	96	119	53	110	58	80.8	105.7	93.2	−3.7
94	87	65	59	100	150	41	87	61	82.7	108.2	95.4	−1.5
114	92	79	59	99	154	63	82	55	88.6	106.8	97.7	+0.8
129	95	84	70	114	154	79	83	80	98.7	108.8	103.7	+6.8
115	97	70	75	115	114	76	76	91	92.1	98.4	95.7	−1.2
		85		107						Mean	96.9	

A_2

July '57	June '67	Aug. '76	May '77	June '80	July '86	May '87	Aug. '89	May '90	Mean
84	85	154	120	118	83	50	125	69	98.7
88	76	139	112	103	85	64	111	68	94.0
86	62	110	106	85	78	67	81	62	81.9
94	62	98	129	88	85	77	107	75	90.6
74	59	75	127	81	77	82	110	76	84.6
82	50	63	136	65	97	104	111	77	87.2
88	55	59	127	85	87	107	102	77	87.4
111	85	70	138	95	86	113	102	86	96.2
135	85	103	117	87	83	125	81	78	99.3
			111		79				

B_2

July '99	Aug. '02	May '03	July '12	June '22	Aug. '31	May '32	Mean	$A_2 \downarrow_2$	Mean	Δ
94	188	113	95	79	118	80	109.6	96.2	102.9	+3.5
84	176	127	103	67	145	86	112.5	99.3	105.9	+6.5
89	153	132	106	60	134	81	107.9	98.7	103.3	+3.9
101	122	129	88	86	147	87	108.5	94.0	101.2	+1.8
116	101	126	103	83	138	86	107.5	81.9	94.7	−4.7
134	94	110	120	92	131	113	113.4	90.6	102.0	+2.6
123	98	89	113	87	104	111	103.6	84.6	94.1	−5.3
110	104	70	124	100	99	118	103.6	87.2	95.4	−4.0
116	105	83	122	81	76	126	101.3	87.4	94.3	−5.1
						140		Mean	99.4	

A_3

Dec. '65	Sept. '66	Nov. '75	Dec. '78	Sept. '79	Nov. '83	Oct. '98	Mean
80	121	132	86	112	114	107	107.5
83	112	116	68	112	99	92	97.5
99	100	122	81	135	92	84	101.9
104	100	116	64	158	87	82	101.5
79	90	129	70	164	82	73	98.2
97	97	134	79	155	100	94	108.0
109	98	143	80	170	135	101	119.4
124	98	134	78	144	134	88	114.3
133	80	138	90	119	128	76	109.1

B_3

Nov. '01	Oct. '11	Dec. '20	Sept. '21	Nov. '30	Dec. '33	Sept. '34	Mean	A_3	Mean	Δ
59	123	68	126	72	55	141	92.0	107.5	99.6	− 5.8
60	114	86	139	75	50	123	92.4	97.5	95.0	−10.4
92	89	121	131	64	56	127	97.2	101.9	99.7	− 5.7
98	83	112	129	53	45	123	91.9	101.5	96.7	− 8.7
89	101	108	142	77	50	132	99.9	98.2	99.0	− 6.4
118	101	122	137	85	73	105	105.9	108.0	107.0	+ 1.6
143	108	116	130	110	77	130	116.3	119.4	117.8	+12.4
144	124	96	115	111	103	142	119.3	114.3	116.8	+11.4
170	122	108	110	120	113	126	124.4	109.1	116.7	+11.3
								Mean	105.4	

TABLE 3.—*Peoria precipitation. The* $15\frac{1}{6}$*-month period*

Sunspots > 20

			A_1									B_1				
Feb. '59	Mar. '64	Apr. '69	Jan. '73	Feb. '83	Jan. '92	Mean	Apr. '93	Mar. '07	Jan. '16	Apr. '17	Feb. '26	Apr. '36	Mean	$A_1\downarrow_5$	Mean	Δ
24	72	127	89	114	110	106.0	120	84	95	93	84	50	87.7	105.0	96.3	— 2.0
02	69	139	98	129	100	106.2	103	64	85	100	83	39	79.0	101.2	90.1	— 8.1
96	80	149	112	136	115	114.7	84	89	86	106	96	41	83.7	89.0	86.3	—12.0
84	75	133	89	114	131	104.3	66	113	60	98	103	75	85.8	94.7	89.7	— 8.6
72	55	116	98	112	129	97.0	49	114	63	106	126	97	92.5	89.5	91.0	— 7.3
74	79	106	97	95	116	94.5	58	106	86	70	155	104	96.5	106.0	101.2	+ 2.9
77	98	94	91	93	104	93.0	63	101	98	68	167	132	104.8	106.2	105.5	+ 7.2
87	115	94	87	107	75	94.2	89	92	106	62	178	148	112.5	114.7	113.6	+15.3
96	107	94	84	102	69	92.0	87	58	109	63	158	132	101.2	104.3	102.7	+ 4.4
89	102	111	104	106	70	97.0	103	83	121	50	136	109	100.3	97.0	98.6	+ 0.3
98	114	87	129	124	78	105.0	96	98	102	69	124	123	102.0	94.5	98.3	0.0
87	125	68	124	107	96	101.2	96	106	84	77	133	106	100.3	93.0	96.7	— 1.6
76	105	49	111	86	107	89.0	89	129	73	83	121	99	99.0	94.2	96.6	— 1.7
73	112	49	115	100	119	94.7	79	142	83	84	149	85	103.7	92.0	97.8	— 0.5
77	101	39	85	111	124	89.5	73	122	77	116	158	88	105.7	97.0	101.3	+ 3.0
				97										Mean	98.3	

			A_2									B_2			
May '60	July '70	June '84	July '94	May '03	Mean	Aug. '04	June '08	May '27	Aug. '28	July '37	July '18	Mean	$A_2\downarrow_5$	Mean	Δ
92	57	109	86	113	91.4	87	122	155	131	70	105	111.7	92.0	101.8	— 0.2
100	87	127	80	127	104.2	76	104	132	132	78	117	106.5	95.4	100.9	— 1.1
103	93	140	84	132	110.4	80	71	137	135	64	120	101.2	99.0	100.1	— 1.9
99	102	139	95	129	112.8	66	67	135	150	73	131	103.7	104.6	104.1	+ 2.1
101	107	153	93	126	116.0	44	54	135	138	102	93	94.3	110.6	102.4	+ 0.4
93	104	154	72	110	106.6	57	53	135	138	110	109	100.3	91.4	95.8	— 6.2
91	89	131	67	89	93.4	78	67	140	130	127	114	109.3	104.2	106.7	+ 4.7
105	93	106	58	70	86.4	87	74	134	129	137	100	110.2	110.4	110.3	+ 8.3
127	91	112	51	83	92.8	100	93	120	112	145	90	110.0	112.8	107.8	+ 5.8
128	82	87	45	93	87.0	108	103	89	137	139	109	109.5	116.6	113.0	+11.0
107	86	79	82	106	92.0	102	104	76	124	150	101	109.5	106.6	108.0	+ 6.0
105	95	90	89	98	95.4	90	109	62	104	138	100	100.5	93.4	96.9	— 5.1
91	118	91	101	94	99.0	92	101	90	113	129	106	105.2	86.4	95.7	— 6.3
81	159	96	98	89	104.6	88	87	95	106	107	111	99.0	92.8	95.9	— 6.1
74	139	108	125	107	110.6	81	109	112	86	87	98	95.5	87.0	91.3	—10.7
84									97				Mean	102.0	

			A_3									B_3						
Nov. '57	Sept. '61	Dec. '62	Dec. '67	Oct. '71	Nov. '81	Sept. '90	Mean	Oct. '95	Nov. '05	Oct. '14	Oct. '19	Nov. '24	Dec. '34	Oct. '38	Mean	$A_3\uparrow_5$	Mean	Δ
74	82	137	55	139	151	76	102.0	127	91	85	98	65	123	68	93.9	101.3	97.6	— 3.
82	76	142	85	109	162	77	104.7	126	101	88	78	67	132	85	95.3	102.1	98.7	— 2.
88	100	135	85	79	143	77	101.0	119	94	88	61	67	105	104	91.1	103.7	97.4	— 3.
111	87	107	113	67	121	86	98.9	121	88	76	81	72	130	120	98.3	105.9	102.1	+ 1.
135	85	79	111	67	116	78	94.4	110	86	83	89	54	142	135	99.9	115.3	107.6	+ 6.
148	103	70	111	56	139	82	101.3	96	84	103	102	64	126	143	102.6	116.1	109.3	+ 8.
159	101	66	91	90	120	88	102.1	93	78	93	102	65	109	133	94.7	114.4	104.5	+ 3.
156	80	72	98	124	110	86	103 7	111	70	102	108	82	112	128	101.9	109.4	105.6	+ 5.
139	113	92	71	135	105	81	105.1	134	82	128	81	101	86	121	105.6	115.7	110.6	+ 9.
127	135	96	102	142	106	99	115.3	136	77	146	57	116	88	97	102.4	109.7	106.0	+ 4.
137	135	113	113	137	88	90	116.1	109	82	111	59	123	88	108	97.1	102.0	99.6	— 1.
144	142	114	106	118	91	86	114.4	116	85	120	59	112	101	90	97.6	104.7	101.0	— 0.
138	139	104	100	88	92	105	109.4	83	114	100	70	99	100	71	91.0	101.0	96.0	— 5.
138	142	85	108	96	126	115	115.7	91	88	108	75	96	98	64	88.6	98.9	93.7	— 7.
149	132	105	90	87	98	91	109.7	77	95	84	68	92	73	69	79.7	94.4	87.0	—14.
			102			99			90				67			Mean	101.1	

Graphical presentation.—The results on the $9\frac{1}{6}$-month periodicity, in tables 1 and 2, are shown graphically in figures 2 and 3. In each of the six charts shown in each figure, the lower curve (*a*), in light lines, represents the first half of the interval. Along with it, in heavy dotted lines (*b*) appears the same curve, shifted in phase as indicated in the tabulation, tables 1 and 2. The medium-heavy full curve above (*c*) in each chart, gives the results tabulated for the second half of

TABLE 4.—*Peoria precipitation. The $15\frac{1}{6}$-month period*

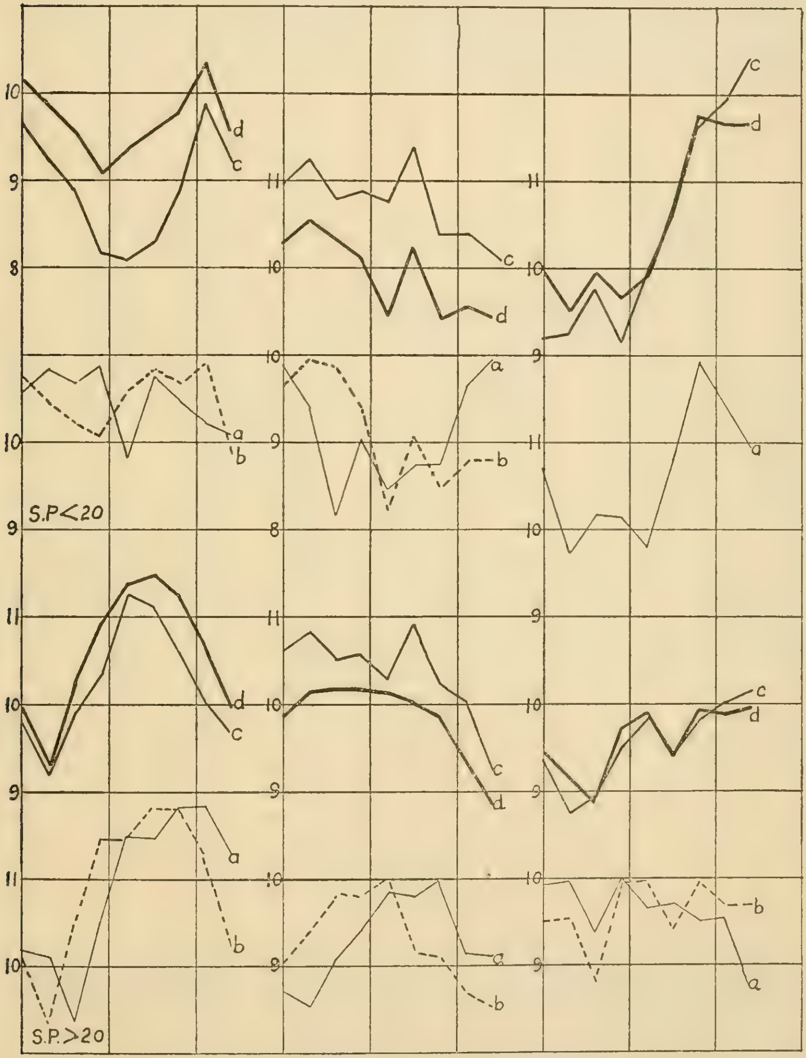
Sunspots < 20

A_1						B_1								
Apr. ’74	Feb. ’78	Mar. ’88	Jan. ’97	Apr. ’98	Mean	Feb. ’02	Mar. ’12	Jan. ’21	Mar. ’31	Apr. ’98	Mean	$A_1{\downarrow}_5$	Mean	Δ
62	111	115	108	140	107.2	98	101	86	77	140	101.0	81.8	91.4	−10.4
54	97	102	105	113	94.2	89	108	121	85	113	106.8	89.4	98.1	− 3.7
83	115	121	108	98	105.0	118	124	112	110	98	111.0	103.2	107.1	+ 5.3
76	104	110	79	108	95.4	143	122	108	111	108	112.2	104.4	108.3	+ 6.5
79	123	126	92	103	104.6	144	95	122	120	103	105.0	110.4	107.7	+ 5.9
88	101	109	65	100	92.6	170	103	116	118	100	109.2	107.2	108.2	+ 6.4
80	109	122	54	107	94.4	188	106	96	145	107	113.5	94.2	103.8	+ 2.0
47	93	110	48	92	78.0	176	88	108	134	92	105.5	105.0	105.2	+ 3.4
65	100	114	67	84	86.0	153	103	126	147	84	115.0	95.4	105.2	+ 3.4
70	80	99	54	82	77.0	122	120	139	138	82	119.8	104.6	112.2	+10.4
65	86	92	93	73	81.8	101	113	131	131	73	112.0	92.6	102.3	+ 0.5
80	68	87	118	94	89.4	94	124	129	104	94	110.5	94.4	102.4	+ 0.6
95	81	82	157	101	103.2	98	122	142	99	101	113.5	78.0	95.7	− 6.1
113	64	100	157	88	104.4	104	110	137	76	88	102.7	86.0	94.3	− 7.5
106	70	135	165	76	110.4	105	77	130	80	76	90.8	77.0	83.9	−17.9
				94				115				Mean	101.8	

A_2							B_2								
Aug. ’56	June ’65	May ’79	Aug. ’80	June ’89	July ’75	Mean	Aug. ’99	June ’13	May ’22	Aug. ’23	June ’32	Mean	$A_2{\uparrow}_2$	Mean	Δ
53	99	79	85	134	132	97.0	84	74	110	100	86	90.8	106.2	98.5	− 4.3
80	118	80	88	128	137	105.2	89	62	79	99	81	82.0	98.0	90.0	−12.8
107	121	78	81	125	125	106.2	101	77	67	114	87	89.2	107.2	98.2	− 4.6
101	115	90	65	111	106	98.0	116	87	60	115	86	93.8	115.3	104.5	+ 1.7
138	95	112	85	81	132	107.2	134	92	86	107	113	106.4	109.7	108.0	+ 5.2
153	109	112	95	107	116	115.3	123	95	83	92	111	100.8	109.8	105.3	+ 2.5
124	80	135	87	110	122	109.7	110	97	92	95	118	102.4	120.8	111.6	+ 8.8
95	83	158	96	111	116	109.8	116	85	87	81	126	99.0	111.2	105.1	+ 2.3
105	99	164	126	102	129	120.8	101	75	100	105	140	104.2	106.3	105.2	+ 2.4
71	104	155	101	102	134	111.2	58	79	81	119	132	93.8	104.5	99.1	− 3.7
80	79	170	85	81	143	106.3	88	58	93	150	118	101.4	107.3	104.3	+ 1.5
84	97	144	99	69	134	104.5	96	65	92	154	114	104.2	111.0	107.6	+ 4.8
88	109	119	122	68	138	107.3	90	79	91	154	101	103.0	115.0	109.0	+ 6.2
86	124	118	122	62	154	111.0	98	84	83	114	110	97.8	97.0	97.4	− 5.4
94	133	103	146	75	139	115.0	100	70	96	106	87	91.8	105.2	98.5	− 4.3
					110								Mean	102.8	

A_3						B_3								
Nov. ’57	Sept. ’66	Nov. ’76	Sept. ’85	Dec. ’86	Mean	Nov. ’00	Sept. ’09	Dec. ’10	Dec. ’29	Sept. ’33	Mean	$A_3{\downarrow}_5$	Mean	Δ
74	121	98	97	97	97.4	84	131	91	114	82	100.4	105.4	102.9	+10.6
82	112	75	102	87	91.6	85	132	97	90	83	97.4	106.8	102.1	+9.8
88	100	63	91	86	85.6	93	152	109	86	76	103.2	103.6	103.4	+11.1
111	100	59	81	83	86.8	80	149	101	87	55	94.4	109.0	103.2	+10.9
135	90	70	77	79	90.2	84	107	112	71	50	84.8	102.4	93.1	+ 0.8
148	97	103	83	50	96.2	85	93	99	54	56	77.4	97.4	87.4	− 4.9
159	98	120	72	64	102.6	94	90	94	53	45	73.2	91.6	82.4	− 9.9
156	98	112	84	67	103.4	73	70	114	41	50	69.6	85.6	77.6	−14.7
139	80	106	67	77	93.8	81	76	129	63	73	84.4	86.8	85.6	− 6.7
127	85	129	72	82	99.0	81	78	115	79	77	86.0	90.2	88.1	− 4.2
137	76	127	83	104	105.4	61	68	123	76	103	86.2	96.2	91.2	− 1.1
144	62	136	85	107	106.8	62	58	114	72	115	84.2	102.6	93.4	+ 1.1
138	62	127	78	113	103.6	59	61	89	75	141	85.0	103.4	94.2	+ 1.9
138	59	138	85	125	109.0	60	55	83	64	123	77.0	93.8	85.4	− 6.9
149	50	117	77	119	102.4	92	80	101	53	127	90.6	99.0	94.8	+ 2.5
												Mean	92.3	

the interval. The reader will perceive a considerable similarity in form between curves (*b*) and (*c*). Owing to the causes producing roughness in the mean results, as explained above, this correspondence is not as close as one could wish. However, it is the best available, and mean curves in heavy lines are plotted in lines (*d*). Their general similarity to the curves (*c*) indicate that the first half of the data,



FIGS. 2 (lower) AND 3 (upper).—Graphs of the $9\frac{1}{16}$-month periodicity.

when in the same phase, supports the second-half determinations of the periodicity.

Amplitudes of Peoria periodicities.—The reader will note that all the curves (*d*) in figures 2 and 3 indicate an amplitude for the $9\frac{1}{6}$-month periodicity of above 10 percent and several of them above 20 percent. Of the 19 periodicities determined in Peoria precipitation, none have a less average amplitude than 5 percent, and 10 of them exceed 20 percent in average amplitude. This may seem extraordinary to those who recall that the solar variations which control these periodicities in precipitation, as recorded in the paper cited above, seldom had amplitudes as great as 0.2 percent. But the explanation is not as yet susceptible to theory; we have to accept the results of tabulations.

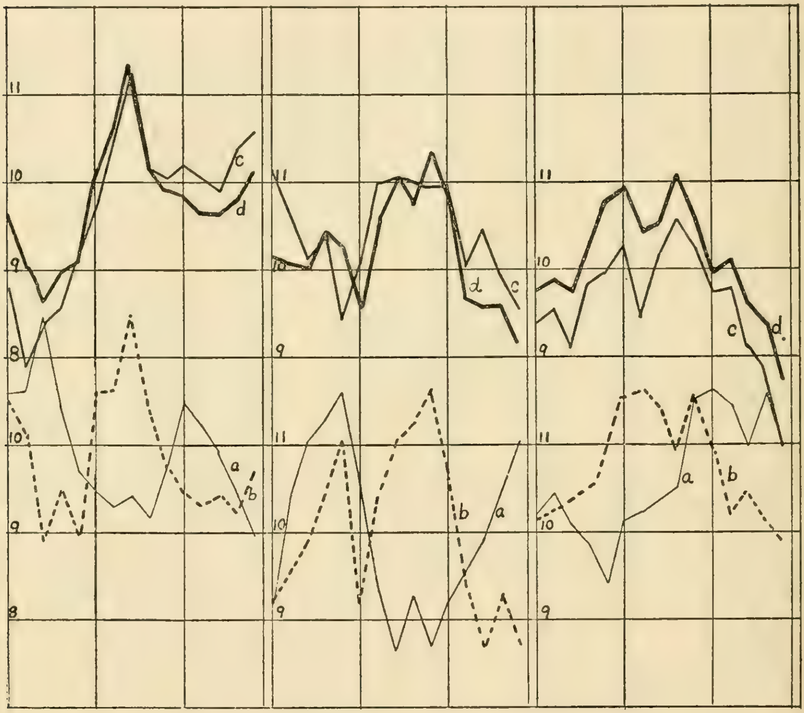


FIG. 4.—Graphs of the $15\frac{1}{6}$-month periodicity.
Wolf numbers > 20.

Figures 4 and 5, suited to Wolf numbers $\gtreqless 20$ for the periodicity of $15\frac{1}{6}$ months, will be understood from the preceding description, relating to $9\frac{1}{6}$ months. It will be noted that in figures 4 and 5 the amplitudes of the curves (*d*) are in all cases about 20 percent.

Forecasts of precipitation for future years.—The reader will perceive that since the periodicities fixed by tabulations of Peoria precipitation employ only data of the years 1856 to 1939, it is perfectly justified to use them to predict from a synthesis the precipitation expected to be observed at Peoria in the years 1940 to 1950. This operation has been performed. The data for it are such as given in the columns Δ of tables 1–4.

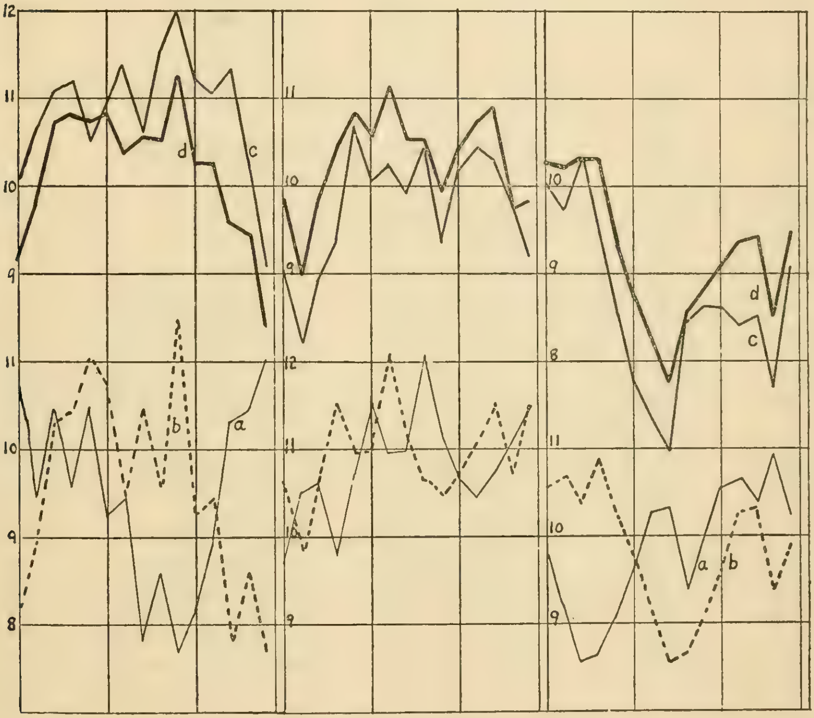


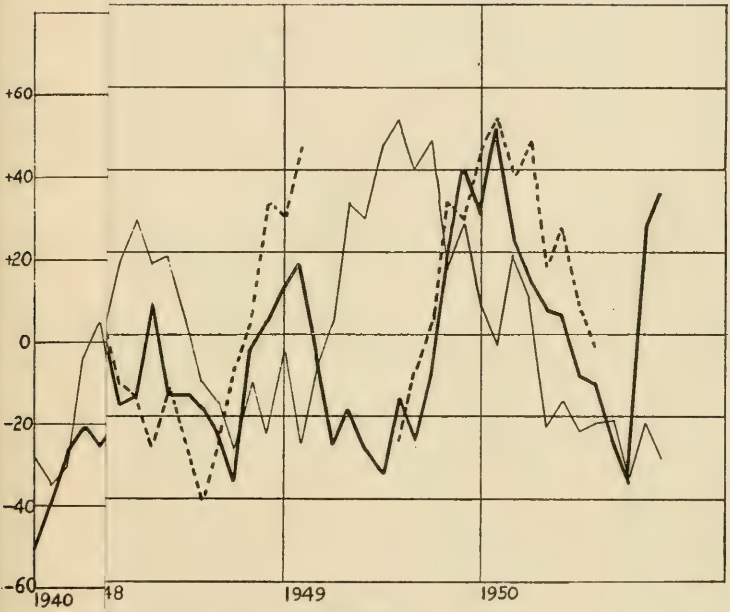
Fig. 5.—Graphs of $15\frac{1}{6}$-month periodicity.
Wolf numbers < 20.

To fix ideas, there is given in table 5 as much of this tabulation as covers the years 1940 and 1950. The summation of the 19 columns purports to show for these future years what will be the percentage departures from the normals that were printed above. In the next to final column of table 5 are given the actual observed departures from those normals, computed from Weather Bureau records. The final column gives the percentage differences between predicted and observed. The reader will recall that all these data were smoothed by 5-month consecutive means before the tabulation.

TABLE 5.—*Sample of synthesis prediction and verification*

Percentages in tenths of percent
Sums given to nearest percent

	4 1/3	5 1/3	6 1/15	7	8 1/8	9 1/8	9 3/4	10 3/5	11 1/5	13 1/10	13 3/5	15 1/8	22 4/5	24 4/5	30 1/3	34 1/5	38 4/5	45 1/2	91 1/2	Σ	Obs	Δ
1940																						
Jan.	+12	−23	−21	+27	+21	− 59	− 12	+ 7	+ 3	−45	+ 68	− 20	−18	−39	− 6	− 19	+ 3	− 65	− 99	−28	−50	+22
Feb.	−28	−13	− 8	+68	+ 1	−125	− 20	+ 52	−43	−34	+ 65	− 81	+27	−36	−28	− 20	+22	− 54	− 94	−35	−39	+ 4
Mar.	− 1	−34	+33	+19	+ 1	− 35	+ 10	+ 48	−39	− 3	+ 24	−120	+ 5	−13	−52	− 22	+ 2	− 34	− 88	−30	−27	− 3
Apr.	+19	− 6	+35	−18	+15	+ 38	+ 49	+100	−22	+31	+ 32	− 86	+ 8	−26	−66	− 6	−36	− 19	− 79	− 4	−20	+16
May	+10	+32	− 6	−16	+45	+ 81	+ 57	+ 73	−47	+31	− 29	− 73	+52	+ 8	−30	− 59	−36	+ 22	− 69	+ 5	−26	+31
June	+26	+35	−31	−61	+25	+ 91	− 26	+ 2	−61	+53	− 47	+ 29	+35	−68	−27	− 28	−35	− 20	− 59	−17	−20	+ 3
July	−28	−17	−10	−21	−46	+ 62	+ 28	− 24	+33	+56	− 65	+ 72	+49	−75	−40	− 60	−21	+ 2	− 49	−15	−35	+20
Aug.	− 9	− 2	−10	+14	−58	+ 8	0	− 27	+ 9	0	− 51	+153	+81	−89	−18	− 53	− 9	+ 22	− 42	− 8	−25	+17
Sept.	± 0	−23	+13	+34	+90	− 61	− 41	− 61	+83	−55	−114	+ 44	+10	−50	−57	+ 8	−19	+ 53	− 31	−17	−25	+ 8
Oct.	+ 9	0	+29	+27	+17	+ 2	− 48	− 92	+36	+11	− 72	+ 3	−22	−75	+ 1	+ 68	−19	+ 62	− 19	− 8	−10	+ 2
Nov.	−31	+ 6	− 2	+12	−31	− 21	+102	− 83	+45	− 1	− 8	0	−51	− 6	− 6	+ 84	−23	+ 60	− 14	+ 3	+ 7	− 4
Dec.	+23	+17	−10	+13	−48	− 39	+ 74	+ 25	+66	−31	+ 16	− 16	−76	+ 5	+40	+114	−56	+ 70	− 5	+18	+11	+ 7
1950																						
Jan.	− 1	−34	−21	+18	−84	− 21	− 74	− 74	+36	+52	+ 16	− 74	+49	+10	+27	− 1	+ 2	+125	+106	+ 6	+29	−23
Feb.	+12	− 6	− 8	+24	−76	− 39	− 77	− 84	+45	+54	+ 77	−141	+81	−48	− 6	+ 30	−36	+ 55	+111	− 3	+50	−53
Mar.	−28	+32	+33	+17	+21	+ 16	− 43	− 27	+ 3	+24	+ 68	− 20	+10	−43	−28	+ 63	−36	+ 25	+112	+19	+23	− 4
Apr.	− 1	+35	+35	+ 8	+ 1	+ 18	0	− 1	−43	+21	+ 65	− 81	−22	−17	−52	+ 31	−35	+ 16	+110	+ 9	+13	− 4
May	+19	−17	− 6	−25	+ 1	− 2	+ 6	+ 20	−39	−22	+ 24	−120	−51	−39	−66	+ 1	−21	0	+106	−29	+ 6	−35
June	+14	− 2	−31	−20	+15	+ 10	+ 13	+ 58	−22	−25	+ 32	− 86	−76	−36	−30	− 26	− 9	− 42	+104	−16	+ 5	−21
July	+10	−23	−10	+14	+45	+ 25	+ 1	+ 78	−47	−49	− 29	− 73	−80	−13	−27	− 80	−19	− 62	+ 96	−24	−10	−14
Aug.	+26	0	−10	+34	+25	− 10	− 4	+ 22	−61	−18	− 47	+ 29	−25	−26	−40	−113	−19	− 63	+ 76	−22	−12	−10
Sept.	−28	+ 6	+13	+27	−46	+ 2	− 10	+ 28	+33	−59	− 65	+ 72	−19	+ 8	−18	− 75	−23	− 70	+ 16	−21	−24	+ 3
Oct.	− 9	+17	+29	+12	−58	− 21	− 56	+ 22	+ 9	−76	− 51	+153	+25	−68	−57	− 38	−56	− 97	− 36	−36	−37	+ 1
Nov.	+ 9	+ 2	− 2	+13	+90	− 39	− 35	+ 24	+83	−36	−114	+ 44	+10	−75	+ 1	− 7	−55	− 69	− 99	−22	+26	−48
Dec.	−31	+24	− 2	−25	+17	+ 16	+ 13	+ 30	+36	+ 4	− 72	+ 3	−16	−89	− 6	− 7	− 5	− 83	−104	−23	+36	−59



d in Smithsonian Publ. 4088.
5-month running means.

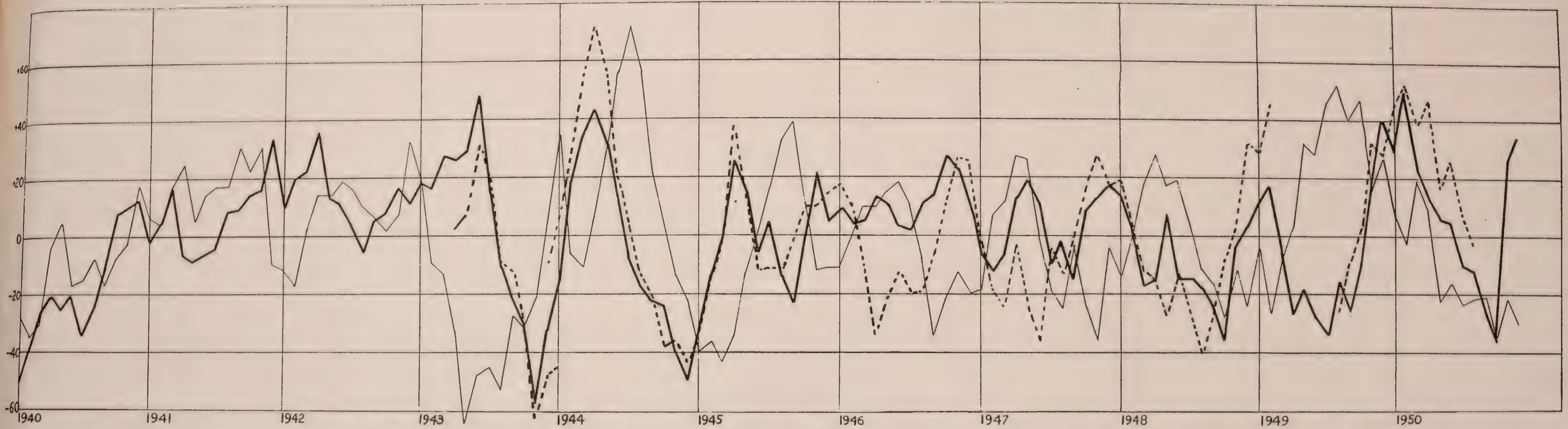


Fig. 6.—Predicted precipitation at Peoria, Ill., 1940 to 1950, and verification. Prediction based on sun's variation as determined in Smithsonian Publ. 4088. Thin line is prediction, thick line is event. Dotted line is prediction altered in phase as stated in text. All curves from 5-month running means.

Graphical comparison of forecast and event.—In figure 6 the whole march of the synthetically forecasted expected departures from normal precipitation at Peoria from 1940 to 1950 are plotted along with the actual departures observed. The reader will still recall that the data were smoothed by 5-month running means before any tabulating was done.

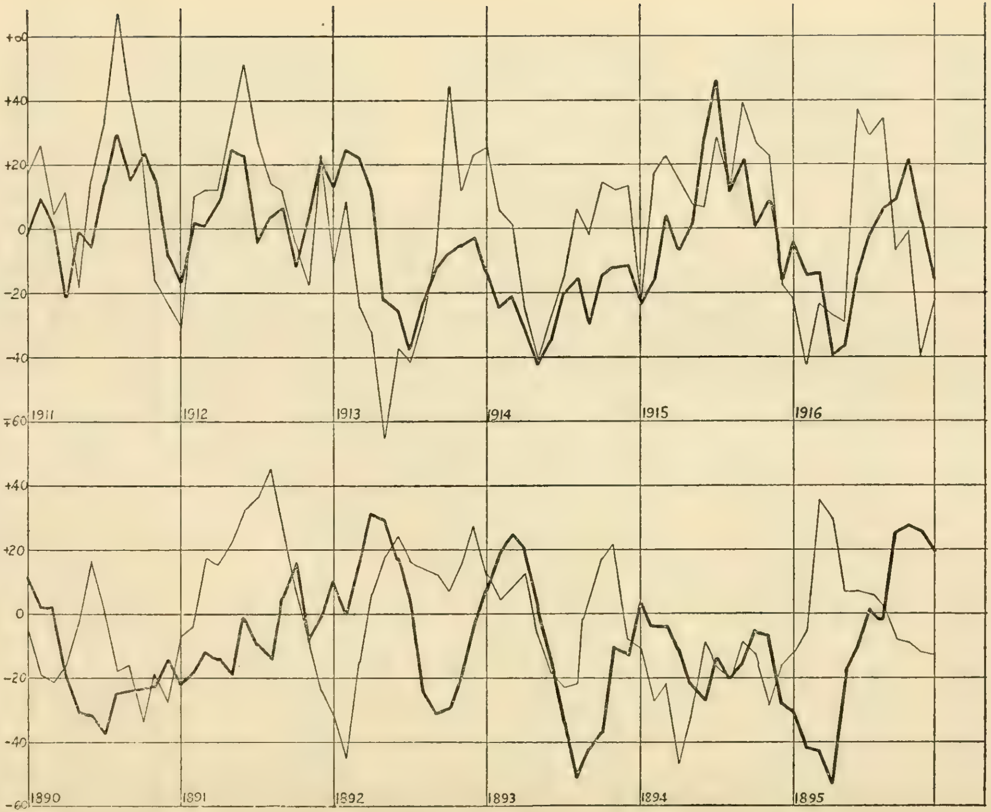
Fit of the curve of prediction.—For 3 years, 1940 to 1942, there is fair agreement between prediction and event. The average divergence between the two curves for 37 months is 13.9 percent. This is quite as close an agreement between prediction and synthesis of periodicities as obtained in the years prior to 1940, when, as one might say, the curves are "tailored to fit." Illustrations of this are given in figures 7 and 8, which deal with the intervals 1890 to 1895 and 1911 to 1916.

Phase changes.—After 1942 came changes of phase, but not of form. Heavy dotted curves are drawn in figure 6 to show the great similarity of form of the two curves when certain changes of phase are permitted. From October 1942 to July 1943 the predicted curve is moved forward 6 months. From March 1944 to June 1945 the predicted curve is moved backward 3 months. Thereafter, for the long interval extending until July 1949, the predicted curve is moved backward bodily 6 months. Finally, from February 1949 to February 1950 the predicted curve is moved forward 6 months.

With these changes of phase admitted, the two curves show for 81 months after 1942 an average divergence between them of 15 percent. Adding the first 3 years, which showed 35 months of fairly close fit, prediction would agree with event for 116 months out of 132, with an average divergence of 15 percent, though including several large swings of from 70 to 90 percent in amplitude. With such a good measure of success an 11-year prediction of precipitation at Peoria would confront us, though based on solar variation alone with no recourse to meteorology, if the several phase changes above suggested could be understood and anticipated.

Taking no consideration whatever of phase changes, the average departure between prediction and event is 14.7 percent for 99 months out of 136. Large divergences occur in the other 37 months.

Quality of representation.—To throw light, if possible, on phase changes, and to expose the roughness of the representation of precipitation by syntheses of periodicities as it stands before attempting a prediction, owing to causes already discussed, two intervals of curves of synthesis and observation prior to 1940 are shown in figures 7 and 8. The intervals chosen are from 1890 to 1895 and from 1911 to 1916. The synthetic curve in figure 7 is at a disadvantage, compared to that



FIGS. 7 (lower) AND 8 (upper).—Comparisons of synthesis with event in years prior to 1940. See comments in text.

in figure 8, because, as stated above, all the mean values from tabulations of the first half of the data were shifted in phase as required to match the phases of the mean values of data of the second half. Hence the general mean used for the syntheses is not so well suited to the first half of the 84-year interval as to the second half.

This disadvantage shows plainly, for figure 7 shows less good agreement than figure 8, yet a considerable part of the curves in figure 7 show fair correspondence. What is particularly interesting in figure 7 is that several cases of phase shifting, similar to those noted above in figure 5, are obvious. Such shiftings appear in the years 1890, 1892, 1893, and notably in 1895. One clearly marked phase shift is seen in the year 1913, in figure 8, and a lesser one in the year 1916.

The reader will see, by comparing figures 7 and 8, which relate to years employed for computing the data for prediction, with figure 6, where the basic periodicities were used for forecasting, that the "tailored to fit" curves, figures 7 and 8, agree no better, if indeed quite as well, with observation as the predicted curve agrees with the event in figure 6.

Solar variation controls weather.—The outcome of this attempt to forecast precipitation for a decade in advance by knowledge of periodicities in solar variation, without recourse to meteorology, is somewhat disappointing because of the phase changes encountered. It had been hoped that forecasts of percentage precipitation for coming seasons over a 10-year interval to within 10 or 15 percent might be made. If this could be done for one station, perhaps it might also be done for many. Then a network of lines of equal percentage precipitation for coming seasons for several years in advance might be laid down on the map. Possibly meteorologists, if they take interest in the idea, may find some means to conquer the phase-changing obstacle, and realize this dream of long-range seasonal forecasts.

Hitherto, for 40 years there has been a reluctance on the part of scientists, and especially meteorologists, to recognize the reality of observed changes of solar radiation. Even if it were admitted that very small solar changes occur, they were thought by these scientists to be insignificant for weather. As one said: "If a room be lighted with 100 lamps, and one is extinguished, no one could notice the loss of illumination." This paper, and Smithsonian Publ. 4088, indicate a contrary conclusion.

SUMMARY

I have sought, in a preceding paper cited above (footnote 1) to demonstrate the reality of 23 periodic changes in the intensity of the solar rays that warm the earth. In this present paper it is shown that periodicities of the same length as 19 of those discovered in solar variation are accompanied by changes of 5 to 20 percent amplitude in the precipitation at Peoria, Ill. By samples graphed in figures 2, 3, 4, 5, and in no way unrepresentative of all the periodicities tabulated, it is shown that these periodic variations of precipitation occur in nearly equal amplitudes and with moderate differences of phase in 12 separate independent intervals, each several years long, between 1856 and 1939.

Using these results as a basis, I predict the precipitation for Peoria from 1940 to 1950. With a range of actual precipitation from 50 to 150 percent of normal, occurring in that interval in the smoothed records, prediction matches the event for 8 out of 11 years to within an average deviation of 14.7 percent. In the other 3 years, large fluctuations in actual precipitation were matched by strikingly similar large fluctuations in the curve of prediction, but with phase differences of from 3 to 6 months. The prediction matches the event as well after 10 years as at the beginning. The fluctuations in the curve of prediction have almost precisely the same scale of range as those in the curve of actual precipitation.

While it is difficult to conceive, theoretically, how solar changes, seldom as large as 0.2 percent, could produce variations of from 5 to 20 percent in precipitation, the facts are there. It may be that adequate theory will eventually be found to explain them. In the meantime it would be of no importance, practically, whether theory had overtaken fact, if it were found that these periodic changes of precipitation could be synthesized to forecast seasons for years in advance.

A partial success in that direction has been achieved. For 3 years in advance the curve of prediction shown in figure 6 follows generally a rise of actual precipitation amounting to 90 percent. For 99 months out of 136, indeed, the average divergence is 15 percent. But the long-range prediction is marred by changes of phase, which, thus far at least, cannot be anticipated and allowed for in advance.

To the interested general reader, unfamiliar perhaps with considering percentages of normal precipitation, the meat of the matter may be expressed as follows: A prediction for 11 years in advance, based on knowledge of the sun's variation, without any consideration of meteorology, fits the rainfall curve at Peoria, Ill., for 99 months out of 136, to within an average error of one medium rainfall per month, or about 0.4 of an inch per month. Sometimes, however, dry or wet spells occur 3 to 6 months from when they are expected. Unless these phase changes can be anticipated, the method fails to come up fully to what is hoped for.

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 117, NUMBER 17

A GENERIC SYNOPSIS OF THE LIZARDS OF THE SUBFAMILY LYGOSOMINAE

BY
M. B. MITTLEMAN

(PUBLICATION 4096)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
NOVEMBER 4, 1952

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 117, NUMBER 17

A GENERIC SYNOPSIS OF THE LIZARDS OF THE SUBFAMILY LYGOSOMINAE

BY

M. B. MITTLEMAN

(Publication 4096)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
NOVEMBER 4, 1952

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

A GENERIC SYNOPSIS OF THE LIZARDS OF THE SUBFAMILY LYGOSOMINAE[1]

BY M. B. MITTLEMAN

As long ago as 1887 Boulenger remarked on the difficulty he had encountered in attempting to make a satisfactory generic arrangement of the Scincidae. In the long interval from Boulenger's day to our own, the skinks have reaffirmed their characteristic refractoriness to systematic order, and by far the most notorious offenders have been those groups of which the genus *Lygosoma* and certain of its allies are representative. These lizards, known loosely as the "lygosome" genera, are as baffling to the taxonomist as they are diverse in the multiplicity of their forms. Probably not the least reason for the perplexity surrounding the lygosomes is the fact that they add or delete many supposedly fundamental characters with the most disconcerting irregularity, while at the same time presumably trivial traits are often maintained through great arrays of species which are distributed over large areas.

The Boulengerian arrangement of genera was based on the recognition of these supraspecific groups according to the presence, absence, or other variation of certain characters accorded "generic" importance. Such a system inevitably becomes unwieldy when applied to lizards displaying the attributes of the lygosomes and results also in some weird zoogeographic and phylogenetic conclusions. On the other hand, in defense of Boulenger's arrangements and the emendations suggested by M. A. Smith (1937), the recognition of a relatively few genera considerably eases the every-day classification of the

---

[1] For many helpful suggestions in the preparation of this study, as well as for the opportunity to examine specimens in his care, I am grateful to Arthur Loveridge, of the Museum of Comparative Zoology. To Dr. Hobart M. Smith, of the University of Illinois, I wish to express my appreciation for the loan of literature, for checking references, and for numerous friendly and constructive criticisms. Finally, I must acknowledge my considerable obligation to the authorities of the Smithsonian Institution for the generous use of facilities at the United States National Museum and for the publication of this paper; and, particularly, to Dr. Doris M. Cochran, who has generously cooperated with me in innumerable ways over the course of several years, has given the present manuscript a careful reading, and has lent me specimens in her care.

lygosomes, and if the ultimate purpose is merely to pigeonhole a particular species at hand, the Boulengerian approach is certainly as good as any other.

The question then arises as to whether some other arrangement is desirable for the lygosome genera and, if so, upon what basis such a system should be predicated. The obvious antithesis of Boulenger's taxonomy is one wherein genera result from the "brigading of demonstrably related species," and where more tightly drawn generic definitions are made. It seems to me that this latter system is incomparably superior to that of Boulenger, for it has the dual advantages of reflecting phylogenetic relationships and of restricting the exercise of arbitrary judgment of characters deemed to be of "generic" importance. The necessity for some such arrangement goes far beyond the private philosophies of the "lumpers" and the "splitters" if any kind of comprehensible and stable arrangement is to be brought to the more than 600 described forms of lygosome lizards.

Since the most recent review of the lygosomes is that of M. A. Smith (op. cit.), reference to and comparison with this author's arrangement of these lizards are necessary. In the summary that follows it will be seen that the supraspecific arrangement suggested here differs from that of Smith in two basic ways: First, that the lygosome genera are regarded as a natural subfamily of the Scincidae, and second, that genera alone are utilized instead of genera, subgenera, and sections. In arriving at the conclusions presented here with respect to genera I have employed the following guiding criteria: First, that genera should be aggregations of species sharing one or more constant traits which set them apart from all other species groups; second, that genera should consist of species of common phylogenetic origin as far as this may appear determinable; third, that, in general, compact and more tightly drawn genera are preferable to loosely defined, all-inclusive groupings. Granting that my generic criteria are probably as personal (and therefore as vulnerable) as may be those of M. A. Smith, I believe they are defensible to the extent that they are essentially consistent and that they indicate relationships, and beyond this I think the genus cannot reasonably be expected to go. In brief, the 600-odd described forms of lygosome lizards individually and collectively constitute the best possible argument for the discrimination of discrete generic groups which are refined beyond the stage of catch-all depositories for widely divergent forms of uncertain origin.

The essence of the arrangement used here, and the differences between this system and that of Boulenger, as emended by M. A. Smith, are as follows:

1. *Lygosoma* and certain related genera are recognized here as constituting a subfamily (Lygosominae) of the Scincidae, which is further divided into three additional subfamilies. Smith does not divide the Scincidae into subfamilies.

2. The subfamily Lygosominae is regarded as consisting of at least 33 genera. Smith recognized 10 genera, 3 sections, and 5 subgenera of *Lygosoma* and its allies.

3. The following lygosome genera are recognized:

Ablepharus Fitzinger, 1823.
Anotis Bavay, 1869.
Ateuchosaurus Gray, 1845.
Carlia Gray, 1845.
Cophoscincopus Mertens, 1934.
Cophoscincus Peters, 1867.
Cryptoblepharus Wiegmann, 1834.
Dasia Gray, 1839.
Emoia Gray, 1845.
Eugongylus Fitzinger, 1843.
Eumecia Bocage, 1870.
Hemiergis Wagler, 1830.
Lampropholis Fitzinger, 1843.
Leiolopisma Duméril and Bibron, 1839.
Leptosiaphos Schmidt, 1943.
Lipinia Gray, 1845.
Lygosoma Hardwicke and Gray, 1827.
Mochlus Günther, 1864.
Nodorha, new genus.
Norbea Gray, 1845.
Ophioscincus Peters, 1873.
Otosaurus Gray, 1845.
Panaspis Cope, 1868.
Rhodona Gray, 1839.
Riopa Gray, 1839.
Ristella Gray, 1839.
Saiphos Gray, 1831.
Scincella Mittleman, 1950.
Sphenomorphus Fitzinger, 1843.
Squamicilia, new genus.
Tachygyia, new genus.
Tribolonotus Duméril and Bibron, 1839.
Tropidophorus Duméril and Bibron, 1839.

4. The supraspecific groups recognized by M. A. Smith are as follows:

Genus:

Ablepharus Fitzinger, 1823.
Ateuchosaurus Gray, 1845.
Cophoscincopus Mertens, 1934.
Dasia Gray, 1839.
Emoia Gray, 1845.
Lygosoma Hardwicke and Gray, 1827.
Otosaurus Gray, 1845.
Rhodona Gray, 1839.
Riopa Gray, 1839.
Tiliqua Gray, 1825.

Subgenus:

Eugongylus Fitzinger, 1843.
Eumecia Bocage, 1870.
Ictiscincus M. A. Smith, 1937.
Panaspis Cope, 1868.
Riopa Gray, 1839.

Section:

Leiolopisma Duméril and Bibron, 1839.
Lygosoma Hardwicke and Gray, 1827.
Sphenomorphus Fitzinger, 1843.

5. The following groups used by M. A. Smith are not recognized here, for the reasons given:

Ictiscincus M. A. Smith, 1937 = *Sphenomorphus* Fitzinger, 1843 (*vide* Loveridge, 1948, p. 352, regarding the supposed distinguishing characteristics of the teeth).

Tiliqua Gray, 1825. Not a lygosome genus (see following discussion and *vide* Waite, 1929, pp. 132-133).

The 33 genera previously enumerated constitute what I conceive to be the subfamily Lygosominae of the family Scincidae. The characteristics of the Lygosominae and of the three other subfamilies of the Scincidae are summarized in the following synopsis:

A. Palatine bones in contact on median line of palate.
  1. Pterygoid bones separated on the median line of palate; palatal notch extending anteriorly to level of centers of eyes .... MABUYINAE
  2. Pterygoid bones in contact anteriorly; palatal notch not extending anteriorly to level of centers of eyes.......... LYGOSOMINAE

B. Palatine bones separated on median line of palate.
  1. Nostril pierced in nasal, or between two adjacent plates, but never touching rostral.................................SCINCINAE
  2. Nostril pierced between rostral and an adjacent plate, thereby contacting rostral, or else within rostral itself..CHALCIDINAE

The Mabuyinae are distributed in Indo-Malaya, Africa, Madagascar, Asia, and the Americas (including the West Indies). The Lygosominae have an approximately similar distribution but occur also in southern Europe, Australasia, and the Pacific Islands. The Scincinae virtually duplicate the Lygosominae in their occurrence, while the Chalcidinae are restricted to Africa, Madagascar, southern Asia, and southern Europe.

The general plan of organization in this paper incorporates a brief diagnosis for each lygosome genus, or else the distinguishing features which set apart the genus from other lygosome genera are enumerated. Included also are the genotype for each genus and the principal synonyms. In addition to an artificial key to the genera, there are appended alphabetical listings of primary generic synonyms and species generically allocated according to the taxonomy suggested here.

Genus **LYGOSOMA** Hardwicke and Gray

Lygosoma HARDWICKE and GRAY, Zool. Journ., vol. 3, p. 228, 1827. (Type: *Lacerta serpens* Bloch = *Anguis quadrupes* Linné.)

Podophis WIEGMANN, Herpetologia Mexicana, p. 11, 1834. (Type: *Anguis quadrupes* Linné.)

Eyelids well developed, movable, the lower one scaly and lacking a more or less translucent or transparent disc; no supranasals; prefrontals small and widely separated; frontoparietals united, distinct from the large interparietal; preanals not, or barely, enlarged; ear opening absent or punctiform, approximating nostril or smaller if present; limbs much reduced, digits 5-5; body elongate, slender.

Distribution.—Australia, Java, Malaya, Siam, Indo-China, Philippine Islands.

Genus **SPHENOMORPHUS** Fitzinger

Eulamprus FITZINGER, Systema reptilium . . . , p. 22, 1843. (Type: *Lygosoma quoyi* Duméril and Bibron.)

Sphenomorphus FITZINGER, ibid., p. 23. (Type: *Lygosoma melanopogon* Duméril and Bibron.)

Hinulia GRAY, Catalogue of the specimens of lizards in the collection of the British Museum, p. 22, 1845. (Type: *Lygosoma quoyi* Duméril and Bibron.)

Elania GRAY, ibid., p. 80. (Type: *Scincus muelleri* Schlegel; non *Elania* Sundevall, 1835.)

Lissonota BLYTH, Journ. Asiatic Soc. Bengal, vol. 22, p. 653, 1853. (Type: *Lissonota maculata* Blyth; non *Lissonota* Gravenhorst, 1829.)

Ictiscincus M. A. SMITH, Rec. Indian Mus., vol. 39, No. 3, p. 222, 1937. (Type: *Scincus muelleri* Schlegel.)

Differs essentially from *Lygosoma* as follows: Prefrontals large, often forming a median suture; frontoparietals paired; preanals enlarged (except in *hallieri*); ear opening always present, large, somewhat smaller than the eye; limbs large and separated slightly or meeting or overlapping when appressed.

Distribution.—Australia, East Indies, New Guinea, India, Indo-China, Malaya.

Note.—This is by far the largest lygosome genus in point of included forms, well over 150 having been described. Quite possibly the genus as here constituted is polyphyletic, but until considerably more information can be accumulated on the individual and population variations of these lizards they are best considered as congeneric despite the fact that certain species groups may be worthy of generic rank.

Genus SAIPHOS Gray

Saiphos GRAY, *in* Griffith's Animal Kingdom, Syn. 9, p. 72, 1831. (Type: *Seps equalis* Gray.)

Peromeles WIEGMANN, Herpetologia Mexicana, p. 11, 1834. (Type: *Seps equalis* Gray.)

Anomalopus DUMÉRIL, Catalogue méthodique de la collection des reptiles . . . , p. 185, 1851. (Type: *Anomalopus verreauxii* Duméril.)

Coloscincus PETERS, Monatsb. Akad. Wiss. Berlin, 1876, p. 532. (Type: *Coloscincus truncatus* Peters.)

Differs essentially from *Lygosoma* as follows: Prefrontals greatly reduced, or often absent; frontoparietals paired; preanals enlarged; ear opening absent; limbs minute, reduced to tridactyle, didactyle, or monodactyle rudiments.

Distribution.—Australia, Sumatra, Malaya.

Genus LEPTOSIAPHOS Schmidt

Leptosiaphos K. P. SCHMIDT, Zool. Ser. Field Mus. Nat. Hist., vol. 24, No. 29, p. 332, 1943. (Type: *Lygosoma meleagris* Boulenger.)

Differs essentially from *Lygosoma* as follows: Frontoparietals paired; limbs well developed, digits 3, 4, or 5.

Distribution.—East Africa.

Genus OTOSAURUS Gray

Otosaurus GRAY, Catalogue of the specimens of lizards in the collection of the British Museum, p. 93, 1845. (Type: *Otosaurus cumingi* Gray.)

Parotosaurus Boulenger, Trans. Zool. Soc. London, vol. 20, p. 257, 1914. (Type: *Parotosaurus annectens* Boulenger.)

Differs essentially from *Lygosoma* as follows: Supranasals usually present, either small and widely separated or else well developed and forming a median suture; frontoparietals paired; preanals enlarged; ear opening large, approximating eye; limbs large, separated slightly or meeting or overlapping when appressed.

Distribution.—East Indies, Borneo, Sarawak, Sumatra, Malaya, New Guinea, Philippine Islands.

Note.—The genus *Parotosaurus* may be used conveniently for those forms possessing reduced nonsuturing supranasals, or else lacking these scales; in this case *Otosaurus* would then be restricted to the species with enlarged supranasals which form a median suture.

Genus **COPHOSCINCUS** Peters

Cophoscincus Peters, Monatsb. Akad. Wiss. Berlin, 1867, p. 19. (Type: *Lygosoma* (*Cophoscincus*) *quadrivittatus* Peters.)

Differs essentially from *Lygosoma* as follows: Preanals enlarged; ear opening absent; limbs robust and either separated by several scale lengths when appressed or else meeting or overlapping.

Distribution.—Australia, Sumatra, Borneo, Malaya, Celebes, Philippine Islands.

Note.—In *quadrivittatus* the lower eyelid is scaly and lacks a transparent or translucent disc, while in other species (cf. *infralineolatus, relictus*) the disc is present. In this group the presence or absence of the palpebral disc is not generically important.

Genus **DASIA** Gray

Dasia Gray, Ann. Mag. Nat. Hist., vol. 2, p. 331, 1839. (Type: *Dasia olivacea* Gray.)

Lamprolepis Fitzinger, Systema reptilium, p. 22, 1843. (Type: *Scincus smaragdinus* Lesson.)

Liotropis Fitzinger, ibid., p. 22. (Type: *Euprepres ernestii* Duméril and Bibron = *Dasia olivacea* Gray.)

Keneuxia Gray, Catalogue of the specimens of lizards in the collection of the British Museum, p. 79, 1845. (Type: *Scincus smaragdinus* Lesson.)

Apterygodon Ederling, Nat. Tijdschr. Med. Ind., vol. 26, p. 483, 1863. (Type: *Apterygodon vittatum* Ederling.)

Theconyx Annandale, Spolia Zeylanica, vol. 3, p. 191, 1906. (Type: *Euprepes halianus* Haly and Nevill; non *Theconyx* Gray, 1845.)

Differs from *Lygosoma* essentially as follows: Supranasals present, occasionally forming a median suture, sometimes partially or nearly completely fused with the nasals; prefrontals large, sometimes forming a median suture; frontoparietals paired; body and limbs robust, the latter often overlapping when appressed, or else separated by only a few scale lengths.

Distribution.—Indian Archipelago, Papuasia, Caroline and Philippine Islands, India, Borneo.

Genus COPHOSCINCOPUS Mertens

Cophoscincopus Mertens, Zoologica (Stuttgart), vol. 32, p. 190, 1934. (Type: *Cophoscincus simulans* Vaillant; non *Cophoscincus* Peters, 1867 = *Tiliqua dura* Cope.)

Differs from *Lygosoma* essentially as follows: Supranasals present and forming a median suture; frontoparietals paired; ear opening present but almost completely covered by overlapping scales; preanals enlarged; limbs robust and long, overlapping when appressed.

Distribution.—West Africa.

Genus ATEUCHOSAURUS Gray

Ateuchosaurus Gray, Catalogue of the specimens of lizards in the collection of the British Museum, p. 107, 1845. (Type: *Ateuchosaurus chinensis* Gray.)

Lygosaurus Hallowell, Proc. Acad. Nat. Sci. Philadelphia, 1860, p. 496. (Type: *Lygosaurus pellopleurus* Hallowell.)

Differs essentially from *Lygosoma* as follows: Frontoparietals paired; frontal long and constricted (longer than frontoparietals and interparietal together); parietals much reduced; ear opening large, about midway in size between eye and nostril; limbs robust, either overlapping when appressed or separated by a few scale lengths.

Distribution.—China, Indo-China, Ryukyu Archipelago.

Genus RIOPA Gray

Riopa Gray, Ann. Mag. Nat. Hist., vol. 2, p. 332, 1839. (Type: *Lygosoma punctata* Gray = *Lacerta punctata* Linné.)

Chiamela Gray, ibid., p. 332. (Type: *Chiamela lineata* Gray.)

Hagria Gray, ibid., p. 333. (Type: *Hagria vosmaerii* Gray.)

Campsodactylus Duméril and Bibron, Erpétologie générale . . . , vol. 5, p. 761, 1839. (Type: *Campsodactylus lamarrei* Duméril and Bibron = *Hagria vosmaerii* Gray; non *Campsodactylus* Duméril, 1837, nom. nud.)

Sphenosoma Fitzinger, Systema reptilium, p. 23, 1843. (Type: *Eumeces punctatus* Wiegmann = *Lacerta punctata* Linné.)

Eyelids well developed, movable, the lower one with a more or less transparent or translucent disc; supranasals present, forming a median suture; prefrontals small, widely separated; frontoparietals paired, distinct from interparietal; preanals not, or barely, enlarged;

ear opening small (punctiform), approximating nostril or smaller; limbs much reduced, digits 5-5 or less; general habitus vermiform.

Distribution.—India, Burma, Kenya.

Genus **EUGONGYLUS** Fitzinger

Eugongylus FITZINGER, Systema reptilium, p. 23, 1843. (Type: *Eumeces oppellii* Duméril and Bibron = *Lacerta rufescens* Shaw (part).)

Differs from *Riopa* essentially as follows: Lower eyelid either uniformly scaly or else with a small opaque disc; supranasals reduced and not forming a median suture; limbs well developed, digits 5-5; body robust, lacertiform.

Distribution.—Australia, Papuasia, Halmahera, Sula Islands.

SQUAMICILIA, new genus

Type: *Eumeces isodactylus* Günther, The reptiles of British India, p. 93, pl. 13, fig. A, 1864.

Differs essentially from *Riopa* as follows: Lower eyelid scaly, lacking a more or less transparent or translucent disc; supranasals reduced and not forming a median suture; frontoparietals usually united, interparietal much reduced; ear opening reduced, often only a small oblique slit.

Distribution.— Siam and Somaliland.

Genus **MOCHLUS** Günther

Mochlus GÜNTHER, Proc. Zool. Soc. London, 1864, p. 308. (Type: *Mochlus punctatus* Günther = *Eumeces* (*Riopa*) *sundevallii* Smith.)

Sepacontias GÜNTHER, Ann. Mag. Nat. Hist., ser. 5, vol. 6, p. 235, 1880. (Type: *Sepacontias modestus* Günther.)

Lepidothyris COPE, Journ. Morph., vol. 7, p. 233, 1892. (Type (by subsequent designation): *Lepidothyris fernandi* Cope = *Tiliqua fernandi* Burton.[2])

Differs essentially from *Riopa* as follows: Lower eyelid scaly, lacking a more or less transparent or translucent disc; limbs robust,

---

[2] Cope's original description of *Lepidothyris* (loc. cit.) is merely that of a scincid genus of lizards with no included species, and appears only in a key to the genera of Scincidae. In accordance with Opinion 46 of the International Commission "the first species published in connection with the genus . . . becomes *ipso facto* the type." Thus the type of *Lepidothyris* is the species *fernandi,* since Cope (1900, p. 617) mentions *Lepidothyris fernandi* briefly. Described with *Lepidothyris* at the same time and in the same fashion are the following genera: *Monophorus, Oncopus, Ollochirus, Tridentulus, Furcillus, Haploscincus,* and *Dimeropus.* All these are scincid genera; presumably Lygosominae, with no included species, and must at present be considered unidentifiable nomina inquirendae, except for *Monophorus* which is clearly unavailable since it is preoccupied by *Monophorus* Deshayes, 1877 (Mollusca).

barely meeting or else separated by several scale lengths when appressed; digits 5-5.

Distribution.—Africa, China, Indo-China, Malaya, Philippine Islands.

TACHYGYIA, new genus

Liosoma FITZINGER, Systema reptilium, p. 22, 1843. (Type: *Eumeces microlepis* Duméril and Bibron; non *Liosoma* Brandt, 1834.)

Type: *Eumeces microlepis* Duméril and Bibron, Erpétologie générale, vol. 5, p. 659, 1839.

Differs essentially from *Riopa* as follows: Lower eyelid scaly, lacking a more or less transparent or translucent disc; frontoparietals united, interparietal reduced; limbs very robust and long, broadly overlapping when appressed.

Distribution.—Friendly Islands, New Caledonia.

Genus EUMECIA Bocage

Eumecia BOCAGE, Journ. Acad. Sci. Lisbon, vol. 3, p. 67, 1870. (Type: *Eumecia anchietae* Bocage.)

Differs from *Riopa* essentially as follows: Prefrontals large, forming a median suture; ear opening large (only slightly smaller than the eye); limbs minute; digits 2-3 (in *Riopa* 3-3 or more).

Distribution.—British East Africa, Nyasaland.

Genus PANASPIS Cope

Panaspis COPE, Proc. Acad. Nat. Sci. Philadelphia, 1868, p. 317. (Type: *Panaspis aeneus* Cope.)

Differs essentially from *Riopa* as follows: Supranasals reduced, not forming a median suture, occasionally partially fused with nasals; ear opening large, approximating eye; limbs short or long, but robust.

Distribution.—West Africa.

Note.—The species *reichenovei* and *africanus* are referred to *Leiolopisma,* although M. A. Smith considers them congeneric with *aeneus, cabindae,* and other West African forms which I regard as members of *Panaspis.* The habitus is such in *reichenovei* and *africanus* as to render these species generically indistinguishable from many forms in the genus *Leiolopisma.* However drastic and improbable the zoogeographic implications may be as a result of placing the West African species in a genus which is largely Pacific in distribution, they are paralleled by other instances of disjunct distribution in the lygosome genera, cf. *Riopa, Poria, Ophioscincus, Ablepharus,* etc.

Genus EMOIA Gray

Eusoma FITZINGER, Systema reptilium, p. 22, 1843. (Type: *Eumeces lessonii* Duméril and Bibron = *Scincus cyanurus* Lesson; non *Eusoma* Germar, 1817.)

Emoia GRAY, Catalogue of the specimens of lizards in the collection of the British Museum, p. 95, 1845. (Type: *Scincus atrocostatus* Lesson.)

Differs from *Riopa* essentially as follows: Supranasals reduced, not forming a median suture; interparietal often fused with the single frontoparietal; limbs robust and long, overlapping when appressed, digits 5-5; general habitus lacertiform.

Distribution.—Borneo, Philippine Islands, New Guinea, Solomon Islands, New Hebrides, Fiji Islands, Friendly Islands, Samoa, Admiralty Islands.

Genus LEIOLOPISMA Duméril and Bibron

Leiolopisma DUMÉRIL and BIBRON, Erpétologie générale . . . , vol. 5, p. 742, 1839. (Type: *Scincus telfairii* Desjardins.)

Oligosoma GIRARD, Proc. Acad. Nat. Sci. Philadelphia, 1857, p. 196. (Type: *Mocoa zeylandica* Gray = *Lygosoma moco* Duméril and Bibron.)

Hombronia GIRARD, ibid., p. 196. (Type: *Hombronia fasciolaris* Girard.)

Lygosomella GIRARD, ibid., p. 196. (Type: *Lygosomella aestuosa* Girard.)

Cyclodina GIRARD, ibid., p. 195. (Type: *Cyclodina aenea* Girard.)

Eyelids well developed, movable, the lower one with a more or less transparent or translucent disc; no supranasals; prefrontals small, separated; frontoparietals paired, distinct from interparietal; preanals not, or barely, enlarged; ear opening rather large, often approximating the eye, always larger than the nostril; limbs well developed, broadly overlapping or meeting or slightly separated when appressed, digits 5-5; general habitus lacertiform.

Distribution.—Australia, New Caledonia, New Zealand, Tasmania, Mauritia, West Africa.

Genus LAMPROPHOLIS Fitzinger

Lampropholis FITZINGER, Systema reptilium, p. 22, 1843. (Type: *Lygosoma guichenoti* Duméril and Bibron.)

Eulepis FITZINGER, ibid., p. 22. (Type: *Lygosoma duperryi* Duméril and Bibron = *Tiliqua trilineata* Gray.)

Mocoa GRAY, Catalogue of the specimens of lizards in the collection of the British Museum, p. 80, 1845. (Type: *Lygosoma guichenoti* Duméril and Bibron.)

Tropidoscincus BOCAGE, Journ. Acad. Sci. Lisbon, vol. 15, p. 230, 1873. (Type: *Tropidoscincus aubrianus* Bocage.)

Lioscincus BOCAGE, ibid., p. 328. (Type *Lioscincus steindachnerii* Bocage = *Lygosoma tricolor* Bavay.)

Sauroscincus PETERS, Sitzb. Ges. Nat. Freunde Berlin, 1878, p. 149. (Type: *Sauroscincus braconnieri* Peters = *Tropidolepisma variabilis* Bavay.)

Differs from *Leiolopisma* essentially as follows: A single frontoparietal, well developed, distinct from interparietal; ear opening moderate (smaller than the eye) to small (approximating nostril or slightly larger).

Distribution.—New Caledonia, Australia, Tasmania, Loyalty Islands, New Hebrides Islands.

Genus CARLIA Gray

Heteropus Duméril and Bibron, Erpétologie générale . . . , vol. 5, p. 757, 1839. (Type: *Heteropus fuscus* Duméril and Bibron; non *Heteropus* Beauvois, 1805, or *Heteropus* Fitzinger, 1826.)

Carlia Gray, Catalogue of the specimens of lizards in the collection of the British Museum, p. 271, 1845. (Type: *Carlia melanopogon* Gray; non *Lygosoma melanopogon* Duméril and Bibron = *Sphenomorphus melanopogon* Duméril and Bibron, part.)

Myophila de Vis, Proc. Roy. Soc. Queensland, vol. 1, p. 77, 1884. (Type: *Myophila vivax* de Vis.)

Lygisaurus de Vis, ibid., p. 77. (Type: *Lygisaurus foliorum* de Vis.)

Differs essentially from *Leiolopisma* as follows: A single well-developed frontoparietal; interparietal usually very small or absent; digits 4-5.

Distribution.—Moluccas, New Guinea, Australia, Papuasia.

Genus ANOTIS Bavay

Anotis Bavay, Mem. Soc. Linn. Normandie, vol. 4, No. 5, p. 29, 1869. (Type: *Anotis mariae* Bavay.)

Nannoscincus Günther, Ann. Mag. Nat. Hist., ser. 4, vol. 10, p. 421, 1872. (Type: *Nannoscincus fuscus* Günther = *Anotis mariae* Bavay.)

Differs essentially from *Leiolopisma* as follows: Prefrontals minute and widely separated (well developed in *Leiolopisma*); ear opening absent or punctiform; limbs much reduced, digits 5-5 or less; general habitus vermiform.

Distribution.—New Caledonia, Australia.

Genus HEMIERGIS Wagler

Tridactylus Cuvier, Règne animal, p. 64, 1829. (Type: *Zygnis decresiensis* Fitzinger; non *Tridactylus* Lacépède, 1799.)

Tetradactylus Cuvier, ibid., p. 64. (Type: *Zygnis decresiensis* Fitzinger; non *Tetradactylus* Merrem, 1820.)

Hemiergis Wagler, Natürliches System der Amphibien . . . , p. 160, 1830. (Type: *Zygnis decresiensis* Fitzinger.)

Peromelis Wagler, ibid., p. 160. (Type: *Zygnis decresiensis* Fitzinger.)

Chelomeles Duméril and Bibron, Erpétologie générale . . . , vol. 5, p. 774, 1839. (Type: *Chelomeles quadrilineatus* Duméril and Bibron.)

Differs essentially from *Leiolopisma* as follows: Preanals enlarged; ear opening minute or absent; limbs greatly reduced, digits 4-4 or less; general habitus vermiform.

Distribution.—Australia.

Genus **LIPINIA** Gray

Lipinia GRAY, Catalogue of the specimens of lizards in the collection of the British Museum, p. 84, 1845. (Type: *Lipinia pulchella* Gray.)

Differs essentially from *Leiolopisma* as follows: Prefrontals large, forming a median suture; frontonasal at least as long as it is wide (wider than long in *Leiolopisma*); preanals prominently enlarged.

Distribution.—Solomon Islands, New Guinea, Philippines, Borneo, Siam, Tenasserim, Malaya, Andaman Islands.

Genus **SCINCELLA** Mittleman

Scincella MITTLEMAN, Herpetologica, vol. 6, No. 2, p. 19, 1950. Type: *Scincus lateralis* Say.)

Differs essentially from *Leiolopisma* as follows: Prefrontals large, often forming a median suture; preanals prominently enlarged.

Distribution.—India, Sarawak, Borneo, North and Middle America, China, Anadaman Islands, Nicobar Islands, Celebes, Hawaiian Islands, Tasmania, Australia.

Genus **RHODONA** Gray

Rhodona GRAY, Ann. Mag. Nat. Hist., vol. 2, p. 335, 1839. (Type: *Rhodona punctata* Gray.)

Soridia GRAY, ibid., p. 335. (Type: *Soridia lineata* Gray.)

Brachystopus DUMÉRIL and BIBRON, Erpétologie générale, vol. 5, p. 778, 1839. (Type: *Brachystopus lineopunctulatus* Duméril and Bibron = *Rhodona punctata* Gray.)

Praepeditus DUMÉRIL and BIBRON, ibid., p. 787. (Type: *Soridia lineata* Gray.)

Ronia GRAY, *in* Grey's Travels in Australia, vol. 2, p. 437, 1841. (Type: *Ronia catenulata* Gray = *Rhodona punctata* Gray.)

Pholeophilus A. SMITH, Illustrations of the zoology of South Africa, p. 15 (App.), 1849. (Type: *Pholeophilus capensis* Smith = *Soridia lineata* Gray.)

Eyelids well developed, movable, the lower one with a more or less transparent or translucent disc; no supranasals; prefrontals absent, or if present then small and widely separated; frontoparietal single, fused with the interparietal into a single large shield; preanals enlarged; ear opening absent or minute; nasals very large and forming a median suture, or else barely separated; anterior limbs much reduced or absent, digits of hind limbs 2 or less; general habitus vermiform.

Distribution.—Australia.

NODORHA, new genus

Leptosoma Fitzinger, Systema reptilium, p. 23, 1843. (Type: *Riopa bougainvillii* Duméril and Bibron (non *Leptosoma* Leach, 1819).)

Type: *Riopa bougainvillii* Duméril and Bibron.

Differs essentially from *Rhodona* as follows: Frontoparietal single or paired, but always distinct from the interparietal; anterior limbs present (except in *N. wilkinsi*), digits 5-5 or less.

Distribution.—Australia, Tasmania.

Genus OPHIOSCINCUS Peters

Ophioscincus Peters, Monatsb. Akad. Wiss. Berlin, 1873, p. 747. (Type: *Ophioscincus australis* Peters.)

Isopachys Lönnberg, Kungl. Svenska Vet.-Akad. Handl., vol. 55, No. 4, p. 10, 1916. (Type: *Isopachys gyldenstolpei* Lönnberg.)

Typhloseps Angel, Bull. Mus. Hist. Nat. Paris, 1920, p. 4. (Type: *Typhloseps roulei* Angel.)

Differs essentially from *Rhodona* as follows: Lower eyelid immovable, with a transparent disc, or else in itself largely transparent; no upper eyelid; frontoparietals paired, distinct from the interparietal; limbs absent.

Distribution.—Siam and Australia.

Genus ABLEPHARUS Fitzinger

Ablepharus Fitzinger, *in* Lichtenstein, Verzeichniss der Doubletten des zoologischen Museums . . . Berlin . . . , 1823, p. 103. (Type: *Ablepharus pannonicus* Fitzinger.)

Lerista Bell, Proc. Zool. Soc. London, 1833, p. 99. (Type: *Lerista lineata* Bell.)

Microblepharus Fitzinger, Systema reptilium, p. 23, 1843. (Type: *Ablepharus menestriesii* Duméril and Bibron.)

Ophiopsis Fitzinger, ibid., p. 23. (Type: *Lerista lineata* Bell.)

Menetia Gray, The zoology of the voyage of H.M.S. *Erebus* and *Terror* . . . , Rep., pl. 5, fig. 4, 1844. (Type: *Menetia greyi* Gray.)

Miculia Gray, ibid., pl. 5, fig. 3. (Type: *Miculia elegans* Gray.)

Blepharosteres Stoliczka, Proc. Asiatic Soc. Bengal, 1872, p. 74. (Type: *Blepharosteres grayanus* Stoliczka.)

Phaneropus Fischer, Arch. Naturg., 1881, p. 236. (Type: *Phaneropus muelleri* Fischer.)

Eyelids immovable, a transparent disc covering the entire eye; supranasals present or absent; frontoparietal single or paired, but always distinct from the interparietal; ear opening absent, or if present quite small; limbs short but well developed; digits 5-5 or less; general habitus lacertiform.

Distribution.—Australia, Africa, southwest Asia, southern Europe.

Genus **CRYPTOBLEPHARUS** Wiegmann

Cryptoblepharus Wiegmann, Herpetologia Mexicana, p. 12, 1834. (Type: *Ablepharus poecilipleurus* Wiegmann.)

Morethia Gray, The zoology of the voyage of H.M.S. *Erebus* and *Terror* . . . , Rep., p. 4, 1844. (Type: *Morethia anomalus* Gray.)

Differs essentially from *Ablepharus* as follows: Frontoparietals and interparietal fused to form a single large shield; ear opening present, large, approximating eye in size.

Distribution.—Australia, New Guinea, East Indies, Madagascar, Africa, Polynesia.

Note.—As remarked by M. A. Smith (1935, p. 309), *Ablepharus* appears to be of polyphyletic origin. The separation of certain species under the generic designation *Crypoblepharus* primarily takes cognizance of slightly more apparent distinctions than many others which occur in *Ablepharus* (sensu lato). It is possible that other species groups in *Ablepharus* are generically distinct.

Genus **RISTELLA** Gray

Ristella Gray, Ann. Mag. Nat. Hist., vol. 2, p. 333, 1839. (Type: *Ristella rurkii* Gray.)

Eyelids well developed, movable, the lower one scaly and lacking a more or less transparent or translucent disc; no supranasals; prefrontals small and well separated, or large and fused into a single large shield; frontoparietals paired, distinct from the interparietal; preanals not enlarged; ear opening well developed; limbs well developed; digits 4-5, claws competely retractile into sheaths.

Distribution.—Southern India.

Genus **TROPIDOPHORUS** Duméril and Bibron

Tropidophorus Duméril and Bibron, Erpétologie générale . . . , vol. 5, p. 554, 1839. (Type: *Tropidophorus cocincinensis* Duméril and Bibron.)

Aspris Blyth, Journ. Asiatic Soc. Bengal, vol. 22, p. 650, 1853. (Type: *Aspris berdmorei* Blyth.)

Enoplosaurus Sauvage, Bull. Soc. Philom., ser. 7, vol. 3, p. 211, 1879. (Type: *Enoplosaurus insignis* Sauvage = *Tropidophorus grayi* Günther.)

Eyelids well developed, movable, the lower one scaly and lacking a more or less transparent or translucent disc; no supranasals; prefrontals well developed, usually forming a median suture; frontoparietal single or paired but always distinct from the interparietal; four principal supraoculars; ear large, tympanum superficial; two or three enlarged preanals; limbs well developed, digits 5-5, claws nonretractile.

Distribution.—Southern China, Indo-China, Philippine Islands, Australia.

Genus **NORBEA** Gray

Norbea Gray, Catalogue of the specimens of lizards in the collection of the British Museum, p. 101, 1845. (Type: *Norbea brookei* Gray.)

Amphixestus Peters, Monatsb. Akad. Wiss. Berlin, 1871, p. 573. (Type: *Amphixestus beccarii* Peters.)

Differs essentially from *Tropidophorus* as follows: Five principal supraoculars; a single greatly enlarged preanal plate.

Distribution.—Sarawak, Borneo, Philippine Islands.

Genus **TRIBOLONOTUS** Duméril and Bibron

Tribolonotus Duméril and Bibron, Erpétologie générale . . . , vol. 5, p. 364, 1839. (Type: *Zonurus novae-guineae* Schlegel.)

Pediporus Roux, Verh. Naturf. Ges. Basel, vol. 41, p. 129, 1930. (Type: *Tribolonotus schmidti* Burt.)

Eyelids well developed, movable, the lower one scaly and lacking a more or less transparent or translucent disc; head with a posteriorly emarginate bony casque; nostril in a single nasal; no supranasals; no prefrontals; frontoparietals paired, distinct from the interparietal; ear opening approximating eye in size; a pair of greatly enlarged preanals; dorsal surfaces of body and tail armed with large spinose scales; neck prominently narrower than the head; limbs large, digits 5-5, claws nonretractile.

Distribution.—New Guinea and Solomon Islands.

ALPHABETICAL GENERIC SYNONYMY

Appended below is an alphabetical listing of the 33 generic names considered valid in this paper, as well as the 62 primary synonyms of these names which have been proposed over the years. Earlier names unavailable because of homonymy are listed simply as straight synonyms of their respective genera. Nomina nuda and new generic names proposed herein are so indicated; nomina inquirendae are omitted.

Ablepharus Fitzinger, 1823. Valid genus.
Amphixestus Peters, 1871 = *Norbea* Gray.
Anomalopus Duméril, 1851 = *Saiphos* Gray.
Anotis Bavay, 1869. Valid genus.
Apterygodon Ederling, 1863 = *Dasia* Gray.
Aspris Blyth, 1853 = *Tropidophorus* Duméril and Bibron.
Ateuchosaurus Gray, 1845. Valid genus.
Blepharosteres Stoliczka, 1872 = *Ablepharus* Fitzinger.
Brachystopus Duméril and Bibron, 1839 = *Rhodona* Gray.

Campsodactylus Duméril, 1837 = nomen nudem.
Campsodactylus Duméril and Bibron, 1839 = *Riopa* Gray.
Carlia Gray, 1844. Valid genus.
Chelomeles Duméril and Bibron, 1839 = *Hemiergis* Wagler.
Chiamela Gray, 1839 = *Riopa* Gray.
Coloscincus Peters, 1876 = *Saiphos* Gray.
Cophoscincopus Mertens, 1934. Valid genus.
Cophoscincus Peters, 1867. Valid genus.
Cryptoblepharus Wiegmann, 1834. Valid genus.
Cyclodina Girard, 1857 = *Leiolopisma* Duméril and Bibron.
Dasia Gray, 1839. Valid genus.
Elania Gray, 1845 = *Sphenomorphus* Fitzinger.
Emoia Gray, 1845. Valid genus.
Enoplosaurus Sauvage, 1879 = *Tropidophorus* Duméril and Bibron.
Eugongylus Fitzinger, 1843. Valid genus
Eulamprus Fitzinger, 1843 = *Sphenomorphus* Fitzinger.
Eulepis Fitzinger, 1843 = *Lampropholis* Fitzinger.
Eumecia Bocage, 1870. Valid genus.
Eusoma Fitzinger, 1843 = *Emoia* Gray.
Hagria Gray, 1839 = *Riopa* Gray.
Hemiergis Wagler, 1830. Valid genus.
Heteropus Duméril and Bibron, 1839 = *Carlia* Gray.
Hinulia Gray, 1845 = *Sphenomorphus* Fitzinger.
Hombronia Girard, 1857 = *Leiolopisma* Duméril and Bibron.
Ictiscincus Smith, 1937 = *Sphenomorphus* Fitzinger.
Isopachys Lönnberg, 1916 = *Ophioscincus* Peters.
Keneuxia Gray, 1845 = *Dasia* Gray.
Lamprolepis Fitzinger, 1843 = *Dasia* Gray.
Lampropholis Fitzinger, 1843. Valid genus.
Leiolopisma Duméril and Bibron, 1839. Valid genus.
Lepidothyris Cope, 1892 = *Mochlus* Günther.
Leptosiaphos Schmidt, 1943. Valid genus.
Leptosoma Fitzinger, 1843 = *Nodorha,* new genus.
Lerista Bell, 1833 = *Ablepharus* Fitzinger.
Lioscincus Bocage, 1873 = *Lampropholis* Fitzinger.
Liosoma Fitzinger, 1843 = *Tachygyia,* new genus.
Liotropis Fitzinger, 1843 = *Dasia* Gray.
Lipinia Gray, 1845. Valid genus.
Lissonota Blyth, 1853 = *Sphenomorphus* Fitzinger.
Lygisaurus de Vis, 1884 = *Carlia* Gray.
Lygosaurus Hallowell, 1860 = *Ateuchosaurus* Gray.
Lygosoma Hardwicke and Gray, 1827. Valid genus.
Lygosomella Girard, 1857 = *Leiolopisma* Duméril and Bibron.
Menetia Gray, 1844 = *Ablepharus* Fitzinger.
Microblepharus Fitzinger, 1843 = *Ablepharus* Fitzinger.
Miculia Gray, 1844 = *Ablepharus* Fitzinger.
Mochlus Günther, 1864. Valid genus.
Mocoa Gray, 1845 = *Lampropholis* Fitzinger.
Morethia Gray, 1844 = *Cryptoblepharus* Wiegmann.

Myophila de Vis, 1884 = *Carlia* Gray.
Nannoscincus Günther, 1872 = *Anotis* Bavay.
Nodorha, new genus.
Norbea Gray, 1845. Valid genus.
Obligosoma Girard, 1857 = *Leiolopisma* Duméril and Bibron.
Ophiopsis Fitzinger, 1843 = *Ablepharus* Fitzinger.
Ophioscincus Peters, 1873. Valid genus.
Otosaurus Gray, 1845. Valid genus.
Panaspis Cope, 1868. Valid genus.
Parotosaurus Boulenger, 1914 = *Otosaurus* Gray.
Pediporus Roux, 1930 = *Tribolonotus* Duméril and Bibron.
Peromeles Wiegmann, 1834 = *Saiphos* Gray.
Peromelis Wagler, 1830 = *Hemiergis* Wagler.
Phaneropus Fischer, 1881 = *Ablepharus* Fitzinger.
Pholeophilus Smith, 1849 = *Rhodona* Gray.
Podophis Wiegmann, 1834 = *Lygosoma* Hardwicke and Gray.
Praepeditus Duméril and Bibron, 1839 = *Rhodona* Gray.
Rhodona Gray, 1839. Valid genus.
Riopa Gray, 1839. Valid genus.
Ristella Gray, 1839. Valid genus.
Ronia Gray, 1841 = *Rhodona* Gray.
Saiphos Gray, 1831. Valid genus.
Sauroscincus Peters, 1879 = *Lampropholis* Fitzinger.
Scincella Mittleman, 1950. Valid genus.
Sepacontias Günther, 1880 = *Mochlus* Günther.
Soridia Gray, 1839 = *Rhodona* Gray.
Sphenomorphus Fitzinger, 1843. Valid genus.
Sphenosoma Fitzinger, 1843 = *Riopa* Gray.
Squamicilia, new genus.
Tachygyia, new genus.
Tetradactylus Cuvier, 1829 = *Hemiergis* Wagler.
Theconyx Annandale, 1906 = *Dasia* Gray.
Tribolonotus Duméril and Bibron, 1839. Valid genus.
Tridactylus Cuvier, 1829 = *Hemiergis* Wagler.
Tropidophorus Duméril and Bibron, 1839. Valid genus.
Tropidoscincus Bocage, 1873 = *Lampropholis* Fitzinger.
Typhloseps Angel, 1920 = *Ophioscincus* Peters.

KEY TO THE GENERA OF LIZARDS OF THE SUBFAMILY LYGOSOMINAE

1. Head broad and distinct from the relatively slender neck, with a posteriorly emarginate bony casque; dorsum of body and tail with large spinose scales.......... *Tribolonotus* Duméril and Bibron
   Head not prominently distinct from neck; no bony casque; body and tail not covered with large spinose scales.................... 2
2. Eyelids absent and/or immovable.................... 3
   Eyelids present and movable.................... 5
3. No upper eyelid, lower lid immovable and without a more or less transparent or translucent disc; no limbs...... *Ophioscincus* Peters

Upper eyelid present but often much reduced and more or less fused with the lower lid which bears a large transparent or translucent disc; limbs present.................................... 4

4. Frontoparietal single or paired, but always distinct from the interparietal; ear opening absent, or smaller than the eye if present ....*Ablepharus* Fitzinger
Frontoparietal and interparietal fused to form a single large shield; ear opening approximates eye opening..*Cryptoblepharus* Wiegmann

5. Lower eyelid scaly, lacking a more or less transparent or translucent disc; occasionally with a small opaque disc............ 6
Lower eyelid with a more or less transparent or translucent disc..... 21

6. Supranasals present (sometimes fused partially with the nasals)...... 7
Supranasals absent 13

7. Ear opening present.. 8
Ear opening absent, or else covered by overlapping scales............ 12

8. Preanals prominently enlarged; ear opening approximates the diameter of the eye..................................*Otosaurus* Gray
Preanals not, or barely, enlarged; diameter of ear opening half or less the diameter of the eye..................................... 9

9. Supranasals reduced, separated by the rostro-frontonasal suture........ 10
Supranasals enlarged, forming a median suture...................... 11

10. Frontoparietals paired; lower eyelid usually uniformly scaly but occasionally with a small opaque disc; 5 supraoculars; limbs robust, body stout........................*Eugongylus* Fitzinger
Frontoparietals united; lower eyelid uniformly scaly, never with a small opaque disc; 4 supraoculars; limbs much reduced and weak, body slender and vermiform....*Squamicilia,* new genus

11. Frontoparietals paired; limbs short, barely meeting or separated by several scale lengths when appressed........*Mochlus* Günther
Frontoparietals united; limbs long, widely overlapping when appressed..................................*Tachygyia,* new genus

12. Preanals not, or barely, enlarged; supranasals not, or rarely, forming a median suture..................................*Dasia* Gray
Preanals prominently enlarged; supranasals large and forming a median suture ....*Cophoscincopus* Mertens

13. True parietals lacking; frontal very long and constricted, longer than frontoparietals plus interparietal; prefrontals small, separated ....*Ateuchosaurus* Gray
True parietals present; frontal not long and constricted, shorter than frontoparietals plus interparietal............................ 14

14. Tympanum superficial 15
Tympanum sunk (if visible at all)................................. 16

15. Enlarged preanals 2 or 3; supraoculars 4. *Tropidophorus* Duméril and Bibron
Enlarged preanal 1; supraoculars 5........................*Norbea* Gray

16. Frontoparietals united 17
Frontoparietals paired 18

17. Preanals not, or barely, enlarged; ear opening usually present but punctiform; limbs much reduced....*Lygosoma* Hardwicke and Gray
Preanals enlarged; ear opening absent; limbs robust, often meeting or overlapping when appressed...........*Cophoscincus* Peters

18\. Claws retractile .... *Ristella* Gray
Claws nonretractile 19
19\. Prefrontals large, often forming a median suture; limbs robust; 5 digits .... *Sphenomorphus* Fitzinger
Prefrontals greatly reduced and widely separated, or else absent; digits 5 or less, limbs reduced and weak 20
20\. Preanals enlarged; supraoculars 3 or 4; ear opening absent; digits 1, 2, or 3 .... *Saiphos* Gray
Preanals not, or barely, enlarged; supraoculars 4; ear opening present although often much reduced; digits 3, 4, or 5. *Leptosiaphos* Schmidt
21\. Supranasals present (sometimes fused partially with the nasals) 22
Supranasals absent 25
22\. Supranasals large, forming a median suture 23
Supranasals reduced, separated by the rostro-frontonasal suture 24
23\. Prefrontals large, usually forming a median suture or else barely separated by the rostro-frontonasal suture; ear approximates eye in size; limbs vestigial, digits 2 or 3 .... *Eumecia* Bocage
Prefrontals small, widely separated; ear opening approximates size of nostril, or smaller; limbs short but robust, digits 3 or more .... *Riopa* Gray
24\. Frontoparietals united and usually fused with the interparietal to form a single large shield, or else if the interparietal is present it is much reduced; limbs large and broadly overlapping when appressed; ear approximates nostril in size .... *Emoia* Gray
Frontoparietals paired and distinct from the well-developed interparietal; limbs separated, just meeting, or overlapping when appressed; ear large, approximating eye in size .... *Panaspis* Cope
25\. Preanals not, or barely, enlarged 26
Preanals prominently enlarged 29
26\. Frontoparietals united 27
Frontoparietals paired 28
27\. Interparietal distinct, usually large; digits 5-5 .... *Lampropholis* Fitzinger
Interparietal very small or absent; digits 4-5 .... *Carlia* Gray
28\. Digits 5-5; limbs well developed, meeting or overlapping when appressed, or else separated by one or two scale lengths; ear opening prominent .... *Leiolopisma* Duméril and Bibron
Digits 5-5 or less; limbs short, separated by several scale lengths when appressed; ear opening absent or punctiform (approximating nostril or smaller) .... *Anotis* Bavay
29\. Frontoparietals and interparietal fused to form a single large shield; anterior limbs always lacking .... *Rhodona* Gray
Frontoparietals united or paired, but always distinct from interparietal; anterior limbs present (except in *Nodorha wilkinsi*) 30
30\. Limbs much reduced or rudimentary, digits 5-5 or less 31
Limbs well developed, often meeting or overlapping when appressed; digits always 5-5 32
31\. Prefrontals large, often forming a median suture; nasals small to moderate in size, usually separated .... *Hemiergis* Wagler

Prefrontals small and widely separated, or absent; nasals large, usually forming a median suture.................*Nodorha,* new genus
32. Ear concealed ....*Cophoscincus* Peters
Ear opening present.. 33
33. Prefrontals forming a median suture longer than half their length; frontonasal at least as long as it is wide, or longer; snout elongated, acute, depressed or concave; rostral deeper (higher) than it is wide...............................*Lipinia* Gray
Prefrontals separated or forming a median suture less than half their length; frontonasal wider than it is long; snout short, obtuse, flat or convex; rostral wider than it is high..*Scincella* Mittleman

ALPHABETICAL LIST OF SPECIES

In the listing that follows, the fundamental intent is to indicate the limits of the genera employed in this paper, through the medium of their included species. In no sense does this list purport to be a check-list of the forms considered valid, nor does it enumerate all the names that have been proposed in the Lygosominae. Considerable latitude regarding the inclusion of a name has been exercised; where a form has been rather universally regarded as a synonym of an older name, the general rule has been to omit the junior name. On the other hand, some names have been included despite their relegation to synonymy by other workers, since in these cases it is believed likely that further study will demonstrate a distinguishable racial entity.

acrocarinata Kopstein, *Emoia,* 1926.
acutus Peters, *Sphenomorphus,* 1864.
adelaidensis Peters, *Cryptoblepharus,* 1874.
adspersa Steindachner, *Emoia,* 1870.
aenea Girard, *Leiolopisma,* 1857.
aeneus Cope, *Panaspis,* 1868.
aerata Garman, *Carlia,* 1901.
aestuosa Girard, *Leiolopisma,* 1857.
africana Gray, *Leiolopisma,* 1845.
africanus Sternfeld, *Cryptoblepharus,* 1918.
ahli Vogt, *Emoia,* 1932.
aignanus Boulenger, *Sphenomorphus,* 1898.
albertisii Peters and Doria, *Carlia,* 1878.
albofasciolatus Günther, *Eugongylus,* 1872.
albopunctatus Gray, *Mochlus,* 1846.
aldabrae Sternfeld, *Cryptoblepharus,* 1918.
alfredi Boulenger, *Sphenomorphus,* 1898.
aloysii-sabaudiae Peracca, *Leptosiaphos,* 1907.
amblyplacodes Vogt, *Sphenomorphus,* 1932.
anchietae Bocage, *Eumecia,* 1870.
anguina Theobald, *Riopa,* 1868.
anguinoides Boulenger, *Ophioscincus,* 1914.
annamiticus Boettger, *Sphenomorphus,* 1901.

annectens Boulenger, *Otosaurus,* 1897.
anolis Boulenger, *Lipinia,* 1883.
anomalopus Boulenger, *Sphenomorphus,* 1890.
anomalus Gray, *Cryptoblepharus,* 1844.
antoniorum Smith, *Sphenomorphus,* 1927.
aruanus Roux, *Sphenomorphus,* 1910.
aruensis Doria, *Sphenomorphus,* 1874.
aruensis Sternfeld, *Emoia,* 1918.
assamensis Annandale, *Tropidophorus,* 1912.
assata Cope, *Scincella,* 1864.
ater Boettger, *Cryptoblepharus,* 1913.
atrigulare Ogilby, *Carlia,* 1890.
atrigularis Stejneger, *Sphenomorphus,* 1908.
atrocostata Lesson, *Emoia,* 1830.
atromaculatus Garman, *Sphenomorphus,* 1901.
aubrianus Bocage, *Lampropholis,* 1873.
australe Gray, *Lygosoma,* 1839.
australe Peters, *Ophioscincus,* 1873.
australis Gray, *Sphenomorphus,* 1839.
autralis Sternfeld, *Cryptoblepharus,* 1918.
austro-caledonicus Bavay, *Lampropholis,* 1869.
balinensis Barbour, *Cryptoblepharus,* 1911.
bampfyledei Bartlett, *Mochlus,* 1895.
bancrofti Longman, *Saiphos,* 1916.
barbouri Stejneger, *Scincella,* 1925.
battersbyi Procter, *Emoia,* 1920.
baudinii Duméril and Bibron, *Emoia,* 1839.
beauforti de Jong, *Sphenomorphus,* 1927.
beccarii Peters, *Norbea,* 1871.
beccarii Peters and Doria, *Carlia,* 1878.
beddomii Boulenger, *Ristella,* 1887.
beddomii Boulenger, *Scincella,* 1887.
berdmorei Blyth, *Tropidophorus,* 1853.
bicarinata Macleay, *Carlia,* 1877.
bilineata Gray, *Scincella,* 1846.
biparietalis Taylor, *Sphenomorphus,* 1918.
bipes Fischer, *Rhodona,* 1882.
bitaeniatus Boettger, *Cryptoblepharus,* 1913.
biunguiculatus Oudemans, *Saiphos,* 1894.
bivittatus Menestries, *Ablepharus,* 1832.
blackmanni de Vis, *Carlia,* 1885.
blanchardi Burt, *Tribolonotus,* 1930.
blochmanni Tornier, *Leptosiaphos,* 1903.
boettgeri Van Denburgh, *Scincella,* 1912.
boettgeri Sternfeld, *Emoia,* 1918.
boettgeri Sternfeld, *Eugongylus,* 1918.
bougainvillii Duméril and Bibron, *Nodorha,* 1839.
boulengeri Van Denburgh, *Sphenomorphus,* 1912.
boutonii Desjardins, *Cryptoblepharus,* 1831.
bowringi Günther, *Mochlus,* 1864.

brachysomus Lönnberg and Andersson, *Sphenomorphus,* 1915.
brandti Strauch, *Ablepharus,* 1868.
breviceps Peters, *Panaspis,* 1873.
brevipes Boettger, *Sphenomorphus,* 1895.
brookei Gray, *Norbea,* 1845.
brooksi Loveridge, *Sphenomorphus,* 1933.
browni Van Denburgh, *Ateuchosaurus,* 1912.
buergersi Vogt, *Emoia,* 1932.
burdeni Dunn, *Cryptoblepharus,* 1927.
burgeoni Witte, *Leptosiaphos,* 1933.
buttikoferi Lidth de Jeude, *Sphenomorphus,* 1905.
cabindae Bocage, *Panaspis,* 1866.
caerulecauda de Vis, *Emoia,* 1892.
callisticta Peters and Doria, *Emoia,* 1878.
cameronicus Smith, *Sphenomorphus,* 1924.
caudaequinae Smith, *Scincella,* 1950.
caudatus Sternfeld, *Cryptoblepharus,* 1918.
celebense Müller, *Otosaurus,* 1894.
celebense de Rooij, *Dasia,* 1915.
challengeri Boulenger, *Leiolopisma,* 1887.
cherriei Cope, *Scincella,* 1893.
chinensis Gray, *Ateuchosaurus,* 1845.
cocincinensis Duméril and Bibron, *Tropidophorus,* 1839.
cognatus Boettger, *Cryptoblepharus,* 1881.
colletti Boulenger, *Sphenomorphus,* 1896.
compressicauda Witte, *Leptosiaphos,* 1933.
comtus Roux, *Sphenomorphus,* 1928.
concinnatus Boulenger, *Otosaurus,* 1887.
consobrinus Peters and Doria, *Sphenomorphus,* 1878.
cophia Boulenger, *Lygosoma,* 1908.
corpulentus Smith, *Mochlus,* 1921.
courcyanus Annandale, *Sphenomorphus,* 1912.
crassicaudus Duméril, *Sphenomorphus,* 1851.
cumingi Gray, *Otosaurus,* 1845.
cuneiceps de Vis, *Emoia,* 1890.
cuprea Gray, *Leiolopisma,* 1839.
cursor Barbour, *Cryptoblepharus,* 1911.
curta Boulenger, *Carlia,* 1897.
curtirostris Taylor, *Otosaurus,* 1915.
cyanogaster Lesson, *Emoia,* 1830.
cyanura Lesson, *Emoia,* 1830.
dahomeyense Chabanaud, *Panaspis,* 1917.
darlingtoni Loveridge, *Lygosoma,* 1933.
darlingtoni Loveridge, *Tropidophorus,* 1945.
decipiens Boulenger, *Sphenomorphus,* 1894.
decresiensis Fitzinger, *Hemiergis,* 1829.
degrijsi Mertens, *Cryptoblepharus,* 1928.
delicata de Vis, *Lampropholis,* 1888.
dendyi Boulenger, *Leiolopisma,* 1902.
deplanchii Bavay, *Sphenomorphus,* 1869.

derooyae de Jong, *Sphenomorphus*, 1927.
deserti Strauch, *Ablepharus*, 1868.
desertora Sternfeld, *Nodorha*, 1919.
devisii Boulenger, *Carlia*, 1890.
diguliense Kopstein, *Carlia*, 1926.
distinguendus Werner, *Ablepharus*, 1910.
divergens, Taylor, *Sphenomorphus*, 1929.
domina de Vis, *Sphenomorphus*, 1888.
doriae Boulenger, *Scincella*, 1887.
dorsalis, Boulenger, *Sphenomorphus*, 1887.
durus Cope, *Cophoscincopus*, 1862.
dussumieri Duméril and Bibron, *Sphenomorphus*, 1839.
elberti Sternfeld, *Dasia*, 1918.
elegans Gray, *Ablepharus*, 1844.
elegans Boulenger, *Scincella*, 1897.
elegans Sternfeld, *Sphenomorphus*, 1918.
elegantoides Ahl, *Scincella*, 1925.
elegantulus Peters and Doria, *Sphenomorphus*, 1878.
emigrans Lidth de Jeude, *Sphenomorphus*, 1895.
entrecasteauxii Duméril and Bibron, *Leiolopisma*, 1839.
equalis Gray, *Saiphos*, 1825.
essingtonii Gray, *Sphenomorphus*, 1842.
euryotis Werner, *Lampropholis*, 1909.
exigua Anderson, *Scincella*, 1878.
fallax Peters, *Sphenomorphus*, 1860.
fasciatus Gray, *Sphenomorphus*, 1845.
fasciolara Girard, *Leiolopisma*, 1857.
fasciolatus Günther, *Sphenomorphus*, 1867.
fernandi Burton, *Mochlus*, 1836.
fischeri Boulenger, *Sphenomorphus*, 1887.
flavigulare Schmidt, *Emoia*, 1932.
flavipes Parker, *Sphenomorphus*, 1936.
florense Weber, *Sphenomorphus*, 1891.
foliora de Vis, *Carlia*, 1884.
forbesi Boulenger, *Sphenomorphus*, 1888.
forbesora Taylor, *Scincella*, 1937.
formosa Blyth, *Leiolopisma*, 1853.
formosensis Van Denburgh, *Scincella*, 1912.
formosensis Van Denburgh, *Sphenomorphus*, 1912.
fragile Günther, *Nodorha*, 1876.
frontalis de Vis, *Ophioscincus*, 1888.
frosti Zeitz, *Nodorha*, 1920.
furcatus Weber, *Cryptoblepharus*, 1891.
fusca Duméril and Bibron, *Carlia*, 1839.
garnieri Bavay, *Tachygyia*, 1869.
gemmingeri Cope, *Scincella*, 1864.
gerrardii Gray, *Nodorha*, 1864.
gloriosus Stejneger, *Cryptoblepharus*, 1893.
gracile Bavay, *Anotis*, 1869.
gracilis de Rooij, *Tribolonotus*, 1909.

graciloides Lönnberg and Andersson, *Anotis,* 1913.
grande Gray, *Leiolopisma,* 1845.
granulatus Boulenger, *Otosaurus,* 1903.
graueri Sternfeld, *Leptosiaphos,* 1912.
grayanus Stoliczka, *Ablepharus,* 1872.
grayi Günther, *Tropidophorus,* 1861.
greyi Gray, *Ablepharus,* 1844.
griffini Taylor, *Dasia,* 1915.
guentheri Peters, *Riopa,* 1879.
guentheri Boulenger, *Ristella,* 1887.
guichenoti Duméril and Bibron, *Lampropholis,* 1839.
guineensis Peters, *Mochlus,* 1879.
gyldenstolpei Lönnberg, *Ophioscincus,* 1916.
hainanus Smith, *Tropidophorus,* 1923.
haliana Haly and Nevill, *Dasia,* 1887.
hallieri Lidth de Jeude, *Sphenomorphus,* 1905.
helenae Cochran, *Sphenomorphus,* 1927.
helleri Loveridge, *Leptosiaphos,* 1932.
herberti Smith, *Mochlus,* 1916.
himalayana Günther, *Scincella,* 1864.
incerta Stuart, *Scincella,* 1940.
inconspicua Müller, *Scincella,* 1894.
indicus Gray, *Sphenomorphus,* 1853.
infralineolatus Günther, *Cophoscincus,* 1873.
infrapunctata Boulenger, *Leiolopisma,* 1887.
iniqua Lidth de Jeude, *Norbea,* 1905.
initialis Werner, *Anotis,* 1910.
inornatus Gray, *Sphenomorphus,* 1845.
intermedius Sternfeld, *Sphenomorphus,* 1919.
intermedius Kinghorn, *Sphenomorphus,* 1932.
iridescens Boulenger, *Emoia,* 1897.
irrorata Macleay, *Emoia,* 1877.
isodactyla Günther, *Squamicilia,* 1864.
isolepis Boulenger, *Sphenomorphus,* 1887.
ixbaac Stuart, *Scincella,* 1940.
jagori Peters, *Sphenomorphus,* 1864.
jakati Kopstein, *Emoia,* 1926.
jamnana Loveridge, *Carlia,* 1948.
jeudei Boulenger, *Sphenomorphus,* 1897.
jobiensis Meyer, *Sphenomorphus,* 1874.
johnstoni Boulenger, *Eumecia,* 1897.
keiensis Roux, *Cryptoblepharus,* 1910.
keiensis Sternfeld, *Emoia,* 1918.
kilimensis Stejneger, *Leptosiaphos,* 1891.
kinabaluensis Bartlett, *Otosaurus,* 1895.
kitsoni Boulenger, *Panaspis,* 1913.
klossi Boulenger, *Emoia,* 1914.
kohtaoensis Cochran, *Scincella,* 1927.
koratensis Smith, *Mochlus,* 1917.
kordoana Meyer, *Emoia,* 1874.

kosciuskoi Kinghorn, *Sphenomorphus,* 1932.
kuekenthali Boettger, *Emoia,* 1895.
kuhnei Roux, *Sphenomorphus,* 1910.
kutuensis Lönnberg, *Leptosiaphos,* 1911.
labillardierii Gray, *Sphenomorphus,* 1838.
ladacense Günther, *Scincella,* 1864.
laeve Oudemans, *Carlia,* 1894.
laeviceps Peters, *Mochlus,* 1874.
laotus Smith, *Tropidophorus,* 1923.
larutense Boulenger, *Saiphos,* 1900.
laterale Say, *Scincella,* 1823.
lateralis de Vis, *Carlia,* 1885.
laterimaculata Boulenger, *Scincella,* 1887.
latifasciatus Meyer, *Sphenomorphus,* 1874.
leae Boulenger, *Sphenomorphus,* 1887.
lentiginosus de Vis, *Saiphos,* 1888.
leonhardii Sternfeld, *Sphenomorphus,* 1919.
leschenaultii Cocteau, *Cryptoblepharus,* 1832.
lesueurii Duméril and Bibron, *Sphenomorphus,* 1839.
leucospilus Peters, *Tropidophorus,* 1872.
leucotaenia Bleecker, *Carlia,* 1860.
leveretti Schmidt, *Sphenomorphus,* 1927.
lichenigera O'Shaughnessy, *Leiolopisma,* 1874.
lineata Gray, *Rhodona,* 1839.
lineata Gray, *Riopa,* 1839.
lineatus Bell, *Ablepharus,* 1833.
lineolata Stoliczka, *Riopa,* 1870.
lineo-ocellata Duméril, *Leiolopisma,* 1851.
lineo-ocellatus Duméril and Bibron, *Cryptoblepharus,* 1839.
lineopunctulata Duméril and Bibron, *Rhodona,* 1839.
llanosi Taylor, *Otosaurus,* 1919.
lobula Loveridge, *Scincella,* 1945.
longicaudatus de Rooij, *Sphenomorphus,* 1915.
longiceps Boulenger, *Lipinia,* 1895.
loriae Boulenger, *Sphenomorphus,* 1897.
louisadensis Boulenger, *Sphenomorphus,* 1903.
luberoensis Witte, *Leptosiaphos,* 1933.
luctuosa Peters and Doria, *Carlia,* 1878.
luzonense Boulenger, *Lygosoma,* 1895.
mabuiforma Loveridge, *Riopa,* 1935.
maccooeyi Ramsay and Ogilby, *Carlia,* 1890.
maccoyi Lucas and Frost, *Anotis,* 1894.
macropisthopa Werner, *Nodorha,* 1903.
macrota Steindachner, *Scincella,* 1869.
macrotympana Stoliczka, *Scincella,* 1873.
maculatus Blyth, *Sphenomorphus,* 1853.
maindroni Sauvage, *Sphenomorphus,* 1879.
malayanus Doria, *Sphenomorphus,* 1888.
manni Brown, *Emoia,* 1948.
mariae Bavay, *Anotis,* 1869.

mayottensis Mertens, *Cryptoblepharus,* 1928.
megalops Annandale, *Sphenomorphus,* 1906.
megaspilus Günther, *Sphenomorphus,* 1877.
mehelyi Werner, *Emoia,* 1899.
melanochlorus Vogt, *Sphenomorphus,* 1932.
melanopogon Duméril and Bibron, *Sphenomorphus,* 1839.
melanopogon Gray, *Carlia,* 1844.
melanosticta Boulenger, *Scincella,* 1887.
meleagris Boulenger, *Leptosiaphos,* 1907.
mentovarius Boettger, *Eugongylus,* 1895.
metallicum O'Shaughnessy, *Lampropholis,* 1874.
metallicus Boulenger, *Cryptoblepharus,* 1887.
miangense Werner, *Lipinia,* 1910.
microcerca Boettger, *Scincella,* 1901.
microlepidota O'Shaughnessy, *Lampropholis,* 1874.
microlepis Duméril and Bibron, *Tachygyia,* 1839.
microlepis Günther, *Tropidophorus,* 1861.
micropa Lidth de Jeude, *Norbea,* 1905.
microta Gray, *Nodorha,* 1844.
mimikanus Boulenger, *Otosaurus,* 1914.
minutus Meyer, *Sphenomorphus,* 1874.
miodactylus Boulenger, *Saiphos,* 1903.
miopa Günther, *Rhodona,* 1867.
miota Boulenger, *Scincella,* 1895.
misaminia Stejneger, *Norbea,* 1908.
mivarti Boulenger, *Emoia,* 1887.
mjobergi Lönnberg, *Sphenomorphus,* 1913.
moco Duméril and Bibron, *Leiolopisma,* 1839.
mocquardi Boulenger, *Norbea,* 1894.
mocquardi Chabanaud, *Mochlus,* 1918.
modesta Günther, *Scincella,* 1864.
modestus Günther, *Mochlus,* 1880.
modigliani Boulenger, *Sphenomorphus,* 1895.
moellendorffi Boettger, *Sphenomorphus,* 1897.
moluccara Barbour, *Dasia,* 1911.
monotropis Boulenger, *Sphenomorphus,* 1887.
monticola Schmidt, *Scincella,* 1927.
morokana Parker, *Scincella,* 1936.
moszkowskii Vogt, *Sphenomorphus,* 1912.
moultonii Barbour and Noble, *Dasia,* 1912.
muelleri Schlegel, *Sphenomorphus,* 1837.
muelleri Fischer, *Ablepharus,* 1881.
munda de Vis, *Carlia,* 1885.
mundivense Browne, *Carlia,* 1898.
murphyi Burt, *Emoia,* 1930.
murrayi Boulenger, *Sphenomorphus,* 1887.
murudensis Smith, *Otosaurus,* 1925.
mustelina O'Shaughnessy, *Leiolopisma,* 1874.
neuhaussi Vogt, *Sphenomorphus,* 1911.
nichollsi Loveridge, *Nodorha,* 1933.

nieuwenhuisi Lidth de Jeude, *Dasia,* 1905.
nigra Hombron and Jacquinot, *Emoia,* 1853.
nigra Sternfeld, *Dasia,* 1918.
nigricaudis Macleay, *Sphenomorphus,* 1877.
nigrigulare Boulenger, *Carlia,* 1897.
nigriventris de Rooij, *Sphenomorphus,* 1915.
nigrofasciolata Peters, *Leiolopisma,* 1869.
nigrolabrus Günther, *Sphenomorphus,* 1873.
nigrolineatus Boulenger, *Sphenomorphus,* 1897.
nigropunctatus Hallowell, *Cryptoblepharus,* 1860.
nimbense Angel, *Panaspis,* 1944.
nitens Peters, *Scincella,* 1871.
noctua Lesson, *Lipinia,* 1830.
nototaenius Boulenger, *Sphenomorphus,* 1914.
novaecaledoniae Parker, *Lampropholis,* 1926.
novaeguineae Schlegel, *Tribolonotus,* 1834.
novaeguineae Meyer, *Carlia,* 1874.
novaeguineae Mertens, *Cryptoblepharus,* 1928.
novocaledonicus Mertens, *Cryptoblepharus,* 1928.
obscura de Jong, *Emoia,* 1927.
ocellata Gray, *Lampropholis,* 1844.
ocellatus Boulenger, *Sphenomorphus,* 1896.
ocelliferus Boulenger, *Sphenomorphus,* 1896.
oligolepis Boulenger, *Sphenomorphus,* 1914.
olivacea Gray, *Dasia,* 1838.
opisthorhodus Werner, *Mochlus,* 1910.
orientale Shreve, *Sphenomorphus,* 1940.
ornatus Gray, *Sphenomorphus,* 1845.
pagenstecheri Lindholm, *Scincella,* 1901.
pallidiceps de Vis, *Emoia,* 1890.
pallidus Günther, *Sphenomorphus,* 1844.
pallidus Mertens, *Cryptoblepharus,* 1928.
palnica Boettger, *Scincella,* 1892.
pannonicus Fitzinger, *Ablepharus,* 1823.
papuensis Macleay, *Sphenomorphus,* 1877.
paraenea Ahl, *Leiolopisma,* 1925.
pardalis Macleay, *Saiphos,* 1877.
parietale Peters, *Emoia,* 1871.
parkeri Smith, *Scincella,* 1937.
partelloi Stejneger, *Norbea,* 1910.
parvus Boulenger, *Sphenomorphus,* 1897.
pectorale de Vis, *Carlia,* 1885.
pellopleurus Hallowell, *Ateuchosaurus,* 1860.
pembanus Boettger, *Mochlus,* 1913.
peronii Fitzinger, *Hemiergis,* 1826.
peronii Cocteau, *Cryptoblepharus,* 1836.
peronii Duméril and Bibron, *Carlia,* 1839.
perplexa Barbour, *Norbea,* 1921.
perviridis Barbour, *Dasia,* 1921.
phaeodes Vogt, *Scincella,* 1932.

philippinica Mertens, *Dasia,* 1929.
physicae Duméril and Bibron, *Emoia,* 1839.
picturata Fry, *Nodorha,* 1914.
plagiocephalus Cocteau, *Cryptoblepharus,* 1836.
planiventrale Lucas and Frost, *Nodorha,* 1902.
poecilopleurus Wiegmann, *Cryptoblepharus,* 1835.
popae Shreve, *Riopa,* 1940.
potanini Günther, *Scincella,* 1896.
pranensis Cochran, *Scincella,* 1930.
pratti Boulenger, *Sphenomorphus,* 1903.
prehensicauda Loveridge, *Scincella,* 1945.
presignis Boulenger, *Sphenomorphus,* 1900.
pretiosum O'Shaughnessy, *Lampropholis,* 1874.
producta Boulenger, *Squamicilia,* 1909.
pseudotropa Günther, *Leiolopisma,* 1844.
pulchella Gray, *Lipinia,* 1845.
pulcher Sternfeld, *Cryptoblepharus,* 1918.
pulchra Boulenger, *Scincella,* 1903.
pulla Barbour, *Carlia,* 1911.
pumila Boulenger, *Lygosoma,* 1887.
punctata Linné, *Riopa,* 1766.
punctata Gray, *Rhodona,* 1839.
punctatolineata Boulenger, *Scincella,* 1893.
punctatovittata Günther, *Nodorha,* 1867.
punctatus Sternfeld, *Cryptoblepharus,* 1918.
punctulata Peters, *Lygosoma,* 1871.
quadridigitatus Werner, *Hemiergis,* 1910.
quadrilineata Duméril and Bibron, *Hemiergis,* 1839.
quadrivittatus Peters, *Cophoscincus,* 1867.
quadrupes Linné, *Lygosoma,* 1766.
quatuordecimlineatus Sternfeld, *Sphenomorphus,* 1919.
quatuordigitata Sternfeld, *Leptosiaphos,* 1912.
queenslandiae de Vis, *Tropidophorus,* 1890.
quinquetaeniatus Günther, *Cryptoblepharus,* 1874.
quoyi Duméril and Bibron, *Sphenomorphus,* 1839.
reevesi Gray, *Scincella,* 1838.
reichenovei Peters, *Leiolopisma,* 1874.
relictus Vinciguerre, *Cophoscincus,* 1892.
renschi Mertens, *Cryptoblepharus,* 1928.
reticulatus Günther, *Saiphos,* 1873.
rhomboidale Peters, *Carlia,* 1869.
richardsoni Gray, *Sphenomorphus,* 1844.
rivulare Taylor, *Norbea,* 1915.
robinsoni Smith, *Tropidophorus,* 1919.
roulei Angel, *Ophioscincus,* 1920.
rouxi Hediger, *Lipinia,* 1934.
rufescens Shaw, *Eugongylus,* 1802.
ruficauda Taylor, *Emoia,* 1915.
ruficaudus Lucas and Frost, *Cryptoblepharus,* 1895.
rufus Boulenger, *Sphenomorphus,* 1887.

rupicola Smith, *Scincella,* 1916.
rurkii Gray, *Ristella,* 1839.
rutilus Peters, *Crytoblepharus,* 1879.
salsburyi Schmidt, *Ateuchosaurus,* 1927.
samoensis Duméril, *Emoia,* 1851.
sanctus Duméril and Bibron, *Sphenomorphus,* 1839.
sanfordi Schmidt and Burt, *Emoia,* 1930.
sarasinorus Boulenger, *Sphenomorphus,* 1897.
scharffi Boulenger, *Anotis,* 1915.
schevilli Loveridge, *Sphenomorphus,* 1933.
schmidti Burt, *Tribolonotus,* 1930.
schoedei Vogt, *Sphenomorphus,* 1912.
schultzei Vogt, *Sphenomorphus,* 1911.
scotophilus Boulenger, *Sphenomorphus,* 1900.
scutirostra Peters, *Lygosoma,* 1873.
sembalunica Mertens, *Carlia,* 1927.
semoni Oudemans, *Scincella,* 1894.
semperi Peters, *Scincella,* 1867.
septentrionale Schmidt, *Scincella,* 1927.
shelfordi Boulenger, *Sphenomorphus,* 1900.
sikkimense Blyth, *Scincella,* 1854.
silvicola Taylor, *Scincella,* 1937.
similis Dunn, *Emoia,* 1927.
simplex Cope, *Saiphos,* 1864.
simus Sauvage, *Sphenomorphus,* 1879.
sinicus Boettger, *Tropidophorus,* 1886.
slevini Loveridge, *Anotis,* 1941.
smaragdina Lesson, *Dasia,* 1830.
smithii Gray, *Leiolopisma,* 1845.
solomonis Boulenger, *Sphenomorphus,* 1887.
sorex Boettger, *Emoia,* 1895.
sowerbyi Stejneger, *Ateuchosaurus,* 1924.
spaldingi Macleay, *Sphenomorphus,* 1877.
speiseri Roux, *Emoia,* 1913.
spinaure Smith, *Carlia,* 1927.
spurrelli, Boulenger, *Panaspis,* 1917.
stanleyana Boulenger, *Scincella,* 1897.
steerei Stejneger, *Sphenomorphus,* 1908.
steindachneri Bocage, *Lampropholis,* 1873.
stejnegeri Taylor, *Norbea,* 1922.
stellatus Boulenger, *Sphenomorphus,* 1900.
stickeli Loveridge, *Sphenomorphus,* 1948.
strauchi Boulenger, *Sphenomorphus,* 1887.
striatopunctulatus Ahl, *Sphenomorphus,* 1925.
striolatus Weber, *Sphenomorphus,* 1891.
stuarti Smith, *Scincella,* 1941.
subcaerulea Boulenger, *Dasia,* 1891.
subnitens Boettger, *Scincella,* 1896.
sulaense Kopstein, *Eugongylus,* 1927.
sumatrense Bleecker, *Saiphos,* 1860.

sumbawanus Mertens, *Cryptoblepharus,* 1928.
sundevalli Smith, *Mochlus,* 1849.
surdus Boulenger, *Cophoscincus,* 1900.
suteri Boulenger, *Leiolopisma,* 1906.
taeniolatus Shaw, *Sphenomorphus,* 1790.
taeniopleurus Peters, *Cryptoblepharus,* 1874.
tamburinensis Lönnberg and Andersson, *Sphenomorphus,* 1915.
tanae Loveridge, *Riopa,* 1935.
taprobanensis Kelaart, *Sphenomorphus,* 1852.
tavesae Smith, *Scincella,* 1935.
taylori Burt, *Otosaurus,* 1930.
taylori Oliver, *Scincella,* 1937.
telfairii Desjardins, *Leiolopisma,* 1831.
tenue Garman, *Sphenomorphus,* 1901.
tenuiculus Mocquard, *Sphenomorphus,* 1890.
tenuis Gray, *Sphenomorphus,* 1831.
terdigitata Parker, *Nodorha,* 1926.
tersus Smith, *Sphenomorphus,* 1916.
tetradactyla Lucas and Frost, *Nodorha,* 1875.
tetradactyla O'Shaughnessy, *Carlia,* 1879.
tetrataenia Boulenger, *Emoia,* 1895.
texta Mueller, *Scincella,* 1894.
thai Smith, *Tropidophorus,* 1919.
thomasi Tornier, *Leptosiaphos,* 1903.
tigrinus de Vis, *Sphenomorphus,* 1888.
timidus de Vis, *Ablepharus,* 1888.
togoensis Werner, *Panaspis,* 1902.
tornieri Vogt, *Sphenomorphus,* 1911.
totocarinatus Vogt, *Sphenomorphus,* 1932.
travancorica Beddome, *Ristella,* 1870.
travankorica Beddome, *Scincella,* 1870.
tricarinata Meyer, *Carlia,* 1874.
tricolor Bavay, *Lampropholis,* 1869.
tridactylus Boulenger, *Hemiergis,* 1915.
trilineatum Gray, *Lampropholis,* 1838.
tropidolepis Boulenger, *Emoia,* 1914.
tropidonotus Boulenger, *Sphenomorphus,* 1897.
truncatus Peters, *Saiphos,* 1876.
tryoni Longman, *Sphenomorphus,* 1918.
tympanus Lönnberg and Andersson, *Sphenomorphus,* 1913.
undulatus Peters and Doria, *Sphenomorphus,* 1878.
unicolor Harlan, *Scincella,* 1825.
unilineatus de Rooij, *Sphenomorphus,* 1915.
vandenburghi Schmidt, *Scincella,* 1927.
variabilis Bavay, *Lampropholis,* 1869.
variegatus Peters, *Sphenomorphus,* 1867.
verreauxii Duméril, *Saiphos,* 1851.
vertebrale de Vis, *Carlia,* 1888.
victoriana Shreve, *Scincella,* 1940.
vigintiserius Sjostedt, *Sphenomorphus,* 1897.

virens Peters, *Lipinia,* 1881.
virgatus Garman, *Cryptoblepharus,* 1901.
viridipunctata Lesson, *Dasia,* 1830.
vittata Ederling, *Dasia,* 1864.
vittigera Boulenger, *Scincella,* 1894.
vivax de Vis, *Carlia,* 1884.
voeltzkowi Sternfeld, *Cryptoblepharus,* 1918.
vosmaerii Gray, *Riopa,* 1839.
vulcania Girard, *Scincella,* 1857.
vyneri Shelford, *Dasia,* 1905.
wahlbergii Smith, *Ablepharus,* 1849.
walkeri Boulenger, *Nodorha,* 1891.
weberi Schmidt, *Leptosiaphos,* 1943.
weeksae Kinghorn, *Leiolopisma,* 1928.
werneri Vogt, *Emoia,* 1912.
wetariensis Mertens, *Sphenomorphus,* 1928.
whitneyi Burt, *Emoia,* 1930.
wilkinsi Parker, *Nodorha,* 1926.
wolfi Sternfeld, *Otosaurus,* 1918.
wolfi Sternfeld, *Sphenomorphus,* 1918.
wollastoni Boulenger, *Sphenomorphus,* 1914.
woodfordii Boulenger, *Sphenomorphus,* 1887.
woodwardi Lucas and Frost, *Hemiergis,* 1894.
yunnanensis Boulenger, *Tropidophorus,* 1887.

BIBLIOGRAPHY

The bibliography of the Lygosominae is enormous, scattered as it is over hundreds of miscellaneous papers, monographs, exploration reports, and general zoological treatises which have appeared during the last 150 years. In consequence, rather than being a compendium of this literature the present bibliography includes only certain standard works and geographic studies to which the interested student is referred for more specific literature treating forms of particular interest.

BARBOUR, THOMAS.
1912. A contribution to the zoogeography of the East Indian islands. Mem. Mus. Comp. Zool., vol. 44, pp. 1-203, pls. 1-8.
1921. Reptiles and amphibians from the British Solomon Islands. Proc. New England Zool. Club, vol. 7, pp. 91-122, pls. 2-4.
BOULENGER, GEORGE A.
1887. Catalogue of the lizards in the British Museum. 2d ed., xii + 575 pp., 40 pls. London.
BURT, CHARLES E., and BURT, MAY D.
1932. Herpetological results of the Whitney South Sea Expedition. VI. Bull. Amer. Mus. Nat. Hist., vol. 63, pp. 461-597, figs. 1-38.
COPE, EDWARD D.
1864. Contributions to the herpetology of tropical America. Proc. Acad. Nat. Sci. Philadelphia, vol. 3, pp. 166-176; vol. 4, pp. 177-181.

1892. On degenerate types of scapular and pelvic arches in the Lacertilia. Journ. Morph., vol. 7, pp. 223-244, pl. 13.

1900. Crocodilians, lizards, and snakes of North America. Ann. Rep. U. S. Nat. Mus. for 1898, pp. 153-1294, figs. 1-347, pls. 1-36.

Duméril, A. M. C., and Bibron, G.

1839. Erpétologie générale. . . . 5 vols., viii + 854 pp. Paris.

Duméril, A., and Bocourt, Marie-Firmin.

1881. Études sur les reptiles et les batraciens. Mission Scientifique au Mexique et dans l'Amérique Centrale, vol. 3, No. 7, pp. 441-488, pls. 22e-22j.

Duméril, A. M. C., and Duméril, M. A.

1851. Catalogue méthodique de la collection des reptiles du Muséum d'Histoire Naturelle de Paris. iv + 224 pp. Paris.

Fitzinger, Leopold J.

1826. Neue Classification der Reptilien. 66 pp., 1 pl. Wien.

1843. Systema reptilium. . . . 106 pp. Vindobonae.

Fitzsimons, Vivian F.

1943. The lizards of South Africa. Transvaal Mus. Mem., vol. 1, xv + 528 pp., 384 figs., 24 pls., map.

Gray, John E.

1831. A synopsis of the species of the class Reptilia. (App., pp. 1-100) *in* Cuvier, The Animal Kingdom. Class Reptilia. Griffith ed., 480 + 100 pp., 54 pls. London.

1845. Catalogue of the specimens of lizards in the collection of the British Museum. xxvii + 289 pp. London.

Günther, Albert C. L. G.

1864. The reptiles of British India. xxvii + 452 pp., pls. 1-26. London.

Hoffmann, C. K.

1881. Klassen und Ordungen des Thier-Reichs, etc. Bd. 6, Abt. 3. Reptilien, Lief. 18-21, pp. 443-1399, pls. 49-107. Leipzig and Heidelberg.

Loveridge, Arthur.

1928. Field notes on vertebrates collected by the Smithsonian-Chrysler East African expedition. Proc. U. S. Nat. Mus., vol. 73, No. 17, pp. 1-69, pls. 1-4.

1933. Reports on the scientific results of an expedition to the southwestern highlands of Tanganyika Territory. VII. Herpetology. Bull. Mus. Comp. Zool., vol. 74, No. 7, pp. 195-416, 3 pls.

1933. New scincid lizards of the genera *Sphenomorphus, Rhodona* and *Lygosoma* from Australia. Occ. Pap. Boston Soc. Nat. Hist., vol. 8, pp. 95-100.

1934. Australian reptiles in the Museum of Comparative Zoology, Cambridge, Massachusetts. Bull. Mus. Comp. Zool., vol. 77, No. 6, pp. 243-383, 1 pl.

1942. Scientific results of a fourth expedition to forested areas in East and Central Africa. IV. Reptiles. Bull. Mus. Comp. Zool., vol. 91, No. 4, pp. 237-373, pls. 1-6.

1948. New Guinean reptiles and amphibians in the Museum of Comparative Zoology and United States National Museum. Bull. Mus. Comp Zool., vol. 101, No. 2, pp. 305-430.

MERTENS, ROBERT.

1928. Neue Inselrassen von *Cryptoblepharus boutonii* (Desjardin). Zool. Anz., vol. 78, pp. 82-89.

1929. Die Rassen des Smaragdskinkes *Dasia smaragdinum* Lesson. Zool. Anz., vol. 84, pp. 209-220.

1930. Die Amphibien und Reptilien der Inseln Bali, Lombok, Sumbawa und Flores. Abh. Senck. nat. Ges., vol. 42, pp. 117-344, pls. 1-4.

1931. *Ablepharus boutonii* (Desjardin) und seine geographische Variation. Zool. Jahrb., vol. 61, pp. 63-210, pls. 2-4.

MITTLEMAN, M. B.

1950. The generic status of *Scincus lateralis* Say, 1823. Herpetologica, vol. 6, No. 2, pp. 17-20.

PETERS, W., and DORIA, G.

1878. Catalogo dei rettili e dei batraci raccolti da O. Beccari, L. M. D'Albertis e A. A. Bruijn nella sotto-regione Austro-Malese. Ann. Mus. Civ. Stor. Nat. Geneva, vol. 13, pp. 323-450, pls. 1-7.

ROOIJ, NELLY DE.

1915. The reptiles of the Indo-Australian Archipelago. I. Lacertilia, Chelonia, Emydosauria. xiv + 384 pp., 132 figs. Leiden.

SCHMIDT, KARL P.

1927. The reptiles of Hainan. Bull. Amer. Mus. Nat. Hist., vol. 54, pp. 395-465, 17 figs., pl. 27.

1927. Notes on Chinese reptiles. Bull. Amer. Mus. Nat. Hist., vol. 54, pp. 467-551, 22 figs., pls. 28-30.

1943. Amphibians and reptiles from the Sudan. Zool. Ser. Field Mus. Nat. Hist., vol. 24, No. 29, pp. 331-338, 1 fig.

SMITH, HOBART M., and TAYLOR, EDWARD H.

1950. An annotated checklist and key to the reptiles of Mexico, exclusive of the snakes. U. S. Nat. Mus. Bull. 199, v + 253 pp.

SMITH, MALCOLM A.

1927. Contributions to the herpetology of the Indo-Australian region. Proc. Zool. Soc. London, 1927, pp. 199-225, 2 pls.

1935. The fauna of British India. . . . Reptilia and Amphibia. 2, Sauria. xiii + 440 pp., 1 pl., 93 figs. London.

1937. A review of the genus *Lygosoma* (Scincidae: Reptilia) and its allies. Rec. Indian Mus., vol. 39, No. 3, pp. 213-234, figs. 1-3.

STEJNEGER, LEONHARD.

1907. The herpetology of Japan and adjacent territory. U. S. Nat. Mus. Bull. 58, xx + 577 pp., 409 figs., 35 pls.

1925. Chinese amphibians and reptiles in the United States National Museum. Proc. U. S. Nat. Mus., vol. 66, No. 25, pp. 1-115, 6 figs.

STERNFELD, RICHARD.

1918. Neue Schlangen und Eidechsen aus Zentralaustralien. Mitt. Senck. Ges., vol. 1, pp. 76-82.

1925. Beiträge zur Herpetologie Inner-Australiens. Abh. Senck. nat. Ges., vol. 38, pp. 221-251.

STUART, LAURENCE C.

1940. Notes on the "Lampropholis" group of Middle American *Lygosoma* (Scincidae) with descriptions of two new forms. Occ. Pap. Mus. Zool., Univ. Michigan, vol. 421, pp. 1-16, 1 fig.

TAYLOR, EDWARD H.

1922. The lizards of the Philippine Islands. Bur. Sci. Manila Publ. 17, 269 pp., 53 figs., 23 pls.

VAN DENBURGH, JOHN.

1912. Concerning certain species of reptiles and amphibians from China, Japan, the Loo Choo Islands and Formosa. Proc. California Acad. Sci., vol. 4, No. 3, pp. 187-258.

WAITE, EDGAR R.

1929. The reptiles and amphibians of South Australia. 270 pp., 192 figs. Adelaide.

ZIETZ, F. R.

1920. Catalogue of Australian lizards. Rec. South Austral. Mus., vol. 1, pp. 181-228.

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 117, NUMBER 18
(END OF VOLUME)

Charles D. and Mary Vaux Walcott Research Fund

THE LOWER EOCENE KNIGHT FORMATION OF WESTERN WYOMING AND ITS MAMMALIAN FAUNAS

(WITH 11 PLATES)

BY
C. LEWIS GAZIN
Curator, Divison of Vertebrate Paleontology
United States National Museum

(PUBLICATION 4097)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
DECEMBER 9, 1952

THE LOWER EOCENE KNIGHT FORMATION OF WESTERN WYOMING AND ITS MAMMALIAN FAUNAS

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 117, NUMBER 18
(End of Volume)

Charles D. and Mary Vaux Walcott Research Fund

THE LOWER EOCENE KNIGHT FORMATION OF WESTERN WYOMING AND ITS MAMMALIAN FAUNAS

(With 11 Plates)

BY
C. LEWIS GAZIN
Curator, Divison of Vertebrate Paleontology
United States National Museum

(Publication 4097)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
DECEMBER 9, 1952

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

CONTENTS

ILLUSTRATIONS

PLATES

(All plates following p. 82.)

FIGURES

Charles D. and Mary Vaux Walcott Reseach Fund

THE LOWER EOCENE KNIGHT FORMATION OF WESTERN WYOMING AND ITS MAMMALIAN FAUNAS

By C. LEWIS GAZIN

Curator, Division of Vertebrate Paleontology
United States National Museum

(With 11 Plates)

INTRODUCTION

The variegated beds of the Wasatch group in southwestern Wyoming have been of much interest to both geologists and paleontologists since their description by Hayden in 1869. To vertebrate paleontologists significance lies largely in their having yielded the first known lower Eocene mammals from North America. Unfortunately, however, the term "Wasatch" was too broadly defined for precise geologic usage and included strata of more than one geologic age. In consequence of this, Veatch in 1907 redefined the term as a group and divided it in ascending order into the Almy, Fowkes, and Knight formations. The last-named formation, including the fossiliferous lower Eocene horizons, is the primary concern of this report.

Investigation by the Smithsonian Institution of the mammalian faunas of the Knight formation was largely an outgrowth of the discovery by U. S. Geological Survey parties of Paleocene vertebrate remains in underlying Almy deposits (Gazin, 1942). Collections by J. B. Reeside, Jr., W. W. Rubey, and B. N. Moore in 1936 and by Rubey and John Rogers in 1939 led us in 1941 to a careful examination of the Almy beds as exposed on La Barge Creek in Lincoln County, Wyo., and to a somewhat desultory search of the nearby Knight exposures along Green River in Sublette County. Examination of the two sets of beds was renewed in 1948, and an intensive search of the Knight exposures was made along the east side of Green River from the vicinity of the "Three Bridges" southeast of Big Piney to 10 or 11 miles south on Fogarty Draw. In 1949 search was extended to both sides of the Green River, on the west side as far south as La Barge, and to about 12 miles north of Big Piney. In 1951 re-examination was made of all the more profitable localities and investigation was carried upward into the New Fork member, a tongue of Wasatchian strata interfingering with the lowermost Green River beds in the same area.

Collections made from the upper Green River basin, together with materials from the Knight beds in the vicinity of Fossil and those of the earlier collections from the Knight on Bear River, result in our now recognizing at least four horizons for fossil mammals in pre-Bridgerian Tertiary of southwestern Wyoming. These include the Clarkforkian Paleocene stage represented by mammalian remains from the Almy on La Barge Creek, equivalent to part of the original Wasatch; a Lysite or about middle-Wasatchian stage represented by collections from the type locality for the Knight, and probably the Knight at Fossil; and apparently two horizons of general Lost Cabin equivalence supported by the collections from the upper Knight beds and New Fork beds along the Green River in Sublette County. The lower Wasatchian or Gray Bull has not been certainly recognized, except in the adjacent Hoback basin (see Dorr, 1952).

ACKNOWLEDGMENTS

In addition to the above-named members of the U. S. Geological Survey, I wish to acknowledge helpful information given me by Dr. G. E. Lewis, who made a small collection from Knight beds near the Green River in 1947 while working with Dr. Rubey on the Big Piney Quadrangle. George Shea, of Billings, Mont., very graciously aided in locating for me materials which he and G. E. Lewis observed in 1947. Acknowledgment is also made of the courtesies extended in connection with my work in 1951 by the geologists of the General Petroleum Co., the Mountain Fuel and Supply Co., and the Shell Oil Co. doing exploratory work in the same area. My field assistants in 1941 included G. F. Sternberg and F. L. Pearce. In 1948 I was aided by my wife, Elisabeth, and son, Chester Gazin; both accompanied F. L. Pearce and myself in 1949.

In the faunal study I am indebted to Dr. Glenn L. Jepsen for permitting me to examine and describe Knight materials in the Princeton University collections and make comparisons with type and other specimens there. Drs. G. G. Simpson, E. H. Colbert, and Bobb Schaeffer extended to me facilities of the American Museum of Natural History and permitted me to study Knight materials from the type locality and various type specimens of lower Eocene mammals in the American Museum collections.

The drawings depicting new forms in figures 2-6 were prepared by William D. Crockett. The photographs of specimens in plates 1, 2 (fig. 1), 5-8, 10, and 11 were made through the kindness of Dr. G. Arthur Cooper. Photographs in text figure 1, plate 2 (figs. 2-5), and plates 3, 4, and 9 were made by the photographic laboratory of the U. S. National Museum.

HISTORY OF INVESTIGATION

Special historic interest, as has been noted, is involved in consideration of the Knight formation and its faunas. Fossil mammalian remains from exposures of this formation along Bear River, near Evanston, Wyo., are apparently the first to be described from the lower Eocene of North America. From here Hayden, or Cleburne according to Marsh (1893, p. 321), in 1871 secured the remains that Cope (1872a) described as *"Bathmodon" radians* and *"Bathmodon" semicinctus,* and part of the material later described as *"Bathmodon" latipes.* In 1872 Cope, assisted by Garman, and while working for the Hayden Survey, collected the type of *Hyracotherium vasacciense* as well as materials that became the types of various turtles (1872b). It is of interest that in 1872 Cope's travels took him to the mouth of La Barge Creek in the general area of upper Knight beds that produced the materials forming the basis of this investigation. It is unlikely, however, that he made any collection there. The same year he obtained from the vicinity of Black Buttes, east of the Rock Springs uplift, teeth from two badly decomposed *Coryphodon* skulls that he named (1873b) *"Metalophodon" armatus.* Apparently again in 1873 Cope went over the exposures along Bear River, southeast of Evanston, and collected the type materials of *Hyracotherium index* and *Phenacodus primaevus* (1873a), and additional material of *Coryphodon radians* and *Coryphodon latipes.*

Cope's investigation in the Knight ended with his transfer of interest to the lower Eocene of New Mexico and our next record of activity in these beds is Marsh's description of *Coryphodon hamatus* in 1877. This was collected in about 1874, from exposures on Bear River, about "35 miles west of Bridger," by R. Veltman of Evanston, Wyo., formerly a storekeeper at Fort Bridger. Veltman first wrote[1] Marsh about having discovered large bones on Bear River in June of 1871. Marsh apparently did not follow up this information until Veltman wrote again in November of 1874, at which time he reported

---

[1] Information kindly furnished me by Dr. J. T. Gregory from the file of Marsh's correspondence.

finding a skull and other bones of a very large animal, offering them for sale. These were evidently of the *Coryphodon hamatus* skeleton that Marsh eventually obtained. About the middle of the same decade Marsh acquired material of *Hyracotherium,* from the vicinity of Black Buttes, that in 1876 he named *Eohippus pernix.* William Cleburne, of the Union Pacific Railroad, in 1875 collected the skull and jaws that Thorpe (1934) described as *Meniscotherium robustum.* The latter was found in a cut on the old grade of the railroad about 2 miles west of Aspen (old location).

I have no further information on early paleontological exploration in these beds until 1906, when Granger and Miller collected about a dozen specimens of small mammals approximately 200 feet up on the bluffs of Bear River south of Knight station and in the vicinity of the railroad bridge. These are specifically mentioned by Granger in 1914 (p. 203) and regarded as Lysite in age.

More recent active interest in the Knight was recorded by Bonillas when, in 1936, with his description of the dentition of *Lambdotherium* from deposits near La Barge, Wyo., he mentioned the field exploration of the California Institute of Technology in these beds and cited briefly the fauna obtained. Their collecting was done largely in the vicinity of La Barge and included search on both sides of the Green River. Field work by parties from Princeton University in the Knight formation resulted in the discovery in 1939 and 1940 of fragmentary mammalian remains in Knight beds 40 to 100 feet below Green River strata about 3 miles northwest of Fossil, Wyo. Also, a jaw of *Ambloctonus* as well as an isolated tooth of *Oxyaena* were found by them southeast of La Barge in 1941. These, together with the above-noted finds of the U. S. Geological Survey and the more extensive exploration and collecting by the Smithsonian Institution, complete the history of paleontological work in the Knight of the Fossil and upper Green River basins, as far as it is known to me.

OCCURRENCE AND PRESERVATION OF MATERIAL

For practical purposes the Knight collections may be regarded as coming from three general localities or areas of exposure in the westernmost part of the State: one in the northwestern part of the upper Green River or Bridger basin and two in the adjacent, small but elongate structural basin to the west which includes the type section. In addition to these are a few isolated occurrences either at remote localities tentatively regarded as Knight or in exposures separated from the general localities by significant faulting.

Fig. 1.—Map of southwestern Wyoming and portions of adjacent States showing Eocene sedimentary basins, with fossil localities in Knight formation numbered as follows: 1, Knight station, type Knight; 2, Fossil; 3, La Barge–Big Piney; 4, New Fork; 5, Rock Springs; 6, Vermilion Creek; 7, Black Buttes; 8, Dad-Baggs; 9, Great Divide basin; 10, Red Desert. Map reproduced from Osborn, U. S. Geol. Surv. Monogr. 55, figs. 9, 49, 1929.

Historically, the more important of the localities would be the exposures along Bear River, in general between Evanston and Knight station. Granger's collection came mostly from the bluffs south of Knight station, and the only detailed statement made by Cope (1872b, p. 473) regarding his collection refers to "upper red and white strata on the bluffs eleven miles S. E. of Evanston, or near the bend of Bear River." Except for the *Coryphodon hamatus* skeleton collected for Marsh, the materials so far recovered from this area have been very fragmentary. Those collected by Granger and Miller occurred in a yellowish or buff sandstone, somewhat conglomeratic, hence conditions of deposition were not the most favorable for preservation of the smaller mammals. The bone portion of the jaws of the smaller mammals is very poorly preserved and only the teeth are in reasonably good condition.

The exposures near Fossil, Wyo., from which Princeton obtained a collection, are about 45 miles due north of Knight station but in the same basin of deposition. The Princeton collection was made in variegated beds from 40 to 100 feet beneath the Green River formation about 3 miles north of Fossil. However, a jaw of *Phenacodus* was obtained by Dr. Dunkle for the Smithsonian Institution in gray exposures beneath the red beds just 3 miles to the east of Fossil. The materials from near Fossil are also fragmentary but the bone has more the appearance of that which occurs in the vicinity of La Barge and Big Piney.

The most prolific collecting ground in beds considered to be a part of the Knight formation are to be found in the vicinity of the Green River in Sublette County—from La Barge, approximately 40 miles northeast of Fossil, to a point about 12 miles north of Big Piney, Wyo. Fossil materials of this area are found in many places on both sides of the Green River; however, certain small patches or coves of exposures have proven much more productive than others. Materials here were encountered at various levels from as near as about 40 feet below Green River strata, to possibly 100 feet lower. A collection was also obtained from the New Fork tongue of Wasatchian beds in the lower part of the Green River section along Alkali Creek and New Fork, tributaries of the Green River to the east and southeast of Big Piney.

The Smithsonian collections, which are almost exclusively from the La Barge–Big Piney area, number a little under 600 and include materials in various states of preservation and completeness. Excellent skulls were found of some forms, showing varying amounts of distortion, but less in general than exhibited by materials from lower Eocene deposits in the Big Horn, Wind River, and San Juan basins. Not all specimens are free of an iron-oxide coating, but the prevalence of this condition is far less than in the Big Horn basin Willwood materials. No one horizon or lithology can be regarded as exclusively fossiliferous, except locally and for short distances, although certain dark reddish to purplish zones to the east of the Green River have been relatively productive, and a soft blue-gray shale at certain places on the west side between La Barge and Big Piney. A rather profitable concentration of materials was encountered about 12 miles north of Big Piney in reddish-buff layers and gray sandy shale.

Isolated occurrences include the Aspen locality for the type of *Meniscotherium robustum* (in the Green River basin of deposition and hence not to be confused with the type Knight), and the occurrence of *Coryphodon* and *Hyracotherium* near the upper reaches of Dry Piney Creek, referred to in 1942. In the eastern part of the Bridger basin, around the Rock Springs uplift, isolated occurrences presumably in the same formation include a *Meniscotherium robustum* skull collected by Roland W. Brown just southwest of Rock Springs; a small collection of fragmentary remains that I made from near the southern extremity of the uplift on a tributary of Vermilion Creek; and the Black Buttes occurrence to the east of the uplift. Still more remote, but nevertheless in the same depositional basin, may be mentioned the occurrences on the eastern margin of the Washakie basin beneath the Tipton tongue of Green River between Dad and Baggs, referred to in Wood el al. (1941, p. 18), and from northeast of Creston made by a U. S. Geological Survey party in 1907.

THE KNIGHT FAUNAS

The following tabulation pertains to the principal occurrences of fossil mammals in the Knight formation as it is exposed in the upper Green River basin (the La Barge and New Fork faunas) and in the adjacent small structural basin west of the Oyster Ridge which includes the type Knight and the occurrence at Fossil, Wyo. The figures used refer to the number of specimens encountered, giving an indication of extent of materials upon which identifications are based, and a suggestion of the relative abundance of various forms in the faunas.

	Knight station	*Fossil*	*La Barge-Big Piney*	*New Fork*
MARSUPIALIA:				
Peratherium edwardi, new species			2	
Peratherium chesteri, new species			1	
INSECTIVORA:				
Diacodon pineyensis, new species			3	
Diacodon, cf. *alticuspis* Cope		1		
Cynodontomys knightensis, new species			13	
Cynodontomys, species	1			
TILLODONTIA:				
Esthonyx, cf. *acutidens* Cope			3	
Esthonyx, species	1			1
PRIMATES:				
Pelycodus? species	1			
Notharctus limosus, new species			24	
Notharctus venticolus Osborn			6	
Absarokius noctivagus Matthew			3	
Paratetonius? sublettensis, new species			1	
TAENIODONTA:				
undetermined stylinodont			4	
EDENTATA:				
Pentapassalus pearcei, new genus and species			2	
RODENTIA:				
Paramys, cf. *buccatus* * (Cope)	1		2	
Paramys, cf. *copei* * Loomis			8	
Sciuravus, possibly *S. depressus* Loomis			1	
Tillomys senior, new species			1	
CARNIVORA:				
Thryptacodon, near *T. antiquus* Matthew			2	
Pachyaena? species				2
Oxyaena, species			1	
Ambloctonus, cf. *major* Denison			1	1
Prolimnocyon elisabethae, new species			3	
Sinopa vulpecula Matthew			5	
Sinopa, cf. *strenua* (Cope)			1	
Didymictis altidens Cope	?		14	
Viverravus lutosus, new species			8	
Uintacyon asodes, new species			1	
Miacis, cf. *latidens* Matthew			3	
Vulpavus asius, new species			6	
CONDYLARTHRA:				
Hyopsodus wortmani Osborn			29	1
Hyopsodus mentalis (Cope)			76	
Hyopsodus browni Loomis	4			
Phenacodus primaevus Cope	1	1 **		
Meniscotherium robustum Thorpe			93	
Meniscotherium, cf. *chamense* Cope				3

* *Paramys,* cf. *buccatus* in Knight is *Paramys excavatus* Loomis; and *Paramys,* cf. *copei* Loomis includes *P. copei, P. major,* and a new species, as determined by A. E. Wood.

** Recorded from a horizon stratigraphically lower than other forms cited in this fauna.

	Knight station	*Fossil*	*La Barge-Big Piney*	*New Fork*
PANTODONTA:				
Coryphodon radians (Cope)	X †		cf. 15	
Coryphodon semicinctus (Cope)	1			
Coryphodon latipes (Cope)	1			
Coryphodon hamatus Marsh	1			
Coryphodon, species		1		
DINOCERATA:				
Cf. *Bathyopsis fissidens* Cope				2
PERISSODACTYLA:				
Hyracotherium index (Cope)	2	1	35	
Hyracotherium vasacciense (Cope)	4		67	
Hyracotherium, cf. *venticolum* Cope		1	4	3
Hyracotherium, possibly *H. cristatum* Wortman	1			
Lambdotherium popoagicum Cope			93	11
Heptodon, cf. *ventorum* (Cope)	1		30	
Heptodon, species		1		4
Hyrachyus, species				1
ARTIODACTYLA:				
Bunophorus, cf. *macropternus* (Cope)			7	
Diacodexis, near *D. secans* (Cope)			1	
Diacodexis, species	2 ‡			
Hexacodus pelodes, new genus and species.			11	
Hexacodus uintensis, new species		1		

† Number of specimens not known and should include material of at least a part of those species listed below which are probably synonyms.

‡ Specimens not seen.

CORRELATION AND AGE OF FAUNAS

Within the formation that may properly be called Knight are clearly three horizons that can be distinguished on the basis of fossil mammalian remains, including the New Fork tongue of Wasatchian material interfingering in the lower part of the Green River series. The lower of these is nearest to Lysite in age and the upper are two distinct zones of Lost Cabin age separated locally by the Fontenelle tongue of Green River. In the absence of evidence of any lower Wasatchian or Gray Bull horizon, except in the Hoback basin (see Dorr, 1952), the Knight may well be regarded as about equivalent to the Wind River series.

Knight station.—Critical examination of the materials derived from the type Knight beds along Bear River lead me to support Granger's (1914, p. 203) conclusion that the horizon there represented is about equivalent to Lysite. The *Cynodontomys* material, as incompletely known, does not appear to be more indicative of a Lysite species than of the later form now known to characterize the La Barge fauna; however, *Hyopsodus browni* is highly suggestive of Lysite and the *Heptodon* material would not appear to be older. The relative frequency with which *Coryphodon* remains have been encountered would appear to have no significance, and although not recorded in the type Lysite they are found in Lost Cabin beds of both Wind River and Green River basins, as well as in the Gray Bull, so that their middle Wasatchian or Lysite representation may well be here. Among the 14 to 16 forms recognized in the fauna, characteristic or peculiarly Gray Bull types are missing, particularly such a dominant form as *Homogalax*. In a like manner, the absence of any representation of Lost Cabin forms as *Meniscotherium* and *Lambdotherium* is equally suggestive. In support of this it should be noted that, with regard to the Lost Cabin equivalent of the Knight in the upper Green River basin, almost a third of the specimens encountered are of one or the other latter forms. In a cursory examination of the upper Knight the percentage of these forms would, because of their size, appear to be even much higher.

Fossil.—The rather limited fauna represented by the small collection from near Fossil, Wyo., is less clearly diagnostic with respect to the horizon represented than is the Bear River Knight. Comparison with horizons of the Wind River and Big Horn basins leaves much to be desired; nevertheless, its closest affinity is with the type Knight. *Heptodon,* taken into consideration with other similarities to the fauna from the Knight on Bear River, tend to restrict comparison to only the middle and perhaps upper Wasatchian levels. On the other hand the species of *Diacodon* and *Hexacodus* represented are distinctly not those found in the Lost Cabin equivalent of the Knight in the Green River basin, and *Hexacodus* is not among the rarer forms represented in the latter beds. *Phenacodus primaevus,* though found at a somewhat lower level than other materials from the Fossil area, is significantly absent from the La Barge fauna. It must be noted, however, the situation with respect to *Phenacodus* is reversed in the Wind River basin. Individually, the elements of the Fossil fauna are inconclusive, but collectively there is a strong presumption toward the Lysite level as that level is indicated by the Knight fauna obtained from the Bear River section.

La Barge.—There would appear to be no doubt of the general equivalance of the La Barge fauna to the Lost Cabin of the Wind

River basin. There is a specific difference between them in many of the genera mutually represented, but this may be largely environmental, or possibly of some small time significance if within a rapidly evolving group. Such a time difference, however, would not be of the magnitude of that between Lysite and Lost Cabin. The Lost Cabin equivalance is indicated by the presence of such genera as *Notharctus, Meniscotherium,* and *Lambdotherium* which first appear, or reach the indicated development, in the Lost Cabin horizon of the Wyoming lower Eocene; by such species as *Esthonyx,* cf. *acutidens; Notharctus venticolus; Absarokius noctivagus; Ambloctonus,* cf. *major; Sinopa vulpecula; Miacis,* cf. *latidens; Hyopsodus mentalis; Hyopsodus wortmani; Hyracotherium,* cf. *venticolum;* and *Lambdotherium popoagicum* which are close or identical to such species more or less characteristic of Lost Cabin in the Wind River or Big Horn basins; and by the developmental stage reached in such species as *Cynodontomys knightensis, Notharctus limosus,* and *Prolimnocyon elisabethae* which are otherwise distinct from related Lost Cabin species.

Suggestive of perhaps a slightly earlier stage than type Lost Cabin, although as noted above these differences may be no more than environmental in nature, are the following: The smaller size, though equivalent dental development, of *Cynodontomys knightensis* in comparison with *Cynodontomys scottianus* in a sequence of species increasing in size; the smaller size and relatively smaller premolars in *Notharctus limosus* than in *N. nunienus;* the weaker hypocone in upper molars of *Notharctus venticolus* of the La Barge fauna; the smaller size (of questionable significance) of *Diacodon pineyensis; Esthonyx,* cf. *acutidens; Absarokius noctivagus; Prolimnocyon elisabethae; Sinopa vulpecula; Didymictis altidens; Viverravus lutosus;* and *Vulpavus asius* in comparison with the same or equivalent Lost Cabin species; and the presence of *Paratetonius?, Thryptacodon,* and *Hyracotherium index.* The above would appear to be of perhaps trifling importance in consideration of relative ages, but on the other hand there is even less to suggest a later stage than type Lost Cabin, although such might be interpreted from the presence of *Sciuravus, Tillomys,* and *Hexacodus.* The evidence for a slightly older age afforded by *Meniscotherium* is perhaps the most interesting, inasmuch as the large *M. robustum* so far not found outside of the Green River basin occurs stratigraphically below *Meniscotherium,* cf. *chamense* of the New Fork tongue. Only the smaller species, regarded as *M. chamense,* is recorded from the Lost Cabin beds of the Wind River basin.

The following tabulation is a comparison of genera now known in the La Barge and Lost Cabin faunas:

	La Barge	*Lost Cabin*		*La Barge*	*Lost Cabin*
Peratherium	X		*Protopsalis*		X
Diacodon	X	X	*Ambloctonus*	X	X
Parictops		X	*Prolimnocyon*	X	X
Didelphodus		X	*Sinopa*	X	X
Palaeosinopa		X	*Didymictis*	X	X
Cynodontomys	X	X	*Viverravus*	X	X
Esthonyx	X	X	*Uintacyon*	X	
Notharctus	X	X	*Miacis*	X	X
Loveina		X	*Vulpavus*	X	X
Shoshonius		X	*Phenacodus*		X
Tetonius		X	*Ectocion*		X
Paratetonius?	X		*Meniscotherium*	X	X
Absarokius	X	X	*Hyopsodus*	X	X
Stylinodon	cf.	X	*Coryphodon*	X	X
palaeanodont		X	*Bathyopsis*		X
Tubulodon		X	*Hyracotherium*	X	X
Pentapassalus	X		*Lambdotherium*	X	X
Paramys	X	X	*Eotitanops*		X
Sciuravus	X		*Heptodon*	X	X
Tillomys	X		*Hyrachyus*		X
Mysops		X	*Bunophorus*	X	X
Thryptacodon	X		*Diacodexis*	X	X
Oxyaena	X	X	*Hexacodus*	X	

New Fork.—The New Fork tongue, separated by Green River beds called the Fontenelle tongue by Donovan (1950) from the Knight along the Green River, has yielded a faunal representation which compares equally well with that of the Lost Cabin, but includes forms not found in the La Barge fauna. The Lost Cabin age is here indicated by *Ambloctonus,* cf. *major; Hyopsodus wortmani; Meniscotherium,* cf. *chamense;* cf. *Bathyopsis fissidens; Hyracotherium,* cf. *venticolum;* and *Lambdotherium popoagicum.* The significant differences to be noted from the La Barge fauna are in (1) the species of *Meniscotherium* represented, (2) the presence of *Bathyopsis?* instead of *Coryphodon,* and (3) the appearance of *Hyrachyus.* I suspect that, were the New Fork better known, *Eotitanops* would be represented, also *Trogosus,* which is known from the Cathedral Bluff tongue in the northwestern part of the Red Desert.

The most significant feature of the discovery of the New Fork fauna is the clear demonstration that the lower beds of the Green River are actually Lost Cabin Wasatchian in age and that the Lost

Cabin fauna can be largely broken up into two stages. Tentatively the lower stage may be regarded as characterized by *Meniscotherium robustum* and *Coryphodon* and the upper stage by *Meniscotherium chamense, Hyrachyus,* species, and possibly *Bathyopsis.* Osborn early regarded the Lost Cabin as comprising two stages, but believed them to be distinguished by *Lambdotherium* and *Eotitanops,* respectively; however, *Lambdotherium* is here found in both levels. Much more of the New Fork fauna needs to be known for a more complete understanding of Lost Cabin zones. This may come when the Cathedral Bluff fauna currently under study by William Morris is placed on record.

ISOLATED OCCURRENCES TO THE EAST OF THE BRIDGER BASIN

Not included in the foregoing tabulation and correlations, and for the most part omitted from consideration in the systematic treatment of the faunas, are the scattered occurrences in the eastern part of the Bridger basin, around the Rock Springs uplift, in the eastern part of the Washakie and Great Divide basins, and in the Red Desert. It is not certainly known but entirely probable that the formation represented by these occurrences is also Knight. An examination of the geologic map of Wyoming leads to the conclusion that the Eocene basin of deposition is the same for these deposits as for those in the vicinity of La Barge and Big Piney, and that the formation is continuous beneath the Green River and Bridger formations, and around the Rock Springs uplift to these widely separated areas.

The more significant of these localities are discussed below:

Rock Springs.—West side of Rock Springs uplift, near fork of Bitter Creek and Little Bitter Creek, about 4 miles southwest of the city of Rock Springs, collected by R. W. Brown in secs. 7, 8, 17, and 18, T. 18 N., R. 105 W.: *Meniscotherium robustum* and *Coryphodon,* species. The rather fortuitous discovery of these forms in the relatively thin zone of Wasatchian beds between Rock Springs and Green River is highly indicative of the upper Knight or La Barge equivalent of Lost Cabin being represented here between Paleocene and Green River strata.

Vermilion Creek.—South of Rock Springs uplift on a tributary to Vermilion Creek (in type Vermilion Creek of King and type Hiawatha of Nightingale) near line between T. 11 N. and T. 12 N., in R. 101 W., northernmost part of Moffat County, Colo., collected by writer: Insectivore, possibly *Diacodon; Paramys bicuspis;* and *Hexacodus,* cf. *pelodes.* The insectivore found here is not significant.

Paramys bicuspis, according to A. E. Wood, who identified the specimen, is suggestive of Lysite; however, *Hexacodus,* cf. *pelodes* would suggest an equivalence with the La Barge fauna.

Black Buttes.—East side of Rock Springs uplift, near Black Buttes, collected in part by Cope and in part by a collector for Marsh: *Coryphodon armatus* and *Hyracotherium pernix.* These give little information other than a Wasatchian age.

Dad-Baggs.—East side of Washakie basin, exposures along highway beneath Tipton tongue, between Dad and Baggs, Wyo., collected by the writer: *Coryphodon,* large species, and *Hyracotherium,* cf. *vasacciense.* A small lot of material from near Baggs was collected by Reeside and Eby in 1924, but this material is not now in the collections. Another collection from near Dad was designated by Wood et al. (1941, p. 18) as "Dad local fauna" and noted by McGrew (1951, p. 54) as having been collected by J. LeRoy Kay for the Carnegie Museum. Of the materials collected by Kay only *Hyracotherium* was mentioned. Of the materials which I have observed none are particularly diagnostic; however, I am inclined to regard the horse as of Knight age rather than lower Wasatchian. It should be noted that Wood et al. (1941, chart) regard the fauna as late Wasatchian. This was based on evidence that I have not examined.

Great Divide basin.—About 18 miles west of Rawlins, Wyo., and about 12 miles northeast of Creston, SE¼SE¼ sec. 32, T. 22 N., R. 90 W., Sweetwater County, collected by E. E. Smith and A. C. Veatch in 1907 while with the U. S. Geological Survey on the North Rawlins Coal field: *Esthonyx,* cf. *acutidens;* cf. *Notharctus venticolus; Coryphodon,* species; and cf. *Heptodon,* species. The materials from this locality in the Great Divide basin are very fragmentary, but cf. *Heptodon* suggests Knight, and *Esthonyx,* cf. *acutidens,* and cf. *Notharctus venticolus* would appear to place the horizon represented in the upper Knight or Lost Cabin equivalent. This occurrence is very near the eastern limit in Wyoming of beds which may be called Knight, still within the Eocene basin of deposition which includes the Bridger basin proper.

Cathedral Bluff tongue.—Northwest part of Red Desert, NW. part of T. 26 N., R. 98 W., collected by R. L. Nace (1939, pp. 17, 26-27) from 75 feet below top of Cathedral Bluff tongue, and identified by Simpson: *Trogosus* or *Tillotherium.* As Simpson has indicated, the evidence is rather strong for a Bridger age. However, I am inclined to regard the Cathedral Bluff and New Fork as equivalent, inasmuch as so marked a retreat of Lake Gosiute as indicated by these tongues would effect the entire periphery, unless complicated by tectonic activity involving tilting or folding. In any case there is presumptive evidence favoring contemporaneity of the occurrences of an extensive tongue of variegated beds encountered interfingering with the lower part of the Green River series in various parts of this basin. This leads to the conclusion that the Cathedral Bluff was deposited during Lost Cabin time and that *Trogosus* may well have appeared before the Bridgerian stage, much as *Hyrachyus,* and have lived as a contemporary of *Esthonyx.*

GEOLOGIC RELATIONS

Sequence of formations.—The sequence of early Tertiary materials in the southwestern part of Wyoming includes as its lowest unit the Evanston; above this the Wasatch group, consisting, as redefined by Veatch (1907, p. 88), of the Almy, Fowkes, and Knight, is followed by the Green River and Bridger formations. To the east of the Bridger basin, around the Rock Springs uplift and along the eastern margin of the Tertiary basin, as shown by R. W. Brown (1949), Paleocene beds generally designated as "Fort Union" are exposed, but whose exact age is not known, having so far produced no known fossil mammal remains. Washakie beds, overlying Green River in the Washakie basin, are equivalent to the upper part of the Bridger and include beds regarded as somewhat later than typical Bridger. To the south of the Rock Springs uplift, in the basin of Vermilion Creek, the Vermilion Creek beds of King, as defined by his map (1876, atlas map 2) are approximately equivalent to the Wasatch of Hayden. The Vermilion Creek includes Paleocene in the vicinity of the Rock Springs uplift, and the Tipton and Cathedral Bluff tongues as well as Knight. The Hiawatha of Nightingale (1930, p. 1023) in the same general area is in a general way equivalent to the Knight. In the northern part of the Bridger basin Donovan's (1950) Fontenelle tongue of Green River is likely equivalent to the Tipton tongue farther south, and as noted above, his New Fork tongue of variegated beds likewise may be Cathedral Bluff tongue, although the identity of these is yet to be proved. Still farther north in the Hoback basin, beds which Schultz (1914) mapped as Evanston and undifferentiated Eocene, and called Hoback formation by the University of Michigan field parties, have produced a Tiffanian and Wasatchian fauna (Dorr, 1952). The equivalence of these beds with others in the Bridger and Fossil basin to the west has not been established. The supposition is that the Paleocene portion may be equivalent to the Evanston, or possibly to a part of the Almy. The Wasatchian horizon may be lower Knight, or possibly Fowkes. It is noted, however, that neither Evanston nor Fowkes were recognized by Veatch or Schultz elsewhere along the western margin of the Bridger basin. Should the beds carrying the Wasatchian fauna in the Hoback basin prove to be a part of the Knight this would then be the only known place where beds which appear to be lower Wasatchian in age are included in the formation.

Relations between basins.—The geologic relations involved in the present study are largely those which exist between the sequence of continental early Tertiary deposits in the upper Green River or Bridger basins, and those in the small, north-south elongated basin which includes the type Knight. The latter, which will be referred to as the Fossil basin, lies in a general way to the west of Oyster Ridge and includes the high plateau area from the upper reaches of Ham's Fork in the north southward beyond the headwaters of Bear River. On the west it is bounded by the intermittent band of pre-Tertiary rocks extending in a general way from Tunp Range in the north to beyond Evanston southward.

Early Tertiary deposition in these two basins appears to have been entirely separate and independent. As we may see from Veatch's (1907) map and sections, the Almy, Knight, and Green River lap successively onto older rocks along both the eastern and western margins of the Fossil basin, and along the western margin of the Bridger or Green River basin, wherever the relation is not actually one of faulting. And although the pre-Tertiary is much folded and faulted in the exposed bands along the east and west margins of the Fossil basin, the Tertiary sediments are for the most part but gently warped or tilted. However, it is evident that the Laramide activity did not completely cease by lower Eocene time so that it would be unsafe to assume that there was entire synchroneity beween the deposits of the Fossil and Bridger basins. This lack of equivalence is more noticeable between the Fossil basin and that next toward the west, in the absence of the Fowkes and in a scant representation of Evanston in the Fossil sequence. It is probable, therefore, that the Knight to the east and that to the west of Oyster Ridge are not entirely equivalent and may have had somewhat earlier or later beginnings and endings, although I suspect a rather general equivalence.

The same may be said of the Green River series which in the two basins was deposited in entirely separate lakes. The ultimate reason for the existence of these two lakes may be the same, or their origins may be tied to the same structural or orogenic control, but again their upper or lower limits may not be entirely contemporaneous in the two basins.

The evidence presented by the fossil mammals in the Knight beds of the two basins is such as to suggest that the upper limit of the Knight may have been as much different as the interval between Lysite and Lost Cabin time. The Lost Cabin fauna in the upper Green River basin extends from a few tens of feet below the Green River to 100 or more feet, whereas in the Fossil basin so far only a Lysite fauna has been certainly recognized. In the vicinity of the town of Fossil, the fauna represented is thought to be equivalent to that of the Lysite as represented by the type Knight farther south, and was likewise found 40 to 100 feet below Green River beds. This reasoning also leads to supposition that the Green River beds in the Fossil basin may include somewhat older strata than in the Green River basin, and that this lake had its origin somewhat earlier in lower Eocene time.

Should a further and more intensive search of the Fossil basin demonstrate beyond doubt the absence of beds of Lost Cabin age immediately underlying the Green River, or interfingering with Green River to the southward, one might argue the advisability of selecting a distinct formation name for beds called Knight in the Green River basin. I would not, however, venture to make such a discrimination, as the lithology is similar and in all probability there is more or less overlap if not precise or complete equivalance in time. Continental deposits are often not clearly definable units, and, of course, notoriously unreliable both as to time and lithology when traced laterally for any considerable distance, even within the same basin of deposition.

SYSTEMATIC DESCRIPTION OF THE MAMMALIA

MARSUPIALIA

DIDELPHIDAE

PERATHERIUM EDWARDI,[2] new species

Plate 1, figures 3, 4

Type.—Left ramus of mandible with last two molars, U.S.N.M. No. 19200.

Horizon and locality.—Upper Knight beds, La Barge fauna, SW$\frac{1}{4}$ sec. 33, T. 32 N., R. 111 W., 12 miles north of Big Piney, Sublette County, Wyo.

---

[2] Named for G. E. Lewis, who first called my attention to the particular locality which has since yielded all the *Peratherium* material from these beds.

Description.—Size significantly smaller than *Peratherium comstocki* Cope (1884, pl. 25a, fig. 15) from the "Wind River" beds, nearer that of *Peratherium marsupium* Troxell (1923b) from the Bridger beds. Cusps of last two molars sharp and well defined, particularly the entoconid and hypoconulid which in the last molar are much better defined than in *P. marsupium,* as represented by National Museum materials. Length M_2-M_3, 5.5 mm. Transverse diameter of penultimate molar, 1.8 mm.

A left maxillary portion, U.S.N.M. No. 19206, of a small marsupial found at the same locality is referred to *Peratherium edwardi.* The specimen retains the last two molars, which occlude well with those of the type. The teeth are rather well worn and show little of diagnostic value. The external margin of the penultimate tooth shows three small, worn, but about equally well-defined stylar cusps between the distinct parastyle and metastyle at the angles at the tooth. There appears, however, but two stylar cusps between the more conspicuous parastyle and metastyle on the last molar. In *Peratherium innominatum* Simpson (1928) material in the National Museum collections from the Bridger, a relatively greater spread between the metastyle and the preceding stylar cusp is noted in the penultimate and antepenultimate molars. Length of last two upper molars combined, 4.3 mm. Transverse diameter of penultimate upper molar, 3.1 mm.

PERATHERIUM CHESTERI,[3] new species

Plate 1, figure 1

Type.—Right ramus of mandible with penultimate molar, U.S.N.M. No. 19199.

Horizon and locality.—Upper Knight beds, La Barge fauna, SW¼ sec. 33, T. 32 N., R. 111 W., 12 miles north of Big Piney, Sublette County, Wyo.

Description.—Smaller than hitherto known species of *Peratherium* from the Eocene. A little smaller than the Bridger species *Peratherium innominatum* Simpson (1928). Penultimate molar length about 1.4 mm. and width about 0.8 mm. The alveoli of the last three molars measure about 4 mm. Trigonid relatively high and talonid small with entoconid and hypoconulid much less prominent than in the larger *P. edwardi.* The tooth has points of resemblance to an insectivore but the character and position of the hypoconulid and anterior cingulum seem certainly marsupial.

---

[3] Named for Chester Gazin, who collected the type specimens of both *P. edwardi* and *P. chesteri.*

INSECTIVORA

LEPTICTIDAE

DIACODON PINEYENSIS,[4] new species

Plate 1, figure 2

Type.—Left ramus of mandible with M_1 to M_3 and part of P_4, U.S.N.M. No. 19204.

Horizon and locality.—Upper Knight beds, La Barge fauna, SW¼ sec. 33, T. 32 N., R. 111 W., 12 miles north of Big Piney, Sublette County, Wyo.

Description.— Size near *Diacodon alticuspis* Cope (1875, pp. 11-12) but with lower molar teeth slightly shorter and distinctly broader. P_4 much larger. Length of molar tooth series 8.3 mm., shorter than in *Parictops multicuspis* Granger (1910, pp. 250-251) or *Diacodon bicuspis* (Cope) (1880a, p. 746; see also Matthew, 1918, p. 575). Also, lower jaw much shallower than in either. *Diacodon pineyensis* is appreciably larger than *Diacodon tauri-cinerei* Jepsen (1930, pp. 124-126) from the lower Gray Bull beds.

Discussion.—A sufficient portion of the heel of P_3 is preserved in U.S.N.M. No. 19203 to show that the Knight species is *Diacodon* rather than *Parictops.* Moreover, absence of a fourth diminutive cusp on the heel of the molars is further evidence supporting reference to *Diacodon.*

In critically examining the type of *Diacodon alticuspis,* I find that the preserved portion of P_4 is quite unlike this tooth in *Diacodon bicuspis, D. tauri-cinerei,* or *D. pineyensis.* The decidedly short P_4 with its narrow, much reduced talonid in *D. alticuspis* might justify resurrecting the generic name *Palaeictops* for *D. bicuspis,* etc. Matthew's reasons for first erecting[5] and then dropping the name *Palaeictops* are not given. However, the differences here noted are as great as, if not greater than, those between *Parictops multicuspis* and *Diacodon bicuspis.* I (1949, p. 221) earlier regarded *Parictops* as probably valid, but the significance of its characters may be no greater than those which seem indicated for *Palaeictops.* It should be noted, moreover, that in the character of P_3 *Diacodon tauri-cinerei* makes a distinct approach toward *Parictops multicuspis.* It is anticipated that new collections currently being made by Dr. Simpson from the San Jose formation in New Mexico will reveal additional material of *Diacodon alticuspis* so that this form will be more clearly defined and the genus better understood.

---

[4] Named for the town of Big Piney, Wyo.

[5] Granger (1910, p. 250) has incorrectly attributed this genus to Cope.

DIACODON, cf. ALTICUSPIS Cope

There is in Princeton's collection, from about 100 feet below Green River beds, 3 miles northwest of Fossil, Wyo., a lower jaw portion, P.U. No. 16171, representing a species of *Diacodon* very close to *D. alticuspis* Cope. The species is clearly not *Diacodon pineyensis.* Compared to the latter the cheek teeth are narrower, particularly the talonids, and the paraconid is placed lower with respect to the much elevated protoconid and metaconid. The narrowness of the talonid is most emphasized in P_4 in which the entoconid is much subdued and the basin restricted. The teeth, except for P_4, are slightly larger than in *D. tauri-cinerei* and the trigonids of the molars are higher, except for the paraconid, and broader. Comparison with *D. alticuspis* suggests a close relationship, but one which is inconclusive owing to the fragmentary nature of the type.

MIXODECTIDAE

CYNODONTOMYS KNIGHTENSIS,[6] new species

Plate 2, figure 1

Type.—Left ramus of mandible with P_4-M_3, U.S.N.M. No. 19314.

Horizon and locality.—Upper Knight beds, La Barge fauna, SW$\frac{1}{4}$ sec. 33, T. 32 N., R. 111 W., 12 miles north of Big Piney, Sublette County, Wyo.

Description.—Size close to that of *Cynodontomys latidens* Cope (1882a, pp. 151-152), much smaller than more nearly contemporaneous *Cynodontomys scottianus* (Cope) (1881a, pp. 188-189). P_4 with paraconid distinct and low, and with metaconid almost as large as protoconid and well separated from it though not so much so as in *Microsyops.* Talonid of P_4 broad and fully molariform, though slightly narrower than in molars, with protoconid, entoconid, and hypoconulid sharp and well defined. P_4 distinctly more progressive than illustrated (Matthew, 1915c, figs. 45, 46) for *Cynodontomys latidens* Cope.

Discussion.—In all there are 13 specimens of this form, all but one are lower jaws and, except for two, are from the same exposures as the type. One lower jaw and an isolated upper molar were obtained southeast of Big Piney, on the east side of the Green River. This interesting species, except for its smaller size, is as fully developed as *Cynodontomys scottianus* in the progressiveness of its fourth lower premolar, as might be expected in this horizon. *Cynodontomys scot-*

---

[6] Named for the Knight formation.

tianus, however, is not represented in this fauna, nor is the relatively gigantic *Cynodontomys lundeliusi* White (1952, pp. 191-192) from the Lost Cabin beds in the Boysen Reservoir area. Though *C. knightensis* and *C. scottianus* are from distinctly separate basins of deposition during upper Wasatchian time, the geographic distance between the occurrences is not particularly great. It seems probable that the difference in species is to be attributed to ecologic differences.

MEASUREMENTS OF TYPE LOWER JAW OF
Cynodontomys knightensis, NEW SPECIES, U.S.N.M. NO. 19314

	mm.
P_2 (alveolus) to M_3, incl.	20.5
P_4 to M_3, incl.	15.2
M_1 to M_3, incl.	11.5
Depth of jaw beneath M_2 (internally)	7.3

CYNODONTOMYS, species

A portion of a left lower jaw including M_2 and M_3, in the collections of the American Museum, from the bluffs of the Bear River south of Knight station is identified as *Cynodontomys.* M_2 in this specimen has the same proportions as in *C. knightensis,* but M_3 is relatively a little shorter as in *Cynodontomys angustidens.* This specimen, A.M. No. 12836, has been labeled *Cynodontomys latidens?* but in the absence of P_4 the progressiveness of the dentition cannot be clearly determined. An unusual feature of the specimen is the remarkable flangelike development of the outward- and forward-turned anterolateral margin of the ascending ramus. An approach to this condition is seen in the prominence of this crest in certain of the specimens of *C. knightensis.*

TILLODONTIA

ESTHONYCHIDAE

ESTHONYX, cf. ACUTIDENS Cope

Two incomplete, isolated upper molars from variegated beds between Big Piney and La Barge, Wyo., and a single lower molar from 12 miles North of Big Piney, may well represent the species *Esthonyx acutidens* Cope (1881a, pp. 185-186). The lower tooth is complete and little smaller than in the type of *E. acutidens.* There is much variation in size of *Esthonyx* material from the Lost Cabin beds but the average is distinctly larger than the older *E. bisulcatus;* moreover, the posterior wall of the trigonid of the lower molars tends to be somewhat less oblique and the talonid basin a trifle larger in *E. acutidens.*

In passing it should be noted that the type of the species, *Esthonyx spatularius,* erroneously recorded as coming from the Wind River beds, is beyond reasonable doubt from the Gray Bull beds of the Big Horn basin. The history and explanation of this error are covered in manuscript now in preparation on the tillodonts, and briefly stated in this paper under the section on *Didymictis.*

ESTHONYX, species

The outer portion of an upper molar in the Knight station material in the American Museum is recognized as belonging to *Esthonyx.* The specimen is too incomplete to warrant specific comparison. An upper molar tooth in the collection from the New Fork tongue also represents *Esthonyx.* The latter tooth is short anteroposteriorly and relatively wide transversely. I am uncertain as to whether or not it is *Esthonyx acutidens.*

PRIMATES

ADAPIDAE

PELYCODUS? species

A fragment of an upper molar, including only the outer half, in the American Museum collection from the Knight beds near Knight station in southwestern Wyoming, is only slightly larger than M^2 in *Notharctus limosus* described below, but has the mesostyle no better developed than in *Pelycodus,* hence is referred tentatively to the latter genus.

NOTHARCTUS LIMOSUS,[7] new species

Plate 1, figures 6-8

Type.—Portions of both rami of the mandible with left P_3-P_4, and right M_1-M_3, inclusive, U.S.N.M. No. 19294.

Horizon and locality.—Upper Knight beds, La Barge fauna, SW$\frac{1}{4}$ sec. 33, T. 32 N., R. 111 W., 12 miles north of Big Piney, Sublette County, Wyo.

Description.—Size of molars a little less than in *Notharctus nunienus* (Cope) (1881a, p. 187) with premolars much smaller and depth of jaw less, particularly beneath premolars. P_4 with metastylid well developed and broadly spaced from protoconid. Upper cheek teeth anteroposteriorly short, most noticeably in the medial and lingual portions. Molars relatively broad transversely with distinct mesostyle and hypocone on M^1 and M^2.

---

[7] From Latin *limosus,* muddy, with reference to Muddy Creek where the type was found.

Discussion.—The smaller of the notharctine primates in the La Barge fauna is represented by about 24 specimens, the majority of which were obtained from exposures about 12 miles north of Big Piney.

The lower molars average noticeably smaller in size than those in American Museum specimens of *Notharctus nunienus* from the Lost Cabin beds, and in only two specimens are teeth found as large as in the smallest of *N. nunienus*. The length of M_2, for example, has a range of from 4.9 to 5.3 mm. in *N. nunienus,* and in *N. limosus* the range would be 4.3 to 4.7 mm. except that one specimen measures 5.0. The average in the two species is 5.2 and 4.6 mm., respectively. The molar teeth are otherwise not particularly distinctive. The paraconid is strong on M_1, but highly variable on M_2 and M_3. M_3 has two cusps in the position of the hypoconulid much as in *N. nunienus,* although this has been noted also in *Pelycodus.*

The difference in size of premolars is more noticeable, and P_3 in particular is relatively much smaller than in *N. nunienus.* P_4, though of distinctly smaller size than in *N. nunienus,* has a metaconid that appears to be relatively more widely separated from the protoconid and exhibits a conspicuous, sharply conical hypoconid. This cusp is also distinct on P_3. In *N. nunienus* material the accessory cusp or hypoconid on P_3 and P_4 is generally weak or blunt. In one specimen of *N. nunienus,* A.M. No. 4736, a rather distinct entoconid was observed on P_4. A rudiment of such a cusp was noted in U.S.N.M. No. 19290 of *N. limosus.*

A well-preserved maxillary portion, U.S.N.M. No. 19293, of *Notharctus limosus,* includes P^3 to M^3. The upper teeth are noticeably less in their fore and aft dimension, taken through their middle and lingual portions, in comparison with A.M. No. 4735 of *N. nunienus,* giving them a less rounded appearance, but they are nearly as wide transversely. As in *N. nunienus,* the mesostyle is distinct on M^1 and M^2, and somewhat weaker on M^3. The hypocone is as well developed on M^1 and M^2, but obscured through wear on M^3.

MEASUREMENTS OF TYPE LOWER JAW OF

Notharctus limosus, NEW SPECIES, U.S.N.M. NO. 19294

		mm.
M_1 to M_3, incl.		14.4
P_3,[8]	anteroposterior diameter: greatest transverse diameter	2.9: 2.0
P_4,	" " " " "	4.0: 2.7
M_1,	" " " " "	4.5: 3.3
M_2,	" " " " "	4.4: 3.8
M_3,	" " " " "	5.8: 3.5

---

[8] The type specimen is at the upper limit for the sample in size of premolars.

NOTHARCTUS VENTICOLUS Osborn

The larger of the notharctine primates in the La Barge fauna is represented by a maxilla, U.S.N.M. No. 19288, with P^4-M^3 and five lower jaws. The size of the teeth in these specimens corresponds well with those of *Notharctus venticolus* Osborn (1902, p. 195). In the upper molars the mesostyle is prominently displayed, but the hypocone, though apparently well developed on M^1, appears subdued on M^2. It is evident, however, that somewhat greater wear would produce a large distinct lake in this position. The lingual portions of all the upper teeth preserved in this specimen appear relatively broader anteroposteriorly than in the *N. limosus* maxilla. P^4 and M^3 are distinctly less nearly triangular.

ANAPTOMORPHIDAE

ABSAROKIUS NOCTIVAGUS Matthew

This species is apparently represented in the La Barge fauna materials by three lower jaw portions, one of which, U.S.N.M. No. 19198, exhibits Dp_4 with what appears to be P_2, as well as P_4 and M_3, just erupting. The first two molars are in position but unworn. If one may judge by the positions of the two erupting premolars, P_3 is yet buried beneath the long slender roots of Dp_3. Two small alveoli anterior to the erupting P_2? are presumably for incisors, or incisor and canine. There is no evidence for an enlarged front tooth as in *Tetonius*. Matthew (1915c, pp. 463-465) was apparently correct in his interpretation of the condition in *Absarokius abbotti* (Loomis) and fully justified in distinguishing *Absarokius*.

The teeth in No. 19198 compare very closely to those in the type of *A. noctivagus* but are very slightly narrower. In U.S.N.M. No. 19196, M_3 is a little smaller than in this type, about the length but not so slender as in a specimen of *Absarokius abbotti* in the American Museum collections. A third specimen in the collections from north of Big Piney, U.S.N.M. No. 19197, includes an M_3 a little larger than in the type of *A. noctivagus,* and the paraconid of this is much less lingual in position. It is possible that the latter specimen does not represent this genus.

PARATETONIUS? SUBLETTENSIS,[9] new species

Plate 1, figure 5

Type.—Left ramus of mandible with P_4-M_2, inclusive, preserved, U.S.N.M. No. 19205.

---

[9] Named for Sublette County, Wyo.

Horizon and locality.—Upper Knight beds, La Barge fauna, SW¼ sec. 33, T. 32 N., R. 111 W., 12 miles north of Big Piney, Sublette County, Wyo.

Description.—Size smaller than *Paratetonius? tenuiculus* (Jepsen) (1930, p. 126), much smaller than *Paratetonius musculus* (Matthew) (1915c, p. 463) or *Paratetonius steini* Seton (1940) from the older Gray Bull or Lysite horizons. P_4 not enlarged but exhibiting a well-defined paraconid, a weak but distinct metaconid, a short but broadly basined talonid with but a very weak posterointernal cusp or entoconid and a somewhat better-defined posteroexternal cusp or hypoconid. Molar cusps more marginally placed than in *Tetonius,* as observed by Seton for *Paratetonius.* Paraconids lingual in position, and in M_2 clearly defined and close to the metaconid. As shown by alveoli, P_3 is two-rooted, not fused as in *P. musculus,* and P_2 apparently has but a single large root, relatively larger than in *P. musculus.* Anterior to the root of P_2 is a very small but deep alveolus, probably for P_1, but possibly for an anterior root of P_2, posteroexternal to the relatively large alveolus presumed to be that of the canine.

Discussion.—As anticipated by Matthew in his description of *Tetonius musculus, Paratetonius* Seton appears to be a clearly distinct group, less specialized than *Tetonius,* and including forms in all horizons of the Wasatchian stage. The latest of these, *Paratetonius? sublettensis,* if correctly referred, is the smallest and in some respects may be the least specialized.

In addition to the probable dental formula, the moderate-sized, relatively low-crowned P_4 implies less progressiveness than, for example, *Tetonius homunculus.* On the other hand, the form of P_4 is distinctly more progressive in its approach to that of the molars, a quite different trend.

It is interesting to note that Loomis's form, *Anaptomorphus minimus* (1906, p. 278), from Gray Bull beds of the Big Horn basin, appears scarcely to have been mentioned since its description, except for having been placed questionably in synonymy with *Nyctitherium celatum* by Matthew (1918, p. 604). The illustration is not too clear, so that generic reference cannot be verified but in size it may be smaller than *Paratetonius musculus.* The dimensions given by Loomis are slightly less than for lower teeth in a Gray Bull specimen in the National Museum collections, No. 19154, tentatively referred to *Paratetonius? tenuiculus,* but close to those of *Paratetonius? sublettensis.*

MEASUREMENTS OF TYPE LOWER JAW OF
Paratetonius? sublettensis, NEW SPECIES, U.S.N.M. NO. 19205

	mm.
Length, P_4 to M_2, incl.	4.5
Length, M_1 to M_2, incl.	3.2
Width, M_2	1.3
Depth of jaw beneath M_2, internally	3.1

TAENIODONTA

STYLINODONTIDAE

Undetermined stylinodont

Plate 2, figures 2-5; plates 3, 4

The articulated portions of two hind limbs and a fore limb, with feet, and including some vertebrae from exposures of upper Knight 12 miles north of Big Piney, are recognized as representing a taeniodont. No skull or jaw material, except for some finely broken and scattered fragments of teeth, was encountered. So far the only determinable taeniodont material from this horizon is the Lost Cabin *Stylinodon? cylindrifer* (Cope) (1881a, pp. 184-185) from the Wind River basin. It is reasonable to suppose that the La Barge fauna includes that species but this cannot be established on the material at hand.

The finding of this material is indeed fortunate as it gives us information previously not known on the structure of the hind foot in this family, and gives a certain amount of skeletal data none of which had been recorded before from the Lost Cabin stage.

Fore limb.—The limb bones are rather badly crushed and those of the fore limb very incomplete. The greater part of an ulna is preserved and though incomplete distally, so that its length cannot be determined, it resembles rather noticeably the ulna figured by Marsh (1897, fig. 5) for *Stylinodon mirus.*

Fore foot—The fore foot is represented by the scaphoid, pisiform, unciform, the fourth and fifth metacarpals and the distal part of the third, together with the phalanges of the second, third, and fourth digits. The scaphoid is a relatively small triangular wedge with the large proximal or superior facet for the radius, converging forward and medially with the somewhat smaller distal facet. These are separated laterally by a still smaller lenticular facet for the lunar. The angle between the lunar and distal facets is about 90°, but between the lunar and radial facets is much more acute, more as anticipated by Matthew (1937, fig. 66) for *Psittacotherium* than as interpreted in rough outline by Patterson (1949, p. 253, fig. 4c) for *Stylinodon mirus.* It cannot be determined from the material at hand whether the moderate-sized "pear"-shaped distal facet articulated with the trapezium, or, as Patterson suggests, the trapezoid. This bone, however, so very closely resembles the scaphoid in *Trogosus,* the distal facet of which articulates with the trapezium, that a reasonable doubt persists.

The pisiform is deeply expanded dorsoventrally in its posterior portion and anteriorly exhibits a large, concave articular surface for the ulna and ventrally a much smaller facet for the cuneiform. The anterior extremity is expanded medially although this projection is not complete.

The unciform is a relatively large carpal bone which articulates distally with the entire proximal end of the fourth metacarpal. It is incomplete laterally so that the surface for the fifth metacarpal is missing. There is no certain evidence that the unciform was in contact with the third metacarpal. The proximodistally long facet on the medial side of the unciform seems to have articulated only with the magnum as Patterson has shown. Proximally, incomplete facets for the lunar and cuneiform, at a sharp angle to one another, are preserved.

The fourth metacarpal, about 35 mm. in length, is a sturdy bone with broadly expanded extremities, but with a constricted shaft. The articulating surface for the fifth metacarpal is rather broadly arcuate and undercut distally in a somewhat conventional way, but facing distinctly more palmar than in many unguiculate types. The proximal surface is nearly triangular and the broad and deep distal articular surface for the proximal phalanx is evenly rounded dorsoventrally but with almost no evidence of a keel. The 2d and 3d metacarpals are seen to have saddle-shaped distal extremities.

The fifth metacarpal is about two-thirds the length of the fourth and has a moderately robust proximal portion with broad articulation with the fourth metacarpal. A facet is seen for articulation with the unciform but this surface is incomplete in the specimen at hand. The distal portion of the fifth metacarpal is very much reduced with but a very small articular surface for the first phalanx, about half the width of that in the fourth.

The phalanges of the second to fourth digits are broad and deep but much shortened proximodistally. Only the proximal portions of the clawed distal phalanges are present, but these are transversely narrow and extremely deep. The largest of the claws is approximately

18 mm. across the widest part of the base proximally, but is about 38.5 mm. deep.

Hind limb.—The stylinodont hind limb and foot, previously unknown but for the meager foot remains belonging to *Psittacotherium* and very fragmentary limb material of *Ectoganus,* are represented by both right and left sides in the Knight material. In the left limb all elements are included, but the tibial and tarsal portions are rather poorly preserved. The right side is in a much better state of preservation; however, the femur, cuboid, part of the external cuneiform, and the proximal portions of the second and fifth metatarsals are missing. Except for the proximal articulating surface on the second metatarsal and much of the cuboid, these can be interpreted from the left side.

The femur, approximately 220 mm. long as measured from about the crest of the greater trochanter, is crushed and distorted, so that detailed description is not feasible. The head is lacking but the greater trochanter is well developed. It is broadly expanded anteroposteriorly and its roughened external surface extends over 80 mm. distally. There does not appear to be a third trochanter but the lesser trochanter beneath the head, though broken off, was evidently well developed for possibly as much as 50 mm. along the shaft. The distal or condylar portion of the femur though transversely crushed would appear to be narrow and moderately deep anteroposteriorly.

The proximal portion of the tibia likewise appears somewhat crushed transversely. Nevertheless, the proximal extremity may be relatively deep anteroposteriorly and transversely narrow, particularly just below the articular portion. The external articular surface is relatively small and immediately beneath its posterior extremity and facing distally is a facet for the fibula. The inner surface of the proximal portion of the tibia is rather flattened and the internal condyle is much more produced anteroposteriorly than the outer. A prominent ridge extends downward on the posterior margin of the shaft from the external condyle, terminating distally in a prominent and unusual-appearing process[10] about 36 mm. below the articular surface. The anterior margin or cnemial crest slopes more or less evenly toward the distal portion of the shaft with no clearly defined

---

[10] This process may well have accommodated in part more than one important muscle. Its direction suggests the *soleus,* participating in the Achilles tendon. However, the groove posterior to the internal malleolus is well developed for the *tibialis posticus* or *flexor longus digitorum,* or both, which also may have originated in part on this process. The flexor muscles were obviously strong, to judge by the claws, and a well-developed *tibialis posticus* might account for a similarly unusual development of the posterointernal margin of the navicular as a point of insertion. The latter muscle would serve as an extensor of the tarsus and in supination of the foot.

lower limit on the material at hand, but the proximal tuberosity stands out ruggedly and well in front of the condylar surfaces. The distal portion of the tibia appears normal and undistorted. The internal malleolus is very well developed and extends downward to cover a large segment of the inner wall of the astragalus. Also, the inner condylar surface of the distal end of the tibia projects much farther posteriorly than the outer.

The fibula is a slender shafted bone with enlarged extremities. Also, the shaft is somewhat curved, longitudinally, with the concavity forward so that the distal extremity or external malleolus is well forward and actually ahead of the tibia. The external malleolus is transversely broad anteriorly and on its inner side exhibits a large and elongate surface facing inward, ventrally, and somewhat posteriorly for articulation with the forward, proximal portion of the external wall of the body of the astragalus.

Hind foot.—The hind foot for the most part has the general appearance of a primitive unguiculate type, but with a combination of distinctive characteristics evidently more or less peculiar to the Taeniodonta. The more notable peculiarities include a transversely, much recurved arrangement of the tarsus and digits. The cuneiforms and proximal extremities of the metatarsals present a triangular aspect so that articulation between them from side to side tends to bring the first and fifth digits relatively close together in a plantar direction. With this arrangement the animal's metatarsals were evidently maintained nearly upright in standing, with the weight to the ground carried largely by the distal extremities of the metatarsals through their large sesamoids, and only in part by the proximal phalanges. It is also interesting to note that the first and fifth digits, though a little shorter than the others, are relatively unreduced, as compared with those of the front feet, and although the various digits diverge noticeably from one another, the first appears to diverge from the second somewhat more sharply. The characteristics of the individual elements of the foot are discussed in more detail below.

The astragalus in proximal aspect rather resembles that in the larger cats, but with the trochlear surface distinctly raised, not continuing more or less smoothly into that of the neck of the astragalus. It is not far from the conception outlined by Matthew (1937, fig. 67) for *Psittacotherium,* although with less anteroposterior extent of the trochlea for the tibia. In plantar aspect, the astragalus is somewhat more distinctive. The large ectal or peroneal facet is less concave than in cats or bears. Posteriorly it converges rapidly with the trochlea rather than extending parallel to it, giving the external wall of the body of the astragalus a triangular rather than lunar outline. Anteriorly the ectal facet turns sharply upward for a short distance. The sustentacular facet is much smaller, slightly concave anteroposteriorly, and elongate, extending from near the navicular facet medially, posteriorly, and plantad with respect to the ectal facet. The head of the astragalus articulates broadly with the navicular and externally in a small part with the cuboid.

The calcaneum is apparently the most distinctive bone in the pes. Its most noticeable characteristic is the dorsoventral expansion of its tuberosity or tuber calcis, recalling on a small scale somewhat the appearance of the posterior margin of this element in certain of the edentates, such as *Hapalops*. Ventrally the expansion projects forward, presumably in part for attachment of the *flexor brevis digitorum* which would be inserted into the second phalanges. Anteriorly the calcaneum exhibits on its superior margin the large ectal facet for the astragalus. Anterior to this and meeting the upturned anterior margin of the ectal facet at a sharp angle is a transversely elongate and concave facet facing forward and medially for the cuboid. The outer surface of the calcaneum is developed anteriorly into a prominent forward projection or process which carries the forward portion of the cuboid facet on its inner surface. The sustentacular portion of the calcaneum is missing.

The navicular is distinguished by its elongation, extending inward well beyond its articulation with the head of the astragalus and the internal cuneiform. The knoblike ventrointernal prominence on the navicular may well represent a sesamoid commonly found in certain groups of mammals on the tibial side of the tarsus, which has here become co-ossified with the navicular. The proximal surface of the navicular is broadly concave with a ventrointernally elongate facet for the head of the astragalus. The external facet for the cuboid is about at right angles to the surfaces for the astragalus and external cuneiform, and moderately short dorsoventrally. Its direction is distinctly acute to that of the dorsal surface of the navicular. Distally, the three facets for the cuneiforms occupy somewhat less than two-thirds the long diameter of the navicular. These facets are of approximately equal width dorsally, but that for the internal cuneiform is the more convex dorsoventrally and turns sharply proximal internally.

Little can be determined of the characteristics of the very poorly preserved cuboid in the left foot; however, from the articular facets of the adjacent bones of the right foot it was clearly of good size. Proximally, it articulated broadly with the calcaneum and extended onto the externoplantar margin of the head of the astragalus. Internally it made contact with the nearly erect and coplanar surfaces of the external walls of the navicular and external cuneiform. Distally, it was evidently broad and covered much of the proximal extremity of the fourth metatarsal and apparently a somewhat larger surface on the fifth metatarsal.

The middle and external cuneiforms are of about equal size and present a nearly rectangular appearance in dorsal view. Their proximal and distal aspects are more nearly triangular, the external cuneiform more so than the middle cuneiform. On their distal surfaces each laps slightly over the next metatarsal external to that directly distal to it. The internal cuneiform is not well preserved but is distinctly larger than the other two. Proximally its articular surface for the navicular is markedly concave and externally it makes contact only with the proximal portion of the inner wall of the middle cuneiform. Distally its articular surface is broad, deep, and slightly convex for the first metatarsal.

The metatarsals are a little shorter, with shafts somewhat constricted, and extremities expanded in comparison with the partial hind foot of *Psittacotherium* figured by Matthew. The first metatarsal is the shortest, about five-sevenths the length of the third metatarsal, but is more robust and the proximal extremity is somewhat larger. The first metatarsal apparently does not articulate with the second. The latter is intermediate in length between first and third metatarsals and has a somewhat broader and flatter shaft than the third. The distal extremity is also a little wider but more compressed toward the first. The third and fourth metatarsals are about the same length, 41 mm., but the fourth metatarsal articulates in a slightly higher position in the foot than the third. The proximal extremities of both are distinctly triangular with the broadest base forward. The shaft and distal extremity of the fourth is slightly wider and shallower than the third. The fifth metatarsal is a little longer than the first, but much less robust, and highly distinctive in appearance. The proximal portion has a wide external flare and the dorsoventrally much-compressed shaft exhibits a much more broadly concave plantar surface than the other metatarsals. The proximal extremity articulates with the full depth dorsoventrally of the external surface of the fourth metatarsal and has a relatively large articular surface for the cuboid. Distally the articulation with the first phalanx is transversely wide but not deep. All the metatarsals show well-rounded distal articulations and sturdy sesamoids, and only the slightest suggestion of a median keel.

The intermediate phalanges of all the digits of the hind foot are much shortened, more so than in *Psittacotherium,* and the proximal of these in digits 2 to 5 are scarcely more than wedges with the thin edge down. Those adjacent to the clawed phalanges show evenly rounded, saddle-shaped articular surfaces distally. The claws are much more robust than in *Psittacotherium,* but not nearly so deep and relatively less compressed transversely than in the fore foot of the Knight individual. Those in the first and fifth digits are fully developed.

EDENTATA

EPOICOTHERIIDAE?

PENTAPASSALUS,[11] new genus

Generic characters.—Dental formula: $I\frac{?}{1}$, $C\frac{1}{1}$, $P\frac{2}{3}$, $M\frac{3}{3}$. Teeth much as in *Tubulodon,* but last premolar and M_2 possessing a single, conical root. M_1 alone of the lower series two-rooted. Cranial portion of skull relatively short and broad, more as in *Epoicotherium* than as in *Palaeanodon* or *Metacheiromys.* Bullae ossified, well inflated and posterior in position. Palate not extended posteriorly and pterygoids not continuous with bullae.

Type species.—*Pentapassalus pearcei,* new species.

PENTAPASSALUS PEARCEI,[12] new species

Text figures 2-4

Type.—Large part of skeleton, including skull and lower jaws, U.S.N.M. No. 20028.

Horizon and locality.—Upper Knight beds, La Barge fauna, east side of Green River, southeast of Big Piney, sec. 14, T. 29 N., R. 111 W., Sublette County, Wyo.

Specific characters.—Size near *Tubulodon taylori,* but with teeth a little smaller and jaw somewhat deeper. Skeletal portions correspond closely in size to those of *Metacheiromys tatusia.* Other specific characters not distinguished from those of the genus.

Material.—The type of *Pentapassalus pearcei* is a somewhat crushed but remarkably complete skull and lower jaws, together with both humeri, portions of both radii, an ulna, femora, parts of the tibiae,

---

[11] From Greek πέντε, five, and πάσσαλος, a peg; with reference to the five peglike postcanine teeth in the skull.

[12] Named for Franklin L. Pearce, who found the type specimen.

incomplete scapula and pelvis, a few vertebrae, ribs, and foot bones. In addition to the foregoing, there is in the collection a left lower jaw portion, U.S.N.M. No. 19214, with the last molar and the alveolus for the molar immediately preceding, which was found about 12 miles north of Big Piney, Wyo.

Description of skull.—Among living forms the skull of *Pentapassalus pearcei* may best be compared with that of the small Argentine armadillo, *Zaëdyus pichiy* Desmarest, rather than with the peculiar *Chlamyphorus truncatus* or *Burmeisteria retrusa.* In superior view (fig. 2) the cranial portion of the skull of *P. pearcei* is wider, and the rostrum much shorter and less attenuated anteriorly than *Z. pichiy.* The anterior extremity of the rostrum is damaged but its extent can be determined by the nasals and lower jaws. Posteriorly the rostrum

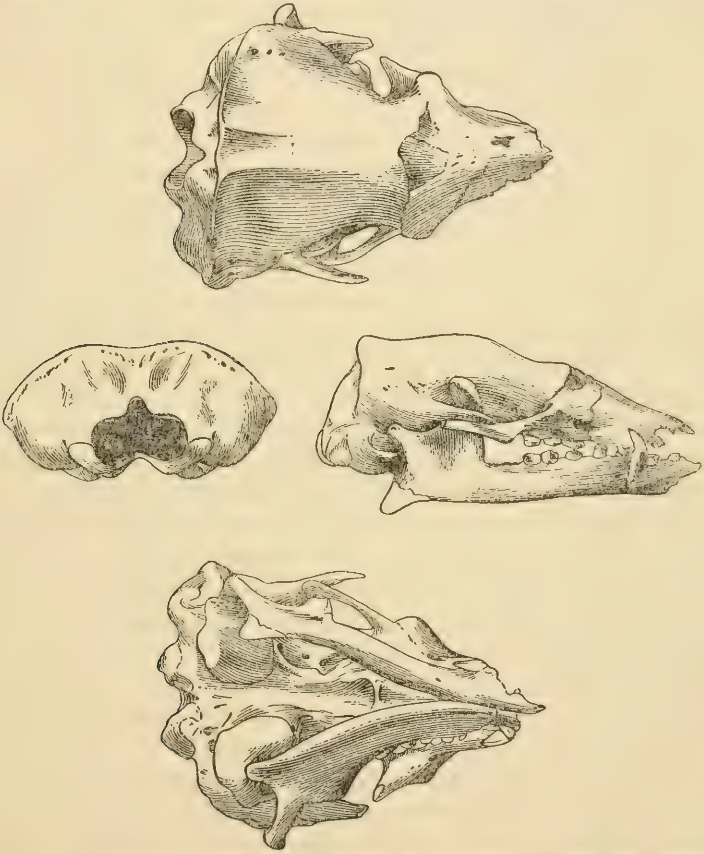


FIG. 2.—*Pentapassalus pearcei,* new genus and species: Skull and mandible (U.S.N.M. No. 20028), type specimen, dorsal, posterior, lateral, and ventral views, natural size. Upper Knight, lower Eocene, Wyoming.

widens abruptly across the frontals, but apparently not to the extent in *Z. pichiy*. The sutures of the fossil skull are for the most part well closed so that no great amount of information on the limitations of the individual bones can be ascertained. However, the indistinct suture between the premaxilla and maxilla appears to curve backward superior to the bulge of the canine. Also, the frontoparietal suture extends almost directly across the cranium at the orbital constriction. There is no sagittal crest, but the weak superior margins of the temporal fossae approach closely and extend nearly parallel fore and aft, somewhat as in *Zaëdyus*. The presence or absence of an interparietal cannot be determined.

In lateral view (fig. 2), the skull of *P. pearcei* exhibits moderate depth posteriorly, relatively a little less than *Zaëdyus pichiy*, but becomes noticeably shallow immediately anterior to the bullae. The midportion of the skull is somewhat crushed, but the basicranium makes a decidedly more acute angle with the palate than in the armadillo or *Orycteropus*. In the latter forms these surfaces are more nearly parallel. The much shorter rostrum in *P. pearcei* does not taper anteriorly so rapidly. The lachrymal portion of the skull is rugged and participates in a marked lateral widening of the skull at the anterior margin of the orbit, much as in *Zaëdyus*, and the lachrymal foramen is conspicuous on the crest of the zygoma immediately beneath a rugose prominence of the lachrymal bone. This foramen is more forward in *Orycteropus* and some material of *Dasypus*. The anterior opening of the infraorbital foramen is large, single, and immediately above M^1. The zygoma is slender with the squamosal portion overlapping the jugal much as in *Orycteropus*. The contact of these elements is quite unlike that in *Dasypus*, and the zygoma is much weaker than in *Zaëdyus*.

In posterior view (fig. 2) the skull is seen to be broad and shallow, actually resembling more closely the much larger *Orycteropus* than any of the armadillos. The resemblance is further emphasized by the way in which the somewhat more inflated mastoid portion is displayed in this view, and in the extension of the well-developed lambdoidal crests outward, above, and lateral to the mastoid prominence. The foramen magnum in *P. pearcei* is notched dorsally somewhat as in *Epoicotherium*.

The ventral aspect (fig. 2) of the *P. pearcei* skull is highly interesting and shows in its anterior part a short, broad palate in contrast to that in armadillos and aardvark. Although somewhat destroyed posteriorly, the palate, as in *Zaëdyus*, apparently did not extend much, if any, posterior to the tooth row. The palatal margin of the posterior narial opening was concave and there is a good indication that it was also curved downward, somewhat as in *Orycteropus*. The pterygoids are partially damaged but apparently turn outward ventrally rather than inward, possibly more so than in *Zaëdyus* or *Orycteropus*, but quite unlike *Dasypus*. The palatopterygoid crests were much longer than in *Zaëdyus*, more as in *Orycteropus* but relatively not so widely separated. These crests also were not continuous with the bullae as in *Burmeisteria* or *Zaëdyus*.

The foramina in the alisphenoid of *Pentapassalus* may not be distinctive, but the identity of all has not been clearly determined. The foramen ovale is in a normal position just above the posterior extent of a subdued lateral sweeping branch of the pterygoid crest. Immediately anterior to the foramen ovale and within the same general depression is a small foramen, noted also by Simpson (1927, p. 289) in *Epoicotherium*, which may be the posterior opening of an alisphenoid canal but is in all probability a venous canal, which extends transversely through the basisphenoid in both armadillos and *Orycteropus*. The presence or absence of an alisphenoid canal cannot be determined in *Pentapassalus* without damage to the skull. It is absent in armadillos and *Orycteropus*, although Gregory (1910, p. 335), following Weber (1904, p. 414), denoted its presence in the latter—a mistaken identification of the foramen ovale, which was corrected in a later edition of Weber's work. Just ahead of the small venous foramen noted above is a circular foramen, somewhat smaller than the foramen ovale which may be a foramen rotundum; however, the position of the alisphenoid-orbitosphenoid suture has not been determined with certainty so that this may well be the sphenoidal fissure. Immediately forward of the latter opening, the bone shows an elongate, natural-appearing margin directed anterodorsally, such as might be expected of the posterior and outer lip of a sphenoidal fissure, but from there forward the orbital cavity is damaged so that the orbital foramen cannot be seen.

The broad basicranium is characterized by the markedly inflated bullae, the medial walls of which are more nearly parallel than in *Zaëdyus*. The anteromedial margin of the bulla is deeply grooved from the medial wall forward to the foramen lacerum medium for the internal carotid. This groove is not covered medially, nor is the bulla perforated ventral and lateral to this position as in *Zaëdyus*. This perforation may well be the eustachian canal in the latter. In *Pentapassalus* the eustachian foramen may be nearly confluent with the foramen lacerum medium ventrally, or be represented by a small opening at the anterior margin of the bulla well separated laterally from the foramen lacerum medium. The external auditory meatus is large and opens immediately beneath the lower extremity of the lambdoidal crest. The glenoid surface for articulation with the lower jaw is well forward from the external auditory meatus and terminates posteriorly in a much-subdued postglenoid process, which carries on its posterior surface a normal postglenoid foramen. In *Dasypus* there is no postglenoid process and the articular surface terminates posteriorly at the opening for the ear. In *Zaëdyus* and *Orycteropus* the postglenoid process of the squamosal is a thin sheet of bone which also forms the anterosuperior margin of the external auditory meatus. The bulla in *Dasypus* and *Orycteropus* is not ossified, only an annular ring is present, whereas in *Zaëdyus* the bulla is ossified, but unlike *Pentapassalus* does not participate in the margin of the external auditory meatus as this is formed entirely by the mastoid and squamosal. Posterolateral to bulla the margin of the skull is formed by the well-inflated mastoids, unlike the armadillos but somewhat more as in *Orycteropus*. Posterior to the bulla the foramen lacerum posterius is evident, and the condylar or hypoglossal foramen is distinct and posterior to it. The stylomastoid foramen would be distinctly marginal in position, immediately posterior to the external auditory meatus. Its exact position and that of the hyoid articulation are somewhat indistinct in the fossil as a result of minor fracturing. The occipital condyles are not so widely separated as in armadillos and these do not so nearly encroach on the mastoids, or bullae.

Comparison of the skull of *Pentapassalus pearcei* with other fossil types shows a marked resemblance to various previously described palaeanodonts; however, important differences were noted which clearly distinguish the genus. The cranium of *P. pearcei* is almost as wide as in Gray Bull *Palaeanodon ignavus* Matthew (1918, figs. 39, 40) but shorter, and the total skull length is very much less. In keeping with the relatively shorter cranium the bullae are placed farther back than are the incompletely ossified bullae or annular rings in *P. ignavus*. The rostrum in *P. ignavus* is markedly elongate but not attenuated as in *Dasypus*. The dentition of *P. ignavus* is much farther forward than in *P. pearcei* and the number of teeth appears to have been less. In an occipital view the mastoid portion is rather similarly developed in the two fossil forms but in *P. ignavus* the lambdoidal crest does not appear to be carried on by the squamosal, above and lateral to the mastoid as in *Pentapassalus*.

The skull differences between *Pentapassalus* and *Metacheiromys* (see Simpson, 1931) are similar to those between *Pentapassalus* and *Palaeanodon*. However, the teeth in the Bridger genus are much further reduced and the bullae are more completely ossified than in *Palaeanodon*. The bullae in *Pentapassalus* resemble very much in form those in *Metacheiromys* but are much more posterior in position.

I find no certain evidence in *Pentapassalus* of an entotympanic, although a somewhat crushed zone around the posteromedial margin of the left bulla is inconclusive, and the right bulla has been thrust medially concealing this area. The glenoid surface for articulation of the lower jaw is transversely much wider and has a better-developed postglenoid process in *Metacheiromys.* The slope of the occiput is similar in the two forms and the lambdoidal crests appear to be similarly developed with respect to the mastoid exposure discussed above. However, the braincase is much more inflated in *Pentapassalus* and the skull is relatively shorter and broader posteriorly.

Comparisons with the Oligocene epoicotheriids show *Pentapassalus* to be more closely allied to the Epoicotheriidae than to the Metacheiromyidae, although known members of the latter family are more nearly contemporaneous. *P. pearcei* strongly resembles the skull form of the much smaller *Epoicotherium unicum* Douglass (1905, pl. 22, figs. 13-16; see also Simpson, 1927, pl. 24). Most noticeable differences, however, lie in the dorsoventral attenuation of the rostrum, the posterior elongation of the palate, the transversely much-constricted choanae, and the continuation of the pterygoid crest onto the bulla in *Epoicotherium.* The lambdoidal crest continues ventrally outside of the mastoid portion, somewhat as in *Pentapassalus,* but the occiput is much more inflated posteriorly in the Chadron form, strikingly as in *Chrysochloris,* as has been noted by others. The dental formula for the upper cheek-tooth series is the same in both fossil forms.

Xenocranium pileorivale Colbert (1942) from the still later Brule beds of Wyoming is distinguished by the remarkable expansion of the mastoid-squamosal region of the skull, much beyond that in either *Epoicotherium* or *Pentapassalus.* The bullae in this form occupy a posterior position but are transversely much elongated. *Xenocranium* has lost one more postcanine tooth, above and below, than has *Pentapassalus.*

Mandible.—The lower jaw of *Pentapassalus pearcei* is quite unlike that in recent armadillos and *Orycteropus.* It corresponds closest in size and form to that in *Metacheiromys marshi* Wortman (1903, pp. 347-352) or *Metacheiromys tatusia* Osborn (1904, p. 165; see also Simpson, 1931, p. 303). The jaw is of nearly uniform depth beneath the cheek teeth, deepening but slightly on the outside posteriorly. Anterior to the single incisor the jaw tapers abruptly, and a short distance posterior to the last molar the anterior margin of the ascending ramus rises rather sharply to about 90° from the line of the tooth row, beneath its posterior deflection near the crest of the coronoid process. The coronoid process is much like that in *Metacheiromys* and is separated by a broad U-shaped concavity from the condyle. The condyle is gently convex, anteroposteriorly, and wider than long. The angle is deflected markedly downward, below the inferior margin of the horizontal ramus, and is widely separated from the condyle, more so than in *Metacheiromys.* The masseteric fossa is a weak triangular depression on the outer surface, and the inferior dental foramen on the lingual side of the jaw has a markedly posterior position in comparison with recent armadillos. Externally, a mental foramen is exhibited beneath a point between the first and second postcanine teeth and somewhat lower between the second and third. The horizontal ramus reaches its thickest at the position of the canine, and again at about the posterior margin of the last molar. The width at the latter position is brought about by a shelflike ridge on the lingual side, which in *Pentapassalus* can scarcely be attributed to a pad as in monotremes, although this has been postulated for the more nearly toothless *Palaeanodon* and *Metacheiromys.*

Comparison of the lower jaw of *Pentapassalus pearcei* with that of *Tubulodon taylori* shows the latter to be less robust but with a little larger teeth and the anterior margin of the ascending ramus rises much more gently. The lower jaw of *Epoicotherium unicum* is not known, but that for *Xenocranium pileorivale* is relatively much more robust, though actually considerably smaller than *P. pearcei.*

Dentition.—The dentition of *Pentapassalus* can be more clearly recognized as the normal mammalian heterodont type than can members of the Metacheiromyidae or other Epoicotheriidae. The presence or absence of any upper incisors cannot be determined, but a single lower incisor, separated from the canine by a small diastema, is present. Strong upper and lower canines are preserved. These are deep-rooted and the crowns are triangular in section, and enamel-covered, except where worn through occlusion. The cheek-tooth series includes five postcanine teeth in the maxilla and six in the lower jaw. In upper series the first of these is close to the canine but separated by a short diastema from the second. These appear to be single-rooted premolars and are followed closely without diastema by three molars. The first and second molars appear from their outline at the alveolar margin to be three-rooted. The third upper molar is more nearly circular at the alveolus but exhibits vestigial roots at the base of the peg or stumplike crown.

There are three lower premolars, the first of which is very small, and apparently pointed. It follows the lower canine by a diastema which permits occlusion of the upper canine. The second and third of the lower premolars are isolated by short diastemata, the last being separated by a somewhat smaller space from the three uninterrupted molars. The roots of the last premolar and second molar were investigated and found to be single; whereas the first molar was found to have two roots, which can be detected even well above the alveolar margin. Presumably, M_3 and the anterior premolars are single-rooted.

The crowns of the cheek teeth are nearly flat with two planes of occlusion meeting at a widely obtuse angle in a low transverse ridge, generally near the middle of the tooth. The angle between these occlusal planes is nowhere nearly so acute as in living armadillos. In the premolar region these occlusal areas also slope more downward and outward than in the molar region. A band of enamel surrounds the crown or appears preserved on the lingual and labial margins, if wear has not progressed too far. Occlusion of each cheek tooth is, of course, with two in the opposite jaw, giving the crown a subdued gable appearance. This is unlike the type of occlusion described for *Xenocranium.*

The lower teeth in *Pentapassalus* are most like those in *Tubulodon taylori* Jepson (1932), but do not exhibit the cuspate development seen in the latter, probably a difference which may be attributed to wear. The most significant difference lies in the persistence of double roots in the last premolar and second molar as well as in the first molar of *Tubulodon.* A superficial similarity is seen in the microscopic tubular structure of the teeth of the two forms. This tooth condition in *Pentapassalus* may not be the same as that in *Tubulodon,* and is here apparently of no taxonomic importance, as it may be observed in bones and teeth of other, quite unrelated forms in this fauna.

Appendicular skeleton.—The limb and foot material of *Pentapassalus pearcei* is so completely like that in *Metacheiromys* that had not the skull and jaws been found the material would have been referred unhesitatingly to that genus. Of the various palaeanodonts, limb material has been described only of *Palaeanodon* and *Metacheiromys.* None so far has been recorded of the Oligocene forms. In almost every instance differences noted from the more nearly contemporaneous *Palaeanodon* have been in the direction of *Metacheiromys.* No special resemblance to *Orycteropus* limb material has been noted. In all elements the limb material of *Pentapassalus pearcei* is the same size or but a little larger than that in *Metacheiromys tatusia* Osborn, as described and figured by Simpson (1931).

Scapula.—The right scapula is preserved, but incompletely along the thin, prescapular border, and the acromion is missing. The exhibited portion of the spine is remarkably high and rugged with the crest turned posteriorly giving strength comparable to that of the postscapular border.

Fore limb.—Comparison of the humerus (fig. 3*a*) is made with that of *Metacheiromys dasypus* inasmuch as this bone in *M. tatusia* is not illustrated; nevertheless, correspondence in form is amazingly similar. Differences noted in the illustration of *P. pearcei* and that of *M. dasypus,* except for size, are due in part to orientation. The lesser tuberosity extends somewhat lower on outer side of the proximal end, and the width of the deltoid process distally appears slightly less, but is incomplete in *P. pearcei.* The supinator ridge and much of the distal extremity are almost identical in the two.

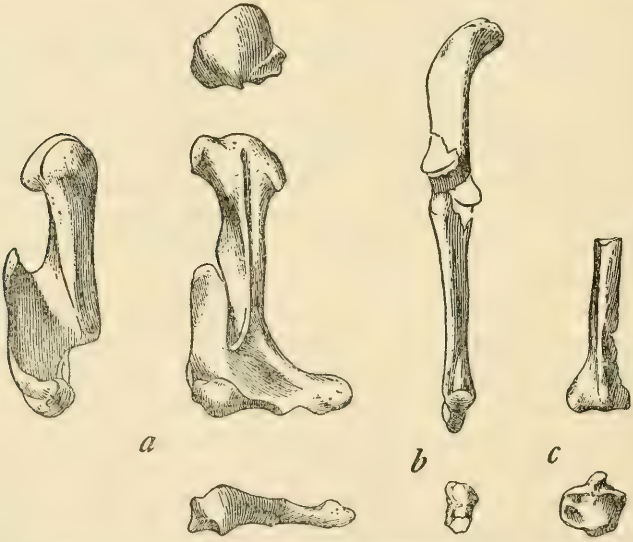


FIG. 3.—*Pentapassalus pearcei,* new genus and species: *a,* Right humerus, restored from left side, proximal, lateral, anterior, and distal views, natural size; *b,* right ulna, anterior and distal views, approximately nine-eighths natural size; *c,* distal portion of right radius, anterolateral and distal views, approximately five-fourths natural size. Type specimen (U.S.N.M. No. 20028). Upper Knight, lower Eocene, Wyoming.

Only the distal portions of the radii (fig. 3*c*) are preserved. These show an anterior crest which is well developed distally, but a short distance (about 7 mm.) from the distal end it is abruptly reduced, giving rise to a noticeable upward-directed process that is better developed in *Metacheiromys.* The distal articular surface shows no distinctive features in comparison with the *Metacheiromys* radius.

The shaft of the ulna (fig. 3*b*) may be somewhat less curved laterally in the anterior view than in *Metacheiromys dasypus* but the olecranon is almost identical in its relative proportions and the inward curvature of its extremity. The sigmoid notch is incomplete in *P. pearcei.*

Pelvis and sacrum.—Portions of right and left innominate bones, together with part of the sacrum are preserved. The right side is more nearly complete than the left, but both lack the pubic portion. The ilium is slender and outwardly curved, extending, as in *Metacheiromys,* well in advance of the sacrolumbar contact. Three elements are involved in the sacrum as indicated by the fused spines, probably about as in *Metacheiromys;* however, as shown in the referred specimen of *M. marshi,* there may have been a fourth centrum fused to this series. The anterior zygapophyses for articulation with the last lumbar are apparently much larger than in *M. tatusia.*

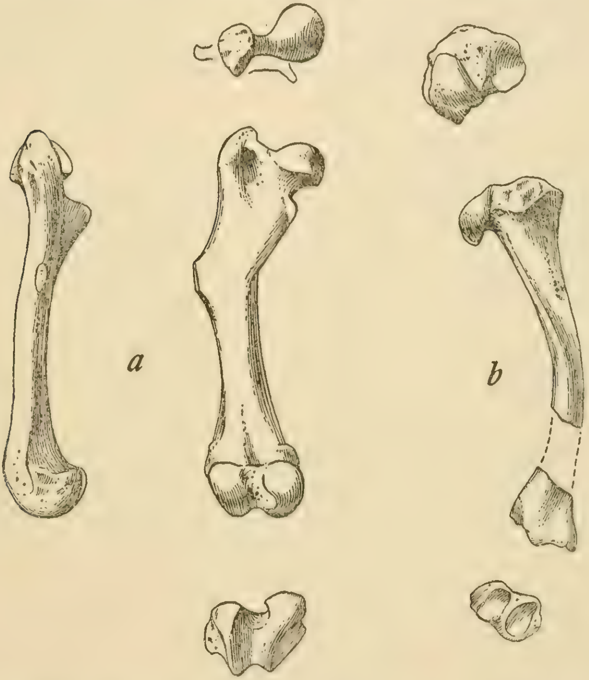


FIG. 4.—*Pentapassalus pearcei,* new genus and species: *a,* Left femur, proximal, lateral, posterior, and distal views, natural size; *b,* left tibia, proximal, posterior, and distal views, approximately five-fourths natural size. Type specimen (U.S.N.M. No. 20028), Upper Knight, lower Eocene, Wyoming.

Hind limb.—Both femora (fig. 4*a*) are included in the *P. pearcei* skeleton, and these so closely resemble the femur of *Metacheiromys* *tatusia* figured by Simpson that no significant differences can be detected. Comparison with *Palaeanodon* is fair, although Matthew's illustration of the femur in his figure 52 (1918), with his description of *P. ignavus,* does not particularly resemble that shown in figure 65B. In *Dasypus novemcinctus* the shaft is curved somewhat as in *P. pearcei* but the greater trochanter is far better developed and the relatively large third trochanter is more distally placed.

The details of the tibia (fig. 4*b*) are also decidedly like those of *M. tatusia.* It is noted, however, in *P. pearcei* that the external tuberosity of the proximal extremity extends a conspicuous process laterally and distally carrying the articular surface for the fibula. Also, the shaft may curve posteriorly somewhat more just beyond the lower limit of the cnemial crest.

Only the proximal extremity of the right fibula is included in the Knight material. This shows little of significance other than being transversely flattened and the articulation for the tibia is a surface almost at right angles to the longitudinal axis of the shaft.

Foot bones.—The foot material of *Pentapassalus pearcei* includes the lunar, magnum, trapezoid, second and third metacarpals, and various phalanges of the manus; but of the pes, only a part of the astragalus is preserved. The lunar would seem to be much like that described by Simpson for *Metacheiromys dasypus;* however, it differs from the illustration of this element in that the radial surface extends entirely to the distal surface at the dorsal margin, much as in *Dasypus novemcinctus.* The distal surface differs from that of the armadillo, as described by Simpson, in that the articulation for the magnum is sharply offset into two parts, the rectangular, more dorsal surface being distinctly more distal and separated from the concave, nearly circular, and more palmar surface by a sharp transverse ridge. A slender, dorsoventrally concave articular surface is seen for the unciform which widens somewhat palmad and distally. Dorsal to this, and more laterally facing, is a facet for the cuneiform.

The trapezoid, in proximal view, is a triangular bone with its acute apex directed palmad. The triangular surface for the scaphoid is dorsoventrally concave in its palmar portion and convex dorsally. A triangular surface is seen dorsally on the inner side for the trapezium, and a plane crescentic surface dorsally on the external side for the magnum. Distally, the trapezoid exhibits two dorsoventrally elongate depressions, with an intervening saddle, the outer of which is the longer, for articulation with the second metacarpal. The trapezoid apparently does not articulate with the third metacarpal, nor is this the case in *Dasypus novemcinctus.*

The proximal surface of the magnum shows, as indicated above, a rectangular shelf and raised, knoblike, more palmar portion for the lunar articulation. The dorsal surface of the magnum is irregular, much as in *Metacheiromys dasypus,* not so nearly rectangular as in *Dasypus novemcinctus.* On the dorsal part of the inner aspect a plane, pentagonal, somewhat proximal facing surface is seen for contact with the trapezoid, and the palmar portion of the inner aspect exhibits a rounded concave surface for a projection of the second metacarpal much as in *Metacheiromys.* The outer surface of the magnum exhibits an irregular concave surface for the unciform. The distal articular surface is a dorsoventrally, deeply concave saddle for the third metacarpal.

The second metacarpal is a very short and sturdy bone, about three-fourths as long as the third metacarpal. The proximal extremity is nearly rectangular, deeply grooved dorsoventrally in the more dorsal portion, and the inner-palmar angle is formed by a prominent rounded knob separated from the articular surface. The dorsal portion of the inner margin shows a small, inward-facing surface for articulation, presumably with the trapezium, and on the dorsal portion of outer margin the facet for the third metacarpal faces somewhat distally. The outer more palmar surface for the magnum is relatively smaller and is not oriented so distinctly proximal as in *Dasypus novemcinctus.* Distally, the surface for articulation with the first phalanx is much broader than the proximal extremity, and is dorsoventrally more constricted on its inner side than on the outer. Dorsally the surface is transversely cylindrical with prominent, symmetrically placed pockets, palmar to the convexity. The shaft of the second metacarpal is very broad dorsally, this aspect being much emphasized by the process for the extensor muscle, which is about midway on the outer margin.

The proximal extremity of the third metacarpal is much more convex, dorsoventrally, than the second. The dorsal portion is relatively broad and concave for articulation of the magnum. A short distance palmar to the dorsal portion the proximal extremity is noticeably constricted transversely, giving the proximal aspect a T-shaped appearance. The external knob of the dorsal expansion articulates with the second metacarpal, whereas the internal knob shows a narrow, limited surface for articulation with the unciform, very much less than in *D. novemcinctus,* but immediately distal to this more proximal surface is a relatively large, outward and palmad-facing concavity, faceted for articulation with the fourth metacarpal. The distal articular surface is for the most part transversely cylindrical with the palmar pockets more feebly developed than in the second metacarpal.

The shaft is sturdy and slightly arched dorsally. The process for the pars brevis of the extensor muscle is very prominent, proximal to the midpoint of the inner margin of the dorsal surface, but somewhat distal to the equivalent process on the second metacarpal. The latter condition is reverse to that seen in *Metacheiromys dasypus.*

The metacarpals and phalanges are not only smaller but relatively shorter than in *Palaeanodon ignavus.* They resemble materials from the Lost Cabin beds attributed by Matthew to *?Palaeanodon,* species, but are rather smaller. These Lost Cabin elements might, of course, represent *Pentapassalus* or *Tubulodon.*

The intermediate phalanges and claw cores are quite like those figured for *Metacheiromys,* except that there is a suggestion that the articulation on the claw may extend somewhat more dorsoventrally around the distal articular surface of the second phalanx than in the Bridger type and the claws may be more curved in a vertical plane.

The head of the astragalus, which is the only part of the hind foot preserved, shows a surface broadly curved transversely for the navicular, and a relatively large, slightly convex sustentacular facet close to that for the navicular. The details are much like those shown by Matthew for *Palaeanodon ignavus.* The body of the astragalus is missing.

Remarks.—Undoubtedly the most significant, and certainly the most interesting find of the several seasons' collecting in the Knight beds is this rare edentate mammal. During the earlier stages of this investigation a rather striking tubular structure noted in the teeth was thought to ally it peculiarly with *Tubulodon* from the Wind River beds, and to place it in some position of relationship to *Orycteropus.* Further observations, however, have shown that so far as the Knight materials are concerned that is not the case. The microscopic, irregular, anastomosing clusters of tubules, quite independent of the Haversian system, were also noted in otherwise dense and somewhat translucent bone and teeth of certain other forms in the fauna, cautioning against regarding the structure as significant in teeth of *Pentapassalus.* The structure noted in the above material was surely of post-mortem development.

Pentapassalus shows very little of importance in the skull structure that would tend to ally it to the Tubulidentata, no more than edentates in general might resemble them. In its general skull form and in retention of the teeth it is most closely allied to the Oligocene *Epoicotherium* of the various palaeanodonts, and is placed in Epoicotheriidae rather than with the longer-skulled, more nearly edentulous and more nearly contemporaneous metacheiromyids. Limb and foot structures are similar to those in *Metacheiromys* but it is very likely that *Epoicotherium* was similarly adapted.

MEASUREMENTS OF TYPE SKELETON OF

Pentapassalus pearcei, NEW GENUS AND NEW SPECIES, U.S.N.M. NO. 20028

	mm.
Skull:	
Length, anterior extremity of nasals to condyles	*a* 59.0
Width at postorbital constriction	*a* 18.0
Length of cranium from postorbital constriction to lambdoidal crest	23.5
Width of cranium across squamosal portions of lambdoidal crests	34.7
Depth of occiput from top of crest to bottom of condyles	19.2
Mandible:	
Length of mandible from anterior extremity to condyle	42.5
Depth of jaw beneath M_1 internally	5.2
Thickness of jaw at widest part immediately behind M_3	4.0
Dentition:	
C to M^3, incl.	15.7
I to M_3, “	21.3
C to M_3, “	18.5
M^1 to M^3, “	8.5
M_1 to M_3, “	6.9
Anteroposterior diameter of last upper premolar	2.0
Anteroposterior diameter of M^2	3.0
Transverse diameter of M^2	2.5
Anteroposterior diameter of last lower premolar	2.2
Transverse diameter of last lower premolar	1.6
Anteroposterior diameter of M_2	2.4
Transverse diameter of M_2	1.9
Fore limb:	
Length of humerus, head to articular surface for ulna	37.0
Transverse width of humerus across proximal tuberosities	12.1
Greatest transverse width of humerus across condyles of distal extremity	21.7
Depth of distal extremity of humerus across capitulum for ulna	5.5
Length of deltoid crest from greater tuberosity	28.0
Length of supinator ridge from surface for ulna	22.0
Width of distal extremity of radius	7.0
Depth of distal extremity of radius incl. longitudinal ridge	7.5
Greatest length of ulna	48.7
Length of olecranon from sigmoid notch	*a* 18.5
Greatest width of distal extremity of ulna	6.0
Length of second metacarpal	7.1
Width of proximal extremity of second metacarpal	3.5
Width of distal extremity of second metacarpal	5.0
Length of third metacarpal	9.5
Width of proximal extremity of third metacarpal	5.5
Width of distal extremity of third metacarpal	5.3

a, Approximate.

Hind limb:	mm.
Greatest length of femur	50.0
Width of proximal extremity of femur across head and greater trochanter	15.0
Width across condyles of distal extremity of femur	13.5
Depth of distal extremity of femur	10.5
Width of proximal extremity of tibia	12.4
Depth of proximal extremity of tibia	10.0
Width of distal extremity of tibia	9.4
Depth of distal extremity of tibia	5.6
Width of proximal extremity of fibula	3.2
Depth of proximal extremity of fibula	6.6

RODENTIA

ISCHYROMYIDAE

PARAMYS, cf. COPEI[13] Loomis

Seven isolated lower-jaw portions and an isolated upper molar, in addition to a specimen, U.S.N.M. No. 19306, including both rami of the mandible with some associated limb and vertebral fragments, represent in the La Barge fauna a moderate-sized paramyine rodent, tentatively referred to the species *Paramys copei* Loomis (1907a, p. 128).

Examination of the teeth of the upper Knight paramyine jaws in comparison with various specimens of Bridger *Paramys* shows little or no significant structural differences upon which, on teeth alone, one could reasonably separate these upper Wasatchian forms generically from true *Paramys*. The lack of definitive characters in the teeth was noted by Matthew (1920) in his description of *Reithroparamys*. *Paramys* appears to be a highly diversified genus, with Wasatchian species assigned to it more than covering the possible size ranges. Moreover, minor differences in teeth attributed to some of these species are probably, in view of Bridger variations, of no systematic significance, so that several of the species are likely invalid. Final allocation of the Knight species herein discussed awaits revision of the paramyids currently under study by A. E. Wood.

---

[13] While this paper was in press, Dr. A. E. Wood, who is revising the paramyids, examined these specimens and informs me that most of them surely represent *Paramys copei*, but that U.S.N.M. Nos. 19305 and 19306 should be referred to *Paramys major*, and a third, No. 19307, may be a new species.

PARAMYS, cf. BUCCATUS[14] (Cope)

An immature lower jaw, U.S.N.M. No. 19302, with the molar teeth broken off, but with the last premolar erupting, is compared, on the basis of the size of P_4, to Cope's (1877, p. 171) species, *Paramys buccatus.* There are also in the upper Knight collection fragments of a skull, including a single upper molar which cannot be distinguished from the type of this New Mexican species. Although Loomis (1907a, p. 130) considered this species as possibly belonging to *Sciuravus,* as Matthew (1910, p. 51) has noted, it is clearly paramyine and not sciuravine.

A left ramus of a mandible with portions of P_4 to M_2, inclusive. No. 12845 of the Knight collection of the American Museum, is very close in size of P_4 to U.S.N.M. No. 19302, and may also represent *Paramys buccatus.* This was included among the materials collected by Granger and Miller in 1906 from the bluffs along Bear River near Knight station.

SCIURAVUS, possibly S. DEPRESSUS Loomis

Recognition of *Sciuravus* in the lower Eocene has in the past been attended by serious doubt. In 1907 (a, p. 130) Loomis described three upper molars and a lower molar as the species *Sciuravus depressus,* from a locality in the Wind River beds near Lost Cabin, Wyo. Matthew, though cognizant of the occurrence in 1910, as shown by his phylogenetic chart and distribution table, did not comment on it, and in 1918 (p. 619) ignored the possibility, and listed *Sciuravus* without comment only in the middle and upper Eocene. Troxell in 1923 (a, p. 385) dismissed the possibility with the comment that from the drawings he judged the form to be not *Sciuravus* but a separate genus. Wilson (1938, p. 129) in his revision of *Sciuravus* based on the Bridger rodents in the Marsh collection cited the occurrence but added Troxell's comment. Again in 1949 (p. 79) Wilson cited *"Sciuravus depressus"* in the Lysite fauna, with the reservation that although this species apparently could not be referred to the genus *Sciuravus* it might be tentatively included in the Sciuravinae. No critical examination of the specimen has been reported since Loomis described it, and Loomis's illustration is clearly unsatisfactory, so that in reality the presence of *Sciuravus* in the lower Eocene has not been entirely discredited.

---

[14] Dr. A. E. Wood has since examined these specimens and indicates that this small Wyoming *Paramys* should be referred to *Paramys excavatus* Loomis rather than the New Mexican *P. buccatus.*

Sciuravus material in the upper Knight collection consists of the left ramus of the mandible, U.S.N.M. No. 19309, with P_4 and M_1, from about 12 miles north of Big Piney, Wyo. The species represented in the La Barge fauna is intermediate in size between *Sciuravus nitidus* Marsh and *Sciuravus bridgeri* Wilson of the Bridger fauna. It appears to be close in size to *Sciuravus depressus,* judging by Loomis's figure of 8 mm. for the lower molariform series.

TILLOMYS SENIOR,[15] new species

Text figure 5

Type.—Right ramus of mandible with P_4 to M_2, inclusive, U.S.N.M. No. 19308.

Horizon and locality.—Upper Knight beds, La Barge fauna, SW¼ sec. 33, T. 32 N., R. 111 W., 12 miles north of Big Piney, Sublette County, Wyo.

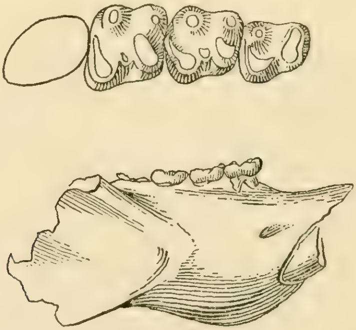


Fig. 5.—*Tillomys senior,* new species: Right ramus of mandible (U.S.N.M. No. 19308), type specimen; occlusal view, ×6; lateral view, ×3. Upper Knight, lower Eocene, Wyoming.

Specific characters.—Size much smaller than *Tillomys senex* Marsh (1872, p. 219) and appreciably smaller than *Tillomys parvidens* (Marsh) (1872, p. 220). Teeth with cusps very low and crests subdued, increasing in size from P_4 to M_2. Tooth row shorter than in *T. parvidens,* but jaw relatively deeper. Masseteric fossa does not extend so far forward with respect to teeth as in *T. parvidens.*

Description.—The above type is the only known specimen but is in a rather good state of preservation. The crowns of the first three cheek teeth are intact though worn to the point of exposing dentine in the central portion of each cusp. The occlusal portion of the incisor and the crown of M_3 are broken off.

---

[15] Older, comparative of *senex;* forerunner of *Tillomys senex.*

The details of the cusp arrangement in *Tillomys senior* are so like those in *T. parvidens* that confusion with other known genera of Eocene rodents seems entirely improbable. The cusps are even more subdued, possibly in part due to wear, than in the Bridger material examined, particularly the metaconid, and the cusps are perhaps more conical with less tendency toward development of crests. The entoconid is isolated with a very weak, posteroexternally directed crest, distinct from the internally directed posterolophid. The mesoconid is a simple conical cusp wedged between the protoconid and hypoconid. The pattern of wear on the protoconid suggests two low spurs directed toward the metaconid. Each of the three preserved teeth shows the trigonid to be narrower than the talonid and each succeeding tooth is wider than that preceding. M_3, though broken off, is clearly longer than M_2, but the width cannot be ascertained.

The teeth in *Tillomys senior* are only slightly larger than in the type of *Mysops kalicola* from the Lost Cabin beds, but the pattern of the crown is essentially different. *M. kalicola* in addition to having highly rugose enamel in the more deeply basined crown has sharper, more arcuate cusps and the crests or lophs are developed more continuously across the crown. Moreover, the jaw of *M. kalicola,* while deeper beneath M_3, becomes shallower forward beneath the anterior cheek teeth, and is transversely more slender.

MEASUREMENTS OF TYPE LOWER JAW OF
Tillomys senior, NEW SPECIES, U.S.N.M. NO. 19308

	mm.
Length of cheek-tooth series	*a* 6.6
Length of P_4 to M_2, incl.	4.6
P_4, anteroposterior diameter: greatest transverse width	1.5 : 1.3
M_1, “ “ “ “ “	1.5 : 1.5
M_2, “ “ “ “ “	1.6 : 1.7
Depth of jaw beneath M_1, on inner side	5.9

a, Approximate.

Remarks.—The occurrence of *Tillomys senior* in the Knight fauna of the Green River basin extends the known geologic distribution of *Tillomys* into the lower Eocene. The principal significance of this fact is the additional evidence afforded of the remarkable conservatism of rodent genera in Eocene time, adding to that of *Paramys* and *Sciuravus.* This is in striking contrast to the still more remarkable evolutionary change which took place in certain other groups of mammals between Lost Cabin and Bridger time. All of which is further proof of the antiquity of the order Rodentia, and arouses speculation as to why so little rodent material is known from the Paleocene, and where their earlier center of dispersal might have been.

CARNIVORA

ARCTOCYONIDAE

THRYPTACODON, near T. ANTIQUUS Matthew

Although Matthew (1915a, p. 7) stated that *Thryptacodon* has not been found in the Lysite or Lost Cabin, Van Houten (1945, p. 452) noted the presence in American Museum collections of a specimen of *T. antiquus* labeled "?Lysite" from the Big Horn basin. The upper Knight materials, which consist of a right upper molar and a tentatively included maxillary fragment with two milk teeth, appear to extend the range to Lost Cabin time.

The isolated upper molar, U.S.N.M. No. 19476, corresponds closely to *Thryptacodon antiquus* material of Gray Bull age in the National Museum collections and is almost identical in size and pattern to the second molar in the type specimen figured by Matthew (1915a, fig. 4). The maxillary portion, U.S.N.M. No. 19343, with the two teeth believed to be deciduous third and fourth premolars, rather resemble P^4 and M^1 of *Thryptacodon,* but are noticeably elongate anteroposteriorly, particularly the labial portion. The appearance and proportions of these teeth are about as one might anticipate in a *Thryptacodon* milk dentition.

MESONYCHIDAE

PACHYAENA? species

Two specimens, a single lower tooth and one associated with bone fragments, would appear to represent *Pachyaena* in the New Fork fauna. The development of the paraconid on these suggests P_4 and M_1. They are rather close in size to these teeth in *Pachyaena gracilis.*

OXYAENIDAE

OXYAENA, species

A single lower molar, obtained by Princeton University in association with the *Ambloctonus* jaw described below, and carrying the number P.U. 16176, was among the Knight materials which Dr. Jepsen has permitted me to include with my study of the Smithsonian collections. This tooth is readily recognized as a first lower molar of *Oxyaena;* however, the species represented is not evident. In size it corresponds very closely to the New Mexican *Oxyaena lupina* Cope. Resemblance on the basis of such limited material, however, scarcely justifies extending the range of this species to the late lower Eocene of Wyoming.

AMBLOCTONUS, cf. MAJOR Denison

Plate 6, figure 2

An *Ambloctonus* lower jaw, obtained by Princeton University from a locality in the upper Knight about 2 miles southeast of La Barge, Wyo., was kindly loaned to me for study by Dr. G. L. Jepsen. This specimen, P.U. No. 14720, includes P_2 to P_4, inclusive, and M_2, and exhibits alveoli for the canine and M_1.

The premolars of the Princeton specimen are a little like those in *Oxyaena forcipata*, but, as in *Ambloctonus*, are distinctly broader, particularly across the talonid, perhaps blunter, and P_4 exhibits a better-developed parastylid. These teeth are relatively longer and apparently less hypsodont than in *Palaeonictis*. M_1 was remarkably large, as indicated by the alveoli, the posterior of which is considerably longer, anteroposteriorly, than the anterior. M_2 is of reduced size, with a much curved shearing blade, no metaconid, and a very small talonid. The narrowness of the talonid and absence of a metaconid on this tooth are characteristic of *Ambloctonus*, and distinguish this form from *Palaeonictis*.

The type of *Ambloctonus major* Denison (1938, p. 176), as figured by Matthew (1915a, fig. 53) under reference to *Ambloctonus hyaenoides*, consists of a fragmentary jaw with M_1 and part of P_4. Direct comparison in not feasible, but the size of the preserved molar in the Lost Cabin type specimen corresponds almost exactly to the space for the missing tooth in the upper Knight jaw.

Among fragments of carnivore teeth found in the New Fork beds is a left P_3 which resembles closely this tooth in the Princeton jaw from near La Barge. It is about the same length but slightly wider. It lacks a paraconid as in both *Ambloctonus* and *Palaeonictis* but its profile in lateral view is much more like *Ambloctonus*.

LIMNOCYONIDAE

PROLIMNOCYON ELISABETHAE,[16] new species

Plate 5, figures 1-3

Type.—Both rami of the mandible with the canine and P_2 to M_2, inclusive, represented, U.S.N.M. No. 19350.

Horizon and locality.—Upper Knight beds, La Barge fauna, north side of "Red Hill," western margin of SW¼ sec. 23, T. 29 N., R. 111 W., about 5 miles southeast of Big Piney, Sublette County, Wyo.

---

[16] Named for my wife, who found the type specimen.

Description.—Teeth a little smaller and much more slender than in *Prolimnocyon antiquus.* P_2 to P_4 with increasingly prominent parastyle. Talonid of molars narrower than in *P. antiquus* and lower jaw a little shorter, shallower, and much more slender. M_3 single-rooted.

Discussion.—In addition to the pair of jaws described above as the type of this species, there are portions of right and left maxillae of one individual, U.S.N.M. No. 19348, including P^4 to M^2 between them, and a third individual, U.S.N.M. No. 19349, represented by a left mandibular ramus with portions of P_4 and M_1.

The type of *Prolimnocyon antiquus* from the Lost Cabin beds consists of right jaw portion with only the heel of M_2 preserved. An isolated M_1 from the opposite side is included with the type and may have been used by Matthew (1915a, fig. 63) to illustrate this tooth in the jaw. The M_1 referred to the type is fairly robust and has a decidedly broad, basined talonid, wider than in M_2 and relatively much larger than in the type of the earlier *Prolimnocyon atavus.* M_1 in the type of *Prolimnocyon elisabethae* is smaller, much more slender and has a considerably smaller talonid than that attributed to *P. antiquus.* The premolars in *P. elisabethae* are almost as long as in *P. antiquus* but more slender as indicated by root portions in the type of the latter. A referred specimen of *P. antiquus,* A.M. No. 2971, shows P_3 and P_4 to have almost no parastyle, and the parastyle is weak or absent in material of Gray Bull *P. atavus.* In *P. elisabethae* the parastyle is weak on P_2 but decidedly prominent on P_4.

Right and left maxillae, U.S.N.M. No. 19348, have between them P^4 to M^2, inclusive. A single small alveolus is preserved of M^3 but the specimen is incomplete lingual to this point so that the presence of additional alveoli for this much-reduced tooth cannot be determined. P^4 shows a single large primary cusp and a sharp high-cusped deuterocone, the latter of which is separated by a deeply indented anterior border from the distinct parastyle. The tritocone is somewhat elongate and approaches the crested form characterizing the first molar. In M^1 the paracone and matacone are distinctly more separated than in *Prolimnocyon atavus* of the Gray Bull stage, and the isthmus to the protocone is a little more constricted, with a better-developed and nearly continuous cingulum around the protocone. Also, the parastyle consists of a complex of two small stylar cusps together with a third small cusp between these and the paracone. M^2 is, of course, transverse with a greatly elongate parastyle, no metastyle, and a vestigial metacone. The striking difference between this tooth in *Prolimnocyon* and that in *Sinopa* is one of function, and Butler (1941) has shown in a study of *Hemicentetes* something of the mechanism or explanation of the transition that may account for the ways and means of divergence between these two creodonts. However, such a separation obviously took place at a much earlier and unspecialized stage of dental development in both lines, and by lower Eocene time this divergence has a basic, nonadaptive significance.

The numerous characters that have been used (Denison, 1938, pp. 241-242) to support transfer of the Limnocyoninae to the Hyaenodontidae are for the most part matters of degree in distinction from the Oxyaeninae, and largely of adaptive significance in comparison with Proviverrinae. Demonstration of a probable common ancestry does not necessarily justify inclusion of two groups of genera in the same family, particularly when these related groups diverge and develop their own taxonomic complex, such as horses and tapirs. Certainly the genera most typical of the family Hyaenodontidae, those included in the Hyaenodontinae, are strikingly distinctive and unlike *Limnocyon* and its allies. All things considered I find inclusion of the Limnocyoninae and Machairoidinae in the Hyaenodontidae untenable. On the other hand, the probable origin of *Prolimnocyon,* or rather of its ancestry, would suggest, although this is uncertain, a polyphyletic Oxyaenidae were the Limmnocyoninae to be retained in that family.

HYAENODONTIDAE

SINOPA VULPECULA Matthew

U.S.N.M. No. 19347, which consists of maxillae and jaws together with fragments of other skeletal portions, is regarded as representing in the La Barge fauna the small Lost Cabin species, *Sinopa vulpecula* Matthew (1915a, pp. 80-82). The teeth are close in size to those in the type but the jaw is slightly shorter, shallower, and straighter, also the coronoid portion not so high. P_1 is absent in both rami, but a slightly rugose depression well ahead of P_2 suggests an earlier presence, but loss before death. Though the animal was evidently not an aged adult, the third molar in both rami was broken to root stubs which were well worn before death. Also, the first molar is missing on the right side and the anterior alveolus for this tooth was completely closed before death.

The upper teeth are undamaged, so far as represented, and in the right maxilla P^2 to M^3 are present. Wear in the molar series was evidently restricted for the most part to occlusion with M_2 and the posterior root of M_3, although earlier occlusion with the trigonid of M_3 is indicated. However, wear resulting from M_1 is very slight, indicating a very early loss of this tooth. The upper molars of No. 19347 are much larger than those in the Lysite specimen figured by Matthew as possibly representing *Sinopa vulpecula.* They are close in size to those of the type of *Sinopa multicuspis* from the Eocene of New Mexico. The most noticeable difference from the latter is a greater lingual extension of the protocone portion in the molars and possibly less development of the parastyle on M^2 of the upper Knight specimen. The slenderness and lingual projection of the protoconal portion is rather noticeable in comparison with middle Eocene forms, such as *Sinopa rapax.*

It is also noted that the upper Knight form may compare favorably in size with *Tritemnodon? whitiae* Cope, but the lower premolars are more robust and longer in the latter, and the talonids of the lower molars are smaller. Upper teeth of a referred specimen of *T.? whitiae,* A.M. No. 4781, show no metacone on M^3 which is present in the Knight material, and P^3 shows a small talon not seen in the Knight specimen referred to *Sinopa vulpecula.*

SINOPA, cf. STRENUA (Cope)

A single left maxillary portion with the last two molars, U.S.N.M. No. 19345, tentatively referred to *Sinopa strenua,* shows the presence of a larger species of *Sinopa* in the La Barge fauna than is represented by the better-preserved material described above as belonging to *Sinopa vulpecula.* Direct comparison with the type of *S. strenua* is not feasible, inasmuch as the New Mexican specimen includes only the lower jaws; however, Matthew (1915a, pp. 74-75) has suggested the possibility of this species being represented by various Lost Cabin specimens. On the basis of size alone No. 19345 might come within the range of *S. strenua.*

MIACIDAE

DIDYMICTIS ALTIDENS Cope

Matthew's (1915a, pp. 19-26) revision of the lower Eocene species of *Didymictis* is an oversimplification of the situation, and includes errors which have led to confusion in attempts to identify Wasatchian materials representing this genus. It seems unlikely that he examined the type of *Didymictis protenus,* as the actual measurements of it are less than the range which he has given for the subspecies of this name. For the record these are P_1-M_2, inclusive, 53 mm.; and M_1-M_2, 18.3 mm. The ranges given for *Didymictis protenus lysitensis* and *Didymictis altidens* would appear to be diagnostic for the Lysite and

Lost Cabin horizons, whereas this is not the case. Several specimens of Lost Cabin *Didymictis* in the National Museum collections are within the range given for *D. p. lysitensis*. This is also true of the upper Knight materials, of which there are some 14 specimens from the vicinity of La Barge and Big Piney, Wyo. I do not believe, however, that a Lysite age is indicated thereby. It seems more probable, as Simpson (1937, p. 15) has suggested, that *Didymictis protenus lysitensis* is either a synonym of *D. altidens,* or a subspecies of the latter rather than of *D. protenus*. On this basis I have referred the upper Knight materials to *D. altidens*. They are scarcely comparable to the type *D. protenus* and only a little smaller than dimensions given by Cope (1880a, p. 746) for *D. altidens.*

Much of the *Didymictis* material in National Museum collections from the Gray Bull exhibits somewhat smaller proportions than *D. protenus,* and should any prove to represent a distinct species, the name *Didymictis leptomylus,* as well as the larger *D. curtidens,* is available. Simpson has shown that *D. leptomylus* possesses a remarkably small M_1; however, he regards the locality for the type as in doubt. This was clarified by Wortman, as reported by Matthew (1915b, p. 314), subsequent to Matthew's work on the Wasatchian carnivores. Hence, *Didymictis leptomylus* Cope, *Haplomylus speirianus* (Cope), and *Esthonyx spatularius* Cope, originally regarded as from Wind River beds, are shown to be Gray Bull, and almost surely lower Gray Bull. This is in accord with locality corrections later made by Cope without explanation.

VIVERRAVUS LUTOSUS,[17] new species

Text figure 6

Type.—Right ramus of mandible with P_2 to M_1, inclusive, U.S. N.M. No. 19339.

Horizon and locality.—Upper Knight beds, La Barge fauna, SW$\frac{1}{4}$ sec. 33, T. 32 N., R. 111 W., 12 miles north of Big Piney, Sublette County, Wyo.

Description.—Size of teeth intermediate between Lost Cabin *Viverravus dawkinsianus* (Cope) and lower Gray Bull *Viverravus acutus* Matthew, but depth of jaw shallow as in *V. acutus*. P_1 two-rooted, P_3 with posterior accessory cusp, but less well developed than in P_4. Talonid of M_1 with trenchant, external hypoconid, and lingual portion distinctly basined.

---

[17] From Latin *lutosus,* muddy, with reference to Muddy Creek where the type was found.

Remarks.—*Viverravus lutosus* material includes approximately eight specimens, all lower-jaw portions except for an isolated P^4. Most of these come from a badland locality on Muddy Creek about 12 miles north of Big Piney. The species is probably closest to *Viverravus dawkinsianus,* particularly in the development of the anterior premolars. However, it has distinctly smaller teeth, particularly P_4, and the lower jaw, though fully mature, is as shallow as in *Viverravus acutus.* The shallowness is most noticeable posteriorly beneath the molars, with the greatest depth beneath P_4. In other Wasatchian species the depth apparently increases posteriorly beneath the molars.

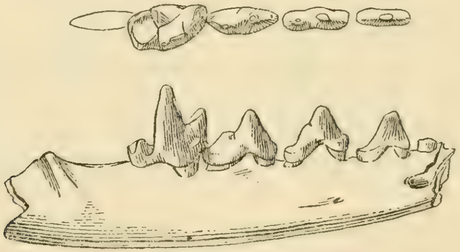


FIG. 6.—*Viverravus lutosus,* new species: Right ramus of mandible (U.S.N.M. No. 19339), type specimen; occlusal and lateral view, × 2. Upper Knight, lower Eocene, Wyoming.

MEASUREMENTS OF TYPE LOWER JAW OF
Viverravus lutosus, NEW SPECIES, U.S.N.M. NO. 19339

	mm.
Length of cheek-tooth series at alveoli, P_1-M_2, incl.	23.7
Length of premolar series, P_1-P_4, incl.	15.4
Length of molar series, M_1-M_2, incl.	8.7
Length of P_4 : width of P_4	4.9 : 1.8
Length of M_1 : width of M_1	5.1 : 2.9
Depth of jaw beneath P_4	5.4
Depth of jaw beneath M_2	5.3

UINTACYON ASODES,[18] new species

Plate 6, figure 1

Type.—Left ramus of the mandible with the canine, P_4, and M_1 preserved, U.S.N.M. No. 19351.

Horizon and locality.—Upper Knight beds, La Barge fauna, SW¼ sec. 33, T. 32 N., R. 111 W., 12 miles north of Big Piney, Sublette County, Wyo.

---

[18] From Greek ἀσώδης, muddy, etc., with reference to Muddy Creek where the type was found.

Description.—Size near that of *Uintacyon massetericus* (Cope), but jaw a little deeper, and teeth wider and more robust. Premolars uninterrupted, except for very small diastemata before and after P_1. P_4 without paraconid. M_2 about 40 percent longer as measured at roots. M_3 single-rooted.

Remarks.—*Uintacyon asodes* is represented by a single specimen which consists of a lower jaw in which are preserved only the canine, last premolar, and first molar. The anterior premolars and posterior molars are indicated by root portions or alveoli. P_1 and M_3 are single-rooted. Comparison of *Uintacyon asodes* with the referred specimen of *Uintacyon massetericus,* which Matthew figured (1915a, fig. 24) instead of the type, shows the carnassial to be wider and the premolars to be less reduced and in closer sequence. Also, the lower jaw is shorter and deeper and would appear to have a straighter inferior margin or profile; however, the anterior part of the specimen Matthew figured is damaged and the restoration may not be correct.

Uintacyon is rare in lower Eocene deposits and this is apparently the first record of its occurrence in beds of Lost Cabin age. Representation in later Wasatchian was to be expected, however, inasmuch as the typical and better-known species are Bridger middle Eocene in age. *Uintacyon asodes* shows a definite trend toward the latter forms.

MEASUREMENTS OF TYPE LOWER JAW OF
Uintacyon asodes, NEW SPECIES, U.S.N.M. NO. 19351

	mm.
Length of dentition from P_1 to M_3, incl., at alveoli	*a* 35.0
Length of premolar series, P_1 (alveolus) to P_4	18.1
Length of molar series, M_1 to M_3 (alveolus)	*a* 17.0
Length of P_4 : width of P_4	6.1 : 3.3
Length of M_1 : width of M_1 at trigonid	7.5 : 5.5
Length of M_2 at roots	5.9
Depth of jaw beneath P_3, lingual side	13.0
Depth of jaw beneath talonid of M_1, lingual side	12.2

a, Approximate.

MIACIS, cf. LATIDENS Matthew

Lower jaw portions of three individuals, all from 12 miles north of Big Piney, exhibit teeth which are more like those in *Miacis* than any of the other miacids. One of these specimens, U.S.N.M. No. 19335, includes portions of both rami and has preserved all the cheek teeth, except P_1, on the left side. The measurements of these are almost the same as those given by Matthew (1915a, p. 34) for the type of *Miacis latidens.* Unfortunately, however, the type exhibits only the last two molars, so that only limited comparisons can be made. The upper Knight jaw has about the same depth beneath P_1 or P_2, but is much deeper beneath the molars, particularly M_3. M_2 corresponds in detail to that in the type and is about the same size; however, M_3 would appear to be slightly more like M_2 in outline than this tooth does in the type.

In addition to the few comparisons permitted with the type, it is further noted in the upper Knight specimen that P_1 and P_2 are isolated by diastemata, but that P_3 to M_3 are in a closed sequence. Of the premolars, only P_4 exhibits an accessory posterior cuspule. The trigonid of M_1 is high but those of the following molars are much reduced. The talonid in each of the molars is basined, though it appears somewhat more trenchant, particularly M_2, than in *Vulpavus australis,* and each tapers somewhat more posteriorly than in the latter. Moreover, M_3 appears more reduced than in *Vulpavus,* and although the crown seems to be a reduced image of M_2, the root portions are not so well separated. In U.S.N.M. No. 19334 the alveolus appears to be a single bilobed opening. The distinctions between species of *Miacis* and *Vulpavus,* though better defined in the middle Eocene, are less clearly discernible in lower Eocene materials, and some of the more fragmentary specimens, including isolated teeth, in the Knight collection could not be assigned with any certainty.

VULPAVUS ASIUS,[19] new species

Plate 5, figure 4

Type.—Portions of both rami of the mandible with P_3 and M_1-M_2, U.S.N.M. No. 19337.

Horizon and locality.—Upper Knight beds, La Barge fauna, SW¼ sec. 33, T. 32 N., R. 111 W., 12 miles north of Big Piney, Sublette County, Wyo.

Description.—Depth of jaw about as in contemporary *Vulpavus canavus* Cope but teeth closer in size to those of *Vulpavus australis* Matthew of the New Mexican San Jose beds. The first two molars are of about the length of those in *V. australis* but relatively wider, and P_4 and M_1, as indicated by root portions, are longer. The trigonid of M_1 is higher, although relatively not so high as in *Miacis,* and the paraconid and metaconid are less widely separated giving the "V" of the trigonid a more acute angle at the protoconid.

Discussion.—*Vulpavus asius* may be represented by some half dozen specimens encountered at various localities in the upper Knight

---

[19] From Greek ἄσιος, slimy, muddy; with reference to Muddy Creek where the type specimen was found.

beds. These appear to represent a form having a jaw about as robust as *Vulpavus canavus,* but with teeth significantly smaller. In this respect *V. asius* approaches Bridger material in the National Museum referred to *V. palustris,* although M_2 is distinctly shorter. The depth of the jaw, however, becomes a little shallower beneath the anterior premolars and, as shown in No. 19336 as well as the type, the symphyseal portion is not so deep as in *V. canavus.*

CONDYLARTHRA

HYOPSODONTIDAE[20]

HYOPSODUS WORTMANI Osborn

There are in the upper Knight collection over 100 specimens belonging to species of *Hyopsodus.* Of these, 29 can be clearly determined as belonging to *Hyopsodus wortmani.* Osborn (1902, p. 185) gave the length of the lower molar series as varying from 11 to 13 mm., whereas Matthew (1915b, p. 317) in his key to *Hyopsodus* cited 10 mm. Probably neither are correct as Osborn likely included some material which Matthew would have placed in *Hyopsodus mentalis lysitensis* and Matthew may have derived the figure of 10 mm. as characterizing the lower molar series from Osborn's dimension for the length of the upper molar series. In the few upper Knight specimens in which all the lower molars are preserved the range is from 10.5 to 11.5 mm. An upper molar series measures 10 mm.

The teeth in the upper Knight materials regarded as representing *H. wortmani* are markedly progressive; exhibiting well-developed hypocones in the upper molars, the trigonid of the lower molars has lost the paraconid, and the metaconid and talonid of P_4 are in an advanced stage of development. The advance is noticeable over Gray

---

[20] The use of the family name Hyopsodontidae appears to have become established through usage, but largely as a result of a series of errors. Hyopsodidae was first used by Schlosser in 1887, but in 1889 Lydekker used Hyopsodontidae, attributing it to Schlosser with the comment "wrongly given as Hyopsodidae." Osborn in 1902 used Hyopsodontidae, also attributing it to Schlosser, and was followed by Weber, and others; however, Hay (Bibliography) in 1902 and Palmer (Index Generum Mammalium) in 1904 correctly credited Hyopsodidae to Schlosser (1887) and Hyopsodontidae to Lydekker (1889), and the earlier spelling was used by Wortman in his revision of the primates in 1903 and by Loomis, with the correct source cited in his revision of *Hyopsodus* in 1905. This was ignored by Matthew who reverted to Osborn in his revision of 1915. In 1930 Hay used Hyopsodontidae but probably because he erroneously gave the date of Lydekker's spelling as 1887. Simpson, in his classification of 1945, used Hyopsodontidae, but without reference to the earlier spelling.

Bull materials, and in particular when comparison is made with the more nearly equivalent-sized *H. simplex*.

In the New Fork materials is a fragmentary right mandibular ramus with M_3. The tooth corresponds well with equivalent material of *H. wortmani* from the upper Knight beds.

HYOPSODUS MENTALIS (Cope)

The much larger series of specimens of *Hyopsodus* in the La Barge–Big Piney collection are referred to the species *Hyopsodus mentalis*. These include materials covering a rather noticeable range in size, but within which no separation seems practical, or can logically be maintained. The dimensions given by Cope (1875, p. 17) for *Hyopsodus mentalis* fall well within the upper limits of this material, but it seems unlikely that the same species of this small mammal would be represented in so widely separated localities. However, on the basis of known material, the upper Knight form, represented by some 76 individuals, appears indistinguishable from the New Mexican species. Moreover, the range of the length of the lower molar series is about 13 to 14.5 mm. This would appear to average less than the range 14 to 15 given by Matthew (1915b, p. 320) for the Lost Cabin and New Mexican materials he included in the New Mexican species, and to overlap the inferred range of his *Hyopsodus mentalis lysitensis* which occurs in Lost Cabin as well as Lysite beds. Matthew's figures here should probably not be relied on as there are differences in cited measurements between key and text for some of the lower Eocene species of this genus.

Matthew (1915b, p. 319) has placed *Hyopsodus lemoinianus* Cope in synonomy with *H. mentalis,* but it should be noted that the dimensions for *H. lemoinianus* are at about the upper limit of the range, and that the type of this species may have come from the older Gray Bull beds. The species of *Hyopsodus* as currently recognized may not be satisfactorily arranged; there is, however, abundant material representing this genus from various Eocene horizons, and this should lend itself rather well to mathematical analysis.

HYOPSODUS BROWNI Loomis

Four specimens of *Hyopsodus* in the American Museum, collected by Granger and Miller in 1906 from the Knight beds near Knight station in southwestern Wyoming, do not appear to be conspecific with any of the *Hyopsodus* material from the Big Piney–La Barge region. Two of these, A.M. Nos. 12838 and 12839, are lower jaws very close to material in the American Museum from the Lysite beds identified as *Hyopsodus browni*. A third lower jaw, No. 12837, has badly worn teeth which are somewhat smaller but may come within the range of *H. browni*. The fourth, a maxilla with P^3 to M^3, inclusive, is also somewhat smaller, corresponding to A.M. No. 12837. The teeth in the maxilla, however, are larger than any in *Hyopsodus* of the La Barge fauna, although an approach is made in one specimen, U.S.N.M. No. 19657, from southeast of Big Piney. Matthew regarded *Hyopsodus browni* Loomis as a subspecies of *H. powellianus,* between the latter and *H. mentalis* in size. He recorded (1915b, p. 322) it as abundant in the Wind River Lysite, rare in the Big Horn Lysite, and doubtful in the Lost Cabin. This form would appear to be rather indicative of a Lysite age for the Knight beds on Bear Creek.

PHENACODONTIDAE

PHENACODUS PRIMAEVUS Cope

The type specimen of this species was found by Cope in the type Knight on Bear River but it appears not to be represented in upper Knight beds of the upper Green River basin. There is, however, a lower jaw portion in the National Museum collections which Dr. D. H. Dunkle obtained in 1950 from lowest exposed Wasatchian beds, just beneath variegated beds, in S½ sec. 11, T. 21 N., R. 117 W., about 3 miles east of Fossil in Lincoln County, Wyo. The specimen includes P_4 and M_1, and compares favorably with *Phenacodus primaevus*.

MENISCOTHERIIDAE

MENISCOTHERIUM ROBUSTUM Thorpe

Plates 7, 8

Beyond doubt the most striking materials recovered from the upper Knight deposits are the well-preserved skulls, jaws, and partial skeletons of the peculiar condylarth *Meniscotherium*. Remains representing *Meniscotherium* are nowhere so abundantly found, outside of the locality of their original discovery in the lower Eocene of New Mexico.

Following Cope's discovery of a maxilla, to which he gave the name *Meniscotherium chamense* (1874, p. 8), David Baldwin obtained considerable material for Marsh and later for Cope from the New Mexican or San Jose beds. The collection obtained for Cope was the basis for an additional species, *Meniscotherium terraerubrae* Cope (1881b, pp. 493-495), founded on a distinctly larger individual than *M. chamense,* but since there seemed to be no clear separation of these two, Granger (1915, p. 359) regarded *M. terraerubrae* as no more than a subspecies of *M. chamense.* Cope's (1882b, p. 470) species, *Meniscotherium tapiacitis,* based on very much smaller material in the Baldwin collection than either of the above, Granger regarded as valid. Subsequent to Cope's work on these, Marsh (1892, pp. 445-449) named *Hyracops socialis* on material in Marsh's Baldwin collection, but a review of this species by both Granger and Thorpe (1934, pp. 406-409) has resulted in its being placed in synonymy with *Meniscotherium chamense terraerubrae.* A very considerable amount of material representing *Meniscotherium* has subsequently been obtained from the San Jose by Simpson and a thorough understanding of these forms is anticipated.

Outside of New Mexico, materials from the Lost Cabin beds were referred by Granger in 1915 to typical *M. chamense* and a form recognized from Clark Fork Paleocene was described as *Meniscotherium(?) priscum* (1915, p. 360). Then in 1934 Thorpe described a skull and jaw in the Marsh collection from 2 miles west of Aspen, Wyo., which was collected by William Cleburne in 1875. To this he gave the name *Meniscotherium robustum.* An examination of Veatch's (1907, pl. 3) geologic map, showing the position of Aspen as it was originally located on the old route of the Union Pacific, shows *M. robustum* type to have come from Knight beds to the east of the general southward extension of the West Oyster Ridge structure and in the Green River basin of Eocene deposition.

Material of *Meniscotherium* in the upper Knight beds of the upper part of the Green River basin are equaled in abundance only by specimens of *Lambdotherium.* Some 93 specimens, including eight skulls, many jaws and maxillae, and various associated skeletal portions in this collection appear to represent a single species which cannot be distinguished from the type of *Meniscotherium robustum.* In addition to the type, and the Smithsonian collections from the vicinity of Big Piney and La Barge, an *M. robustum* skull was found also by R. W. Brown in a relatively thin zone of Knight beds exposed on Little Bitter Creek between Rock Springs and Green River, Wyo. A detailed description of the skull and other portions of the skeleton of this Knight species will be omitted in deference to studies of related forms in the San Jose fauna currently under way by Simpson.

MENISCOTHERIUM, cf. CHAMENSE Cope

A surprising and rather significant discovery with respect to the occurrence of *Meniscotherium* is that the material obtained from the New Fork tongue represents a distinct species from the typical upper Knight, *M. robustum.* Three individuals from separate localities along Alkali Creek in Sublette County are all immature, but can be readily compared with material of equivalent maturity belonging to the upper Knight *M. robustum.* The New Fork specimens are seen to represent a species distinctly smaller than *M. robustum.* The permanent anterior upper molars preserved in two of the specimens are closely comparable in size, and apparently cannot be distinguished otherwise from these teeth in the type of *Meniscotherium chamense* from the San Jose lower Eocene beds of New Mexico.

PANTODONTA

CORYPHODONTIDAE

CORYPHODON, cf. RADIANS (Cope)

Plate 9

Fragmentary remains of *Coryphodon* are not among the more common materials encountered during a search of upper Knight beds in the vicinity of La Barge or Big Piney. Isolated teeth or tooth portions representing some 13 individuals were preserved, although, to my recollection, probably a much greater amount of very poorly preserved or scarcely identifiable material was discarded or not collected. However, a complete skull, U.S.N.M. No. 16701, in a rather poor state of preservation, was found in SW¼ sec. 24, T. 28 N., R. 114 W., on a branch of Dry Piney Creek in Sublette County, Wyo. Attention was called to the occurrence of this specimen in the Knight lower Eocene in a short paper concerned primarily with the first collections obtained from the Almy Paleocene (Gazin, 1942, p. 217). The skull was discovered in beds separated by faulting, as mapped by A. R. Schultz (1914, pl. 1), from the general area of upper Knight in the Green River basin. The locality was early regarded as possibly somewhat older, and the preservation of the specimen together with the lithology appeared nontypical; nevertheless, a jaw of *Hyracotherium,* cf. *vasacciense* was discovered on the same outcrop, supporting a lower Eocene age.

No less than 24 specific names and six generic names have been applied to American *Coryphodon,* and revisions by Earle (1892), Osborn (1898, pp. 188-218), and Matthew (1899, pp. 33, 36), while differing in detail, have reduced the genera finally to one, and cut the number of species almost in half. Four of the specific names proposed, *Coryphodon radians, Coryphodon semicinctus, Coryphodon latipes,* and *Coryphodon hamatus,* were based on materials from the type Knight exposures, the oldest of which is *Coryphodon radians* Cope (1872a), and which, incidentally, has priority over all others in the North American Eocene.

M^3 in U.S.N.M. No. 16701 is slightly smaller than in the type of *Coryphodon radians,* as reported by Osborn (1898, p. 198), measuring about 31 by 40 mm. instead of 32 by 43 mm. It differs in form from the type in the absence of a posterior spur from the metacone, the presence of which was believed to distinguish *C. radians.* The length of the premolar-molar series, about 160 mm., is intermediate between that of *Coryphodon hamatus* and *Coryphodon elephantopus.* It differs most noticeably from *C. hamatus* Marsh (1884, p. 52, fig. 55) in the absence of the distinctive hypocone development seen in the upper molars of Marsh's type. *C. elephantopus,* as represented by U.S.N.M. No. 111, cited by Osborn as a cotype, has transversely narrower upper premolars than the Dry Piney Creek specimen. Without attempting to revise or determine synonymy of *Coryphodon* species, a task of major proportions, the specimen is referred tentatively to *C. radians.* Some separate teeth of another individual, found in Fogarty Draw, near the Green River, NW¼ sec. 20, T. 28 N., R. 111 W., include a second upper molar which measures about 37 by 43 mm. and may represent a larger species, but this is not certain.

DINOCERATA

UINTATHERIIDAE

Cf. BATHYOPSIS FISSIDENS Cope

A pair of lower jaws, U.S.N.M. No. 19990, including the greater part of the left ramus with P_3 to M_3 and a smaller part of the right ramus with portions of P_2 to M_3, of a uintathere was found in the New Fork tongue of Knight on Alkali Creek about 10 miles above its junction with the Green River. The jaws are rather poorly preserved and the teeth, particularly in the right ramus, are noticeably checked.

Details of the teeth correspond very well to those of the type of *Bathyopsis fissidens* Cope (1881a, p. 194) although those in the New Fork specimen are better worn. The posterior crest of the talonid of the molars is truly a crest and not cuspate as in *Probathyopsis.* The teeth are close to the same size, but slightly larger than in *Bathyopsis* *fissidens*. However, from the measurements given by Cope it would appear that P_4 in the type is much smaller than in the New Fork specimen. The length given is appreciably less than the width, a condition not verified in the figures. The relative size of P_4 corresponds more nearly to the illustration. It seems likely that Cope's dimension is in error and that the length of P_4 is 0.0150 M instead of 0.0105 M.

In spite of the similarity of the teeth, marked divergence is noted in the form of the lower jaw. Preservation of the bone is very poor but there is no doubt that the New Fork specimen lacked the massive inferior flange characterizing the type. Wear of the teeth is evidence of greater maturity than the type, and there is some evidence that the diastema back of the canine was longer; nevertheless, the inferior margin of the jaw would appear to be somewhat like that of the smaller and more primitive *Probathyopsis praecursor* Simpson (1929, p. 2). This striking difference of form would suggest generic, or at least specific, difference; however, a dimorphic condition has been postulated by J. A. Dorr (1952, p. 89) with respect to *Probathyopsis* materials from Hoback Canyon, so that the possibility of such a situation in the upper Wasatchian materials should not be ignored. Pending possible future discoveries clarifying the relationships, the New Fork specimen is tentatively referred to *Bathyopsis fissidens* and regarded as possibly female.

PERISSODACTYLA

EQUIDAE

HYRACOTHERIUM INDEX (Cope)

The specimens of *Hyracotherium* in the La Barge fauna readily fall into three fairly well-defined groups, those of the smallest species belong almost certainly to *Hyracotherium index*. Approximately 35 specimens are in this group including jaws and maxillae which give a good representation of the cheek-tooth series.

Measurements of M_2 in seven lower jaws having this tooth show a range of 6.3 to 6.8 mm. in length and 4.5 to 4.8 mm. in width with an average of 6.6 and 4.6 mm., respectively. M_2 in the type of *Hyracotherium index* measures 6.7 and 4.7 mm.; a close correspondence. The probability of identity would appear to be increased by the fact that the type of *H. index* is also from the Knight formation, but at its type locality on Bear Creek and hence evidently somewhat older. Moreover, it is interesting to note that *H. index* is the second species of *Hyracotherium* to have been described from North America, the first being *Hyracotherium vasacciense* and from the same beds.

Two upper teeth representing *Hyracotherium index* are also included in the Princeton University collection, No. 16172, from Knight beds about 100 feet below Green River strata, 3 miles northwest of Fossil, Wyo. These compare very favorably with *H. index* material from the vicinity of Big Piney and La Barge.

HYRACOTHERIUM VASACCIENSE (Cope)

A much larger number of specimens, approximately 67, from the upper Knight are in a size group clearly distinct from that of *H. index*. The range in size of M_2 in 14 jaws, in which this tooth is present and certainly determined, is 7.4 to 8.4 mm. in length and 5.5 to 6.5 mm. in width, with an average of 7.8 and 5.9 mm., respectively. The type of *Hyracotherium vasacciense* consists of a jaw portion with only M_2 preserved. This tooth measures 8.2 mm. in length and 6.0 mm. in width across both trigonid and talonid, a striking correspondence and well within the range. Granger (1908, p. 222) was inclined to suppress this name but I find it advisable to revive it as the most logical and applicable designation for the rather large series of specimens from these beds. Suppression of this name was awkward inasmuch as there is no question of its representing *Hyracotherium* and it is the oldest for North American species. So far as being indeterminate, the Knight collections under consideration would appear to give it definition and practical significance.

In addition to the above collection from upper Knight beds of the upper Green River basin, there are three right upper molars (A.M. No. 12841) of one individual from the Knight on Bear River near Knight station in the American Museum collection which are about the right size and surely represent *Hyracotherium vasacciense*.

HYRACOTHERIUM, cf. VENTICOLUM Cope

Four specimens in the upper Knight collection appear rather large to be included in the group identified as *Hyracotherium vasacciense*. They do not include M_2, but other teeth are found to be 10 to 20 percent larger on various selected measurements than some of the large individuals of *H. vasacciense*. These unusually large specimens are tentatively referred to the Lost Cabin species, *Hyracotherium venticolum* Cope (1881a, pp. 198-199).

A left maxilla with P_2, P_4, and M_1 in the Princeton collection, No. 16173, from near Fossil, Wyo., first thought to be tapiroid, is probably also to be referred to *Hyracotherium venticolum*. The P_4 shows a prominent anterolingual crest, but with little evidence of accessory cuspules. It resembles P^3 in *Homogalax,* but can be matched in fourth premolar material in the upper Knight collection from the Green River basin referred to *Hyracotherium.* The first molar is more equine than tapiroid and is certainly not *Heptodon.*

Isolated upper and lower teeth in the New Fork collection compare favorably with *Hyracotherium venticolum.* Various measurements of these teeth are very close to those in the type of this Lost Cabin species.

HYRACOTHERIUM, possibly H. CRISTATUM Wortman

Some lower teeth (A.M. No. 12842) among the materials collected by Granger from the type Knight appear too large to be included in *H. vasacciense* or *H. venticolum* and may represent one of the larger species such as *H. cristatum.* They are too narrow to belong to the Wind River *H. craspedotum.*

BRONTOTHERIIDAE

LAMBDOTHERIUM POPOAGICUM Cope

Plate 10

As many specimens of this earliest known titanothere were found in the upper Knight beds as of *Meniscotherium,* and several were obtained from the New Fork; however, the material for the most part was more fragmentary than that of *Meniscotherium.* Nevertheless, one of those rarities in collections of *Lambdotherium,* an almost complete skull, is included.

There is surprisingly little published information on the skull of *Lambdotherium.* The reconstruction in Osborn's (1929, fig. 233) monograph on the titanotheres is based on a maxilla and jugal, a portion of the top of the cranium, the zygomatic process of the squamosal, and a condyle. U.S.N.M. No. 19761, from a locality 12 miles north of Big Piney, Wyo., though somewhat crushed and distorted, in essential details lacks only the basicranium. The rostrum of this skull is broad and the nasals strong and protruding. As noted in *Eotitanops borealis* (Cope) (see Osborn, 1929, fig. 251) the skull is very broad between the orbits, and the postorbital processes are prominent and partially enclose the orbit posteriorly. The most notable difference from *Eotitanops borealis,* in dorsal aspect, is that the sagittal crest extends much farther forward, and the anterior margins of the temporal fossae curve more forward as well as inward from the postorbital processes to meet in the sagittal crest. In *Eotitanops* and later genera the anterior portions of the temporal fossae are widely separated and are divided by a sagittal crest only in their posterior parts. By virtue of this difference the postorbital processes of the frontals are directed backward in *Lambdotherium* instead of forward as in *Eotitanops* and others.

The equine occiput in posterior view is high, narrow, and somewhat rectangular above the mastoid portion, and is directed backward rather than being erect as in Osborn's figure of Gregory's restoration. Two rather prominent vascular foramina are noted in the anteroventral portion of the occiput; apparently the forward of these is between the periotic and squamosal and the posterior and larger between the periotic and exoccipital, somewhat as in horses.

In the absence of the basicranial portion, little of importance, other than the dentition, is observed in the ventral view of the skull. It is noted, however, that the posterior narial opening extends forward between the tooth rows to a point about even with the posterior margin of M^2. Also, the postglenoid process of the squamosal is not nearly so prominent and the circular canal for the audital tube is not so nearly enclosed below by the squamosal from behind.

A study of the dentition together with a revision of the known species of *Lambdotherium* was made by Bonillas (1936) on the basis of materials in the California Institute of Technology from Knight beds between La Barge and Big Piney. Little need be added to his description of the permanent teeth, except perhaps to comment on the character of the so-called mesostyle and other details of P^3 and P^4. The nearly median external style is not in the true position of a mesostyle but appears to be a continuation onto the cingulum of the external rib of the metacone, posterior to the position of the mesostyle between the paracone and metacone seen in the molars. It is weak or absent on these teeth. Also the transverse lophs of P^3 are variable and may or may not exhibit intermediate cuspules. Moreover, Bonillas noted a strong internal cingulum on P^4, but this is variable, as in the molars, and may be discontinuous.

Several milk dentitions are included in the Knight collection which call for some comment. Dp^1 appears to be identical to this tooth in the permanent series and may indeed be the same, although it is in a position immediately anterior to Dp^2 without the diastema of the permanent series. Dp^2 to Dp^4 are, of course, decidedly more progressive than their counterparts in the replacing series. Dp^2 is very much like P^2 except for sharper, better-developed cusps. Dp^3 and particularly Dp^4 are molariform. In Dp^3 the cusp having the position of a protocone, as in other perissodactyles of the Eocene, is not so lingual in position as the hypocone, and the transverse lophs with their accessory cuspules, are not developed. However, the crown of Dp^4 appears to be identical in every respect, except smaller size, to M^1. Both of the posterior upper milk teeth have fully developed mesostyles.

In the lower series Dp_2 is an elongate tooth with a distinct paraconid and metaconid, but scarcely more than a prominent cingulum and a buttresslike rugosity posteroexternal to the metaconid, representing the talonid. The trigonid of Dp_3 is also elongate and the three cusps are almost equally developed; however, no metastylid was noted. The talonid of this tooth is molariform; broad and basined with a well-developed hypoconid and entoconid. Dp_4 is smaller than M_1, but apparently molariform in all respects.

HELALETIDAE

HEPTODON, cf. VENTORUM (Cope)

Remains of *Heptodon* from the upper Knight in the Big Piney–La Barge area are next in abundance to those of horses; however, among the 30-odd specimens none are outstanding or particularly comment-worthy. They consist for the most part of jaw fragments with one to three teeth preserved. One jaw (U.S.N.M. No. 19784), however, is almost entire and although only P_2 and P_3 are preserved the alveolar or root portions of all the remaining teeth from the incisors to M_3 can be seen and over-all proportions determined.

No. 19784 shows a single small alveolus for P_1 immediately anterior to P_2. The presence or absence of P_1 is probably not significant although Seton (1931, p. 47) noted its presence in *Heptodon brownorum* in comparison with other species. The diastema between the canine alveolus and that for P_1 is about 22 mm. The length of P_2 to P_4, inclusive, is about 22.5 mm. and for M_1 to M_3 about 38.5 mm. These proportions are distinctly less than in *Heptodon posticus* or *Heptodon brownorum* and somewhat greater than in *Heptodon calciculus*. The correspondence is closest to *Heptodon ventorum* although measurements of teeth in the type are greater than in most of the Knight specimens. There is some variation in size of teeth between specimens in the collection, but I am inclined to regard them as representing a single species which may well be *H. ventorum*.

Among the specimens collected by Granger and Miller from beds in the vicinity of the type locality of the Knight formation is a fragment of a tapiroid lower jaw (A.M. No. 12840) with P_3, P_4, and the anterior portion of M_1. Like the upper Knight materials from the vicinity of Big Piney and La Barge, the teeth are a little smaller than in the type of *Heptodon ventorum* but apparently not closer to *H. calciculus.* The better development of the entoconid on P_4, moreover, suggests *H. ventorum* rather than *H. calciculus* as represented by their types.

A single lower tooth in the Princeton material, No. 16174, from near Fossil, Wyo., can be almost exactly duplicated by Dp_4 in *Heptodon* material from the upper Green River basin and in American Museum *Heptodon* material from the Wind River basin.

HEPTODON, species

In the New Fork collections are various isolated teeth and tooth portions, including an M_3 which is a little larger than in the upper Knight material referred to *Heptodon ventorum.* The M_3 has about the length and width of this tooth in the type of *Heptodon posticus;* however, on this basis it cannot be clearly distinguished from *H. brownorum.*

HYRACHYIDAE

HYRACHYUS, species

A complete last upper molar and fragments of other teeth represent a species of *Hyrachyus* in the New Fork fauna not far in size from *Hyrachyus agrestis,* or *H. modestus* as revised by Wood, from the Bridger middle Eocene. McGrew (*in* Donovan, 1950, p. 64) recognized the presence of *Hyrachyus* in the New Fork on the basis of tooth fragments collected by J. H. Donovan, a student at the University of Utah, however, in the absence of other, more critical evidence, regarded the beds as of Bridger age. *Hyrachyus* has been found, though rarely, in Lost Cabin beds. The New Fork M^3 measures 20.3 mm. anteroposteriorly by 22.9 mm. in its greatest transverse diameter.

ARTIODACTYLA

DICHOBUNIDAE

DIACODEXIS, near D. SECANS (Cope)

A single specimen, U.S.N.M. No. 19218, from north of Big Piney, consisting of lower jaw portions and including M_1 from both right and left sides, and left M_3, is regarded as belonging to a species of *Diacodexis* close in size to *Diacodexis olseni* Sinclair (1914, pp. 292-293) or *Diacodexis secans* (Cope) (1881a, pp. 187-188). M_1 is the same length as the tooth in *D. secans* or *D. olseni* but is appreciably narrower than in the latter. M_3 in Sinclair's type is not complete so that the length cannot be determined, but its width is also much greater than that in No. 19218. M_3 in *D. secans* is only a little wider and longer. The length and greatest width of M_1 in the Knight specimen are 4.6 and 3.4 mm., respectively. The dimensions for M_3 are 5.5 and 3.7 mm. There is a likelihood that the Knight specimen represents *Diacodexis secans* although it is noted that the apices of the cusps in the type are noticeably closer together transversely, and the entoconid of M_3 is much weaker. Moreover, in the absence of P_4, which is surely distinctive of *D. secans,* no certain assignment can be made.

Sinclair's revision of *Diacodexis* brought some order out of chaos, but left something to be desired in omitting consideration of *Diacodexis nuptus* and *Diacodexis secans.* Also, from a consideration of the measurements of the type of *Diacodexis chacensis* and other material from the San Jose beds, together with a large suite of specimens from the Gray Bull, I am inclined to regard the Gray Bull species as specifically distinct from *Diacodexis chacensis.* The specimen that Sinclair referred to as a paratype of *D. chacensis* did not come from the San Jose and is appreciably smaller than the type, as measured by Cope (1875, p. 15). The position of the type specimen of *D. chacensis* at the upper limits, or distinctly beyond the upper limits of Gray Bull materials, in various measurements, coupled with geographic and horizon differences, would lead one to regard the species as distinct. For this reason I would prefer to revive the oldest Gray Bull name, *Diacodexis metsiacus* (Cope) for these specimens. *Diacodexis brachytomus* (Cope) and *Diacodexis laticuneus* (Cope) are probable synonyms. *Diacodexis robustus* Sinclair from the Gray Bull is apparently valid. *Diacodexis nuptus* (Cope) and *Diacodexis secans* (Cope) are described from the Wind River beds, hence, according to Simpson (1933, pp. 115-116), are from the Lost Cabin horizon. *D. nuptus* is exceedingly small in comparison with Gray Bull materials, and the paraconid in the preserved lower molar is rather well forward in position and slightly less lingual than observed in the Gray Bull species. *D. secans,* on the other hand, has large teeth, and is particularly characterized by the relatively large size of P_4. It is further observed that the molars in *D. secans* have the apices of their cusps relatively closer together transversely than in any other *Diacodexis* material observed. *Diacodexis olseni,* as noted above, is characterized by the relatively greater width of the molars. No data exist on the variation in this respect, nor in the characters of *D. secans*. It is noted that the difference in length of P_4 between *D. secans* and *D. olseni* is a little greater than Sinclair has shown as the variation of the length of this tooth in Gray Bull materials.

DIACODEXIS?, species

Van Houten (1945, p. 458) noted the presence of *Diacodexis* material from the Knight formation in the collections of the American Museum. Two lower jaws are so recorded in their catalog but these could not be found. They were collected by Granger and Miller from vicinity of the type Knight section on Bear Creek, near Knight station. There is no evidence as to the species represented.

BUNOPHORUS, cf. MACROPTERNUS (Cope)

Difficulty was early encountered in attempting to identify, as representing *Bunophorus* or *Wasatchia,* certain materials in the upper Knight or La Barge collection. Review of the dental characters, outlined by Sinclair (1914, pp. 268-276) as distinguishing these two genera, would appear to be resolved into inflation of the lower premolars, the extent to which the paraconid is developed on lower molars, and the form of M_3. The premolar difference is largely one of degree, the presence or absence of a weak or vestigial paraconid is not always significant in other groups, and the form of M_3 is likely variable as in *Diacodexis*. However, the combination of the characters outlined by Sinclair, together with the development of the hypoconulid, which was noted to be more distinctive in those specimens exhibiting a more distinctive paraconid, might justify retention of both genera.

The upper Knight collections include five lower-jaw portions very close to one another in size and form of teeth, and surely represent a single species. The best of these is a right mandibular ramus, U.S.N.M. No. 19210, with P_4 to M_3, inclusive. The teeth in this are moderately worn so that the presence or absence of a paraconid cannot be determined; however, P_4 would appear to be somewhat more inflated than in figures of *Wasatchia.* M_2 and M_3 in No. 19208 are slightly worn and do not appear to have had a paraconid, and M_3 conforms to the description of *Bunophorus* except that the talonid is nearly as wide as trigonid. In No. 19209 P_4 is a little larger and more inflated than in No. 19210, and M_1 shows a very small enamel lake representing the paraconid. M_1 in No. 19207 also shows definite evidence of a paraconid, whereas M_2 does not. However, M_2 in No. 19213 shows a small paraconid but is otherwise not distinctive. Sinclair observed the presence of a small paraconid on M_1 of *Bunophorus macropternus* and a vestige on M_3 but not on M_2. The upper Knight material, though limited, lacks a vestige of this cusp on M_3, but in one instance includes it on M_2. The correspondence of the upper Knight form would appear to be closer to *Bunophorus* than to *Wasatchia* and in size is very near *Bunophorus macropternus.*

In addition to the lower jaws there are two specimens showing upper teeth, believed to be of the same species. One of these, U.S.N.M. No. 19212, includes M^1 and M^2 and the other is an isolated molar, probably M^2. Upper teeth of *Bunophorus* have not previously been described, and as may be anticipated, their resemblance is very close to those figured of *Wasatchia.* The upper Knight superior teeth are relatively little worn and the most striking feature is their extremely bunodont appearance. The cusps are all blunt, nearly circular cones, with but slight buttresses on the anterior and posterior slopes of paracone and metacone, and between the protocone and the two accessory cusps, the protoconule and metaconule. There is no great disparity in size of cusps, although the protocone is slightly larger than the about-equal paracone and metacone. Slightly smaller than the latter two are the approximately equivalent protoconule, metaconule, and hypocone. The hypocone is at the posterolingual extremity of the cingulum, which surrounds all but the lingual surface of the tooth.

HEXACODUS,[21] new genus

Generic characters.—Tooth structure much as in *Sarcolemur* Cope, but P_4 appears more inflated medially with metaconid incipient or weak. Trigonid of lower molars with inner pair of cusps higher than protoconid and anteroposteriorly compressed, but less so than in *Sarcolemur.* Paraconid and metaconid less closely appressed than *Sarcolemur,* and metaconid rather than paraconid the larger and higher. Cross crests of trigonid weak and oblique crest from hypoconid less distinctly developed on posteroexternal slope of metaconid. Hypoconid crescentic and entoconid conical with hypoconulid on posterior cingular shelf, distinct and decidedly posterior to hypoconid and entoconid, as in *Sarcolemur.*

Type species.—Hexacodus pelodes, new species.

---

[21] From Greek ἕξ, six; ἀκή, point; ὀδούς, tooth—with reference to the six cusps, including the hypoconulid, of the lower molars.

HEXACODUS PELODES,[22] new species

Plate 11, figures 1-3

Type.—Left ramus of mandible with P_4 to M_2, inclusive, U.S.N.M. No. 19215.

Horizon and locality.—Upper Knight beds, La Barge fauna, SW¼ sec. 33, T. 32 N., R. 111 W., 12 miles north of Big Piney, Sublette County, Wyo.

Specific characters.—Teeth slightly smaller and relatively a little narrower than in *Sarcolemur pygmaeus.* Other characters not distinguished from those of genus.

Description.—Eleven specimens, all lower-jaw portions or lower teeth, belong to *Hexacodus pelodes.* The material was first thought to represent *Diacodexis,* but upon more critical examination it was found that only one specimen in the upper Knight collections of the upper Green River basin represents *Diacodexis.* The remainder of these smaller dichobunids are recognized to be of a form more closely related to Bridger *Sarcolemur.*

The fourth lower premolar in the type of *H. pelodes* is perhaps a little more rounded or inflated externally than in *S. pygmaeus* but the metaconid, well developed in the latter, is incipient or scarcely more than a flexure or swelling on the lingual side of this tooth in the earlier type. The paraconid as in *Sarcolemur* is prominent and turned sharply inward. On the rather small heel of P_4 in the *H. pelodes* type a distinctly isolated entoconid is observed. Two other specimens of *H. pelodes* exhibit P_4, and in one this tooth is more inflated and the accessory cusps are more obscure. In the other, the tooth is only slightly wider and has the equivalent parastyle, a better-developed metaconid, but apparently no entoconid.

The lower molars of *H. pelodes* are less specialized in the peculiarities of the trigonid noted in *Sarcolemur pygmaeus,* although the talonids are very similar in the two forms. In *S. pygmaeus* it is noted that the arcuate anterior crest of the trigonid may be somewhat higher than the posterior, and the paraconid is set slightly inward and a little higher than metaconid. Both are higher than the protoconid and these differences in height are further emphasized by the manner in which the tooth is worn through occlusion. Moreover, in *Sarcolemur* the metaconid appears to be joined from near its summit to the anterior wing of the crescentic hypoconid. In some third molars the metaconid-

---

[22] From Greek πηλώδης, muddy; with reference to Muddy Creek, where the type specimen was found.

hypoconid crest is more conspicuous than that between the metaconid and protoconid. In *H. pelodes* the paraconid and metaconid, though high and close together, are not so closely appressed as in *Sarcolemur* and the metaconid is a little the larger; however, in wear the metacone may be reduced so that the tooth more closely resembles *Sarcolemur.* The crest from the hypoconid rises on the posterointernal slope of the metaconid, but not so high and with less emphasis.

The talonid of the first two molars, as in *Sarcolemur,* exhibits a crescentic, though high-cusped, hypoconid which likewise does not connect directly with the prominent conical entoconid, but sends a weak spur posteriorly from the horn of the crescent to the hypoconulid which is situated on a prominent posterior ledge or cingulum. The structure of this portion of the tooth is entirely unlike that in *Diacodexis.* In M_3 of *H. pelodes* the hypoconulid is an exaggeration of the condition noted in preceding molars, and with this portion of the heel transversely more constricted than in *Diacodexis.* A central crest extends forward from the hypoconulid to the cleft between the hypoconid and entoconid, much as in *Sarcolemur.*

Discussion.—Hexacodus pelodes would appear to be the first authentic record of the *Sarcolemur* or *Antiacodon* type of dichobunid in the lower Eocene, although species from Wasatchian beds have been referred to this group. Erroneously allocated have been *Antiacodon mentalis* and *Antiacodon crassus.* The first of these is now included in *Hyopsodus,* and the second does not represent this group, as may be inferred from Cope's illustration (1877, pl. 45, fig. 15) and as he later recognized (1884, p. 233), although its correct allocation is not known. A third name, *Sarcolemur bicuspis,* was listed without description by Loomis (1907b, p. 357) in a faunal list of materials collected from the lower levels of Tatman Mountain in the Big Horn basin. The name is a nomen nudem and there may be some doubt as to whether the material which he so designated represented this genus. Simpson (1945, p. 143) has listed *Sarcolemur* as lower Eocene and *Antiacodon* as middle Eocene, and although it seems likely that the letter L, there used for lower Eocene, is a typographical error, a shadow of a doubt persists for the following reason: The type of *Sarcolemur* is *S. furcatus,* the type specimen of which was collected by Cope in 1872 "from the bluffs of the Upper Green River" (1873b, p. 608). That year, according to Cope's account (ibid., p. 545), he traveled up the Green River from about 17 miles above the town of Green River, as far as La Barge Creek, so there is the remote possibility that *S. furcatus* came from the upper Knight near

La Barge Creek. However, much of the material similarly labeled in Cope's collection is Bridger in age and none so far as known is Knight; moreover, the type of *S. furcatus* resembles other Bridger materials rather than *Hexacodus pelodes.*

In all probability *Sarcolemur* is a synonym of *Antiacodon.* Cope originally referred his species to Marsh's genus, but later erected *Sarcolemur* because he felt Marsh's description was inadequate (1877, p. 148). *Antiacodon venustus* Marsh (1872, p. 210) has never been figured, nor the type, so far as I know, compared with that of *Sarcolemur furcatus,* so that the equivalence of these two genera remains in doubt. Nevertheless, the pertinent Bridger materials in the National Museum collections, apparently representing but a single species, are cataloged as *Antiacodon pygmaeus.*

MEASUREMENTS OF TYPE LOWER JAW OF
Hexacodus pelodes, NEW SPECIES, U.S.N.M. NO. 19215

	mm.
Length of P_4 to M_2, incl.	12.8
P_4, anteroposterior diameter: transverse diameter	4.5: 2.8
M_1, anteroposterior diameter: greatest transverse diameter	4.2: 3.0
M_2, " " " " "	4.4: 3.7
Depth of jaw beneath point between M_1 and M_2, lingually	6.7

HEXACODUS UINTENSIS,[23] new species

Plate 11, figure 4

Type.—Left ramus of mandible with M_1 and M_2, Princeton University collection No. 16175.

Horizon and locality.—Knight beds, 100 feet below Green River formation, about 3 miles northwest of Fossil, Uinta County, Wyo.

Description.—Distinctly larger than *Hexacodus pelodes* with trigonid relatively of somewhat greater anteroposterior extent. Paraconid and metaconid more distinctly separated. Talonid much as in *H. pelodes* with hypoconulid on posterior cingulum and distinctly posterior to low divide between hypoconid and entoconid.

Discussion.—This species of *Hexacodus* from the Princeton locality near Fossil is clearly distinct from that of the La Barge fauna, and is somewhat more removed from the middle Eocene *Sarcolemur* in the construction of its lower molars. In this respect it is a trifle more generalized and less removed from the *Diacodexis* type of artiodactyl molar.

---

[23] Named for Uinta County, Wyo.

REFERENCES

Bonillas, Ygnacio.

1936. The dentition of *Lambdotherium*. Journ. Mamm., vol. 17, No. 2, pp. 139-142, figs. 1-3.

Brown, Roland W.

1949. Map showing Paleocene deposits of the Rocky Mountains and plains. Preliminary map of U. S. Geological Survey.

Butler, P. M.

1941. A comparison of the skulls and teeth of the two species of *Hemicentetes*. Journ. Mamm., vol. 22, No. 1, pp. 65-80, figs. 1-11, pl. 1.

1946. The evolution of carnassial dentitions in the mammals. Proc. Zool. Soc. London, vol. 116, pt. 2, pp. 198-220, figs. 1-13.

Colbert, Edwin H.

1942. An edentate from the Oligocene of Wyoming. Notulae Naturae, No. 109, pp. 1-16, figs. 1-3, 1 pl.

Cope, Edward D.

1872a. On *Bathmodon*, an extinct genus of ungulates. Proc. Amer. Philos. Soc., vol. 12, pp. 417-420.

1872b. On a new genus of Pleurodira from the Eocene of Wyoming. Proc. Amer. Philos. Soc., vol. 12, pp. 472-477.

1872c. On the dentition of *Metalophodon*. Proc. Amer. Philos. Soc., vol. 12, pp. 542-545.

1873a. Fourth notice of extinct Vertebrata from the Bridger and Green River Tertiaries. Palaeont. Bull. No. 17, pp. 1-4.

1873b. On the extinct Vertebrata of the Eocene of Wyoming observed by the expedition of 1872, with notes on the geology. 6th Ann. Rep. U. S. Geol. Surv. Terr., pp. 545-649, 6 pls.

1874. Report upon the vertebrate fossils discovered in New Mexico with descriptions of new species. Geogr. Expl. and Surv. West of 100th Meridian (Wheeler). Appendix FF, Ann. Rep. Chief of Engineers, 1874, pp. 1-18.

1875. Systematic catalogue of Vertebrata of the Eocene of New Mexico, collected in 1874. Geogr. Expl. and Surv. West of 100th Meridian (Wheeler), pp. 1-37.

1877. Report upon the extinct Vertebrata obtained in New Mexico by parties of the expedition of 1874. Rep. U. S. Geogr. Surv. West of 100th Meridian (Wheeler), vol. 4, pt. 2, pp. i-iv, 1-370, pls. 22-83.

1880a. The badlands of the Wind River and their fauna. Amer. Nat., vol. 14, pp. 745-748.

1880b. The northern Wastach fauna. Amer. Nat., vol. 14, pp. 908-909.

1881a. On the Vertebrata of the Wind River Eocene beds of Wyoming. U. S. Geol. and Geogr. Surv. Terr. (Hayden), vol. 6, No. 1, art. 8, pp. 183-202.

1881b. On some Mammalia of the lowest Eocene beds of New Mexico. Proc. Amer. Philos. Soc., vol. 19, pp. 484-495.

1882a. Contributions to the history of the Vertebrata of the lower Eocene of Wyoming and New Mexico, made during 1881. I. The fauna of the Wasatch beds of the basin of the Big Horn River. Proc. Amer. Philos. Soc., vol. 20, pp. 139-191, 1 fig.

1882b. Supplement on a new *Meniscotherium* from the Wasatch epoch. Proc. Amer. Philos. Soc., vol. 20, pp. 470-471.

1884. The Vertebrata of the Tertiary formations of the West. Book 1. Rep. U. S. Geol. Surv. Terr. (Hayden), vol. 3, pp. i-xxxiv, 1-1009, figs. 1-38, pls. 1-75a.

DENISON, ROBERT H.

1937. Early lower Eocene mammals from the Wind River basin, Wyoming. Proc. New England Zool. Club, vol. 16, pp. 11-14, fig. 1.

1938. The broad-skulled pseudocreodi. Ann. New York Acad. Sci., vol. 37, art. 3, pp. 163-256, figs. 1-32.

DONOVAN, J. H.

1950. Intertonguing of Green River and Wasatch formations in part of Sublette and Lincoln Counties, Wyoming. Wyoming Geol. Assoc., 5th Ann. Field Conf., Southwest Wyoming Guidebook, pp. 59-67, 2 pls.

DORR, JOHN A., JR.

1952. Early Cenozoic stratigraphy and vertebrate paleontology of the Hoback basin, Wyoming. Bull. Geol. Soc. Amer., vol. 63, pp. 59-94, figs. 1-6, pls. 1-7.

DOUGLASS, EARLE.

1905. The Tertiary of Montana. Mem. Carnegie Mus., vol. 2, No. 5, pp. 203-224, pl. 22.

EARLE, CHARLES.

1892. Revision of the species of *Coryphodon*. Bull. Amer. Mus. Nat. Hist., vol. 4, No. 1, pp. 149-166, figs. 1-2.

GAZIN, C. LEWIS.

1942. Fossil Mammalia from the Almy formation in western Wyoming. Journ. Washington Acad. Sci., vol. 32, No. 7, pp. 217-220, figs. 1-2.

1949. A leptictid insectivore from the middle Eocene Bridger formation of Wyoming. Journ. Washington Acad. Sci., vol. 39, No. 7, pp. 220-223, fig. 1.

GRANGER, WALTER.

1908. A revision of the American Eocene horses. Bull. Amer. Mus. Nat. Hist., vol. 24, art. 15, pp. 221-264, figs. 1-5, pls. 15-18.

1910. Tertiary faunal horizons in the Wind River basin, Wyoming, with descriptions of new Eocene mammals. Bull. Amer. Mus. Nat. Hist., vol. 28, art. 21, pp. 235-251, figs. 1-6, pls. 20-23, 1 map.

1914. On the names of lower Eocene faunal horizons of Wyoming and New Mexico. Bull. Amer. Mus. Nat. Hist., vol. 33, art. 15, pp. 201-207.

1915. A revision of the lower Wasatch and Wind River faunas. Pt. 3—Order Condylarthra. Families Phenacodontidae and Meniscotheriidae. Bull. Amer. Mus. Nat. Hist., vol. 34, art. 10, pp. 329-361, figs. 1-18.

GRANGER, WALTER, and GREGORY, WILLIAM K.

1917. A revision of the Eocene Primates of the genus *Notharctus*. Bull. Amer. Mus. Nat. Hist., vol. 37, art. 34, pp. 841-859, pls. 103-107.

GREGORY, WILLIAM K.

1910. The orders of mammals. Bull. Amer. Mus. Nat. Hist., vol. 27, pp. 1-524, figs. 1-32.

HAYDEN, FERDINAND V.

1869. Preliminary report (3d ann.) of the U. S. Geological Survey of Colorado and New Mexico, pp. 91-92.

JEPSEN, GLENN L.

1930. New vertebrate fossils from the lower Eocene of the Bighorn basin, Wyoming. Proc. Amer. Philos. Soc., vol. 69, No. 4, pp. 117-131, pls. 1-4.

1932. *Tubulodon taylori,* a Wind River Eocene tubulidentate from Wyoming. Proc. Amer. Philos. Soc., vol. 71, No. 5, pp. 255-274, 1. pl.

KING, CLARENCE.

1876. Atlas, maps 1, 2. U. S. Geol. Expl. 40th Par.

LOOMIS, FREDERIC B.

1905. The Hyopsodidae of the Wasatch and Wind River basins. Amer. Journ. Sci., vol. 19, pp. 416-424, figs. 1-8.

1906. Wasatch and Wind River Primates. Amer. Journ. Sci., vol. 21, pp. 277-285, figs. 1-8.

1907a. Wasatch and Wind River rodents. Amer. Journ. Sci., vol. 23, pp. 123-130, figs. 1-7.

1907b. Origin of the Wasatch deposits. Amer. Journ. Sci., vol. 23, pp. 356-364, figs. 1-3.

MARSH, OTHNIEL C.

1872. Preliminary description of new Tertiary mammals. Amer. Journ. Sci., vol. 4, pp. 122-128, 202-224.

1876. Notice of new Tertiary mammals. Amer. Journ. Sci., vol. 12, pp. 401-404.

1877. Principal characters of the Coryphodontidae. Amer. Journ. Sci., vol. 14, pp. 81-85, pl. 4.

1884. Dinocerata. A monograph of an extinct order of gigantic mammals. Monogr. U. S. Geol. Surv., vol. 10, pp. i-xviii, 1-237, figs. 1-200, pls. 1-56.

1892. A new order of extinct Eocene mammals (Mesodactyla). Amer. Journ. Sci., vol. 43, pp. 445-449, figs. 1-2.

1893. Restoration of *Coryphodon.* Amer. Journ. Sci., vol. 46, pp. 321-326, fig. 1, pls. 5-6.

1897. The Stylinodontia, a suborder of Eocene edentates. Amer. Journ. Sci., vol. 3, pp. 137-146, figs. 1-9.

MATTHEW, WILLIAM D.

1899. A provisional classification of the fresh-water Tertiary of the West. Bull. Amer. Mus. Nat. Hist., vol. 12, art. 3, pp. 19-75.

1910. On the osteology and relationships of *Paramys,* and the affinities of the Ischyromyidae. Bull. Amer. Mus. Nat. Hist., vol. 28, art. 6, pp. 43-71, figs. 1-19.

1915a. A revision of the lower Eocene Wasatch and Wind River faunas. Pt. 1. Order Ferae (Carnivora). Suborder Creodonta. Bull. Amer. Mus. Nat. Hist., vol. 34, art. 1, pp. 1-103, figs. 1-87.

1915b. A revision of the lower Eocene Wasatch and Wind River faunas. Pt. 2. Order Condylarthra, family Hyopsodontidae. Bull. Amer. Mus. Nat. Hist., vol. 34, art. 9, pp. 311-328, figs. 1-10.

1915c. A revision of the lower Eocene Wasatch and Wind River faunas. Pt. 4. Entelonychia, Primates, Insectivora (part). Bull. Amer. Mus. Nat. Hist., vol. 34, art. 14, pp. 429-483, figs. 1-52, pl. 15.

1918. A revision of the lower Eocene Wasatch and Wind River faunas. Pt. 5. Insectivora (cont.), Glires, Edentata. Bull. Amer. Mus. Nat. Hist., vol. 38, pp. 565-657, figs. 1-68.

1920. A new genus of rodents from the middle Eocene. Journ. Mamm., vol. 1, No. 4, pp. 168-169.

1937. Paleocene faunas of the San Juan basin, New Mexico. Trans. Amer. Philos. Soc., n.s., vol. 30, pp. i-viii, 1-510, figs. 1-85, pls. 1-65.

McGrew, Paul O.

1950. Tertiary vertebrate fossils of the Green River basin. Wyoming Geol. Assoc., 5th Ann. Field Conf., Southwest Wyoming Guidebook, pp. 68-74, 2 figs. and chart.

1951. Tertiary stratigraphy and paleontology of south-central Wyoming. Wyoming Geol. Assoc., 6th Ann. Field Conf., South-central Wyoming Guidebook, pp. 54-57, 1 pl., 1 chart.

Nace, Raymond L.

1936. Summary of the late Cretaceous and early Tertiary stratigraphy of Wyoming. Geol. Surv. Wyoming Bull. 26, pp. 1-271.

1939. Geology of the northwest part of the Red Desert, Sweetwater and Fremont Counties, Wyoming. Geol. Surv. Wyoming Bull. 27, pp. 1-51, 6 figs., 3 pls.

Nightingale, William T.

1930. Geology of Vermilion Creek gas area in southwest Wyoming and northwest Colorado. Bull. Amer. Assoc. Petrol. Geol., vol. 14, No. 8, pp. 1013-1040, figs. 1-5, 2 tables.

Osborn, Henry F.

1898. Evolution of the Amblypoda, Part 1. Taligrada and Pantodonta. Bull. Amer. Mus. Nat. Hist., vol. 10, art. 11, pp. 169-218, figs. 1-29.

1902. American Eocene primates, and the supposed rodent family Mixodectidae. Bull. Amer. Mus. Nat. Hist., vol. 16, art. 17, pp. 169-214, figs. 1-40.

1904. An armadillo from the middle Eocene (Bridger) of North America. Bull. Amer. Mus. Nat. Hist., vol. 20, pp. 163-165.

1929. The titanotheres of ancient Wyoming, Dakota, and Nebraska. U. S. Geol. Surv. Monogr. 55, vols. 1 and 2, pp. i-xxiv (1), i-xi (2), 1-953, figs. 1-797, pls. 1-236.

Patterson, Bryan.

1949. Rates of evolution in taeniodonts. *In* Genetics, Paleontology and Evolution, No. 13, pp. 243-278, figs. 1-7. Princeton.

Schultz, Alfred R.

1914. Geology and geography of a portion of Lincoln County, Wyoming. U. S. Geol. Surv. Bull. 543, pp. 1-141, figs. 1-8, pls. 1-11.

Seton, Henry.

1931. A new *Heptodon* from the Wind River of Wyoming. Proc. New England Zool. Club, vol. 12, pp. 45-48.

1940. Two new primates from the lower Eocene of Wyoming. Proc. New England Zool. Club, vol. 18, pp. 39-42, pl. 8.

Simpson, George G.
1927. A North American Oligocene edentate. Ann. Carnegie Mus., vol. 17, No. 2, pp. 283-298, pl. 24.
1928. American Eocene didelphids. Amer. Mus. Nov., No. 307, pp. 1-7, figs. 1-5.
1929. A new Paleocene uintathere and molar evolution in the Amblypoda. Amer. Mus. Nov., No. 387, pp. 1-9, figs. 1-9.
1931. *Metacheiromys* and the Edentata. Bull. Amer. Mus. Nat. Hist., vol. 59, pp. 295-381, figs. 1-23.
1933. Glossary and correlation charts of North American Tertiary mammal-bearing formations. Bull. Amer. Mus. Nat. Hist., vol. 67, art. 3, pp. 79-121, figs. 1-8.
1937. Notes on the Clark Fork, upper Paleocene, fauna. Amer. Mus. Nov., No. 954, pp. 1-24, figs. 1-6.
1945. The principles of classification and a classification of mammals. Bull. Amer. Mus. Nat. Hist., vol. 85, pp. i-xvi, 1-350.

Sinclair, William J.
1914. A revision of the bunodont Artiodactyla of the middle and lower Eocene of North America. Bull. Amer. Mus. Nat. Hist., vol. 33, art. 21, pp. 267-295, figs. 1-28.

Sinclair, William J., and Granger, Walter.
1911. Eocene and Oligocene of the Wind River and Big Horn basins. Bull. Amer. Mus. Nat. Hist., vol. 30, art. 7, pp. 83-117, figs. 1-4, pls. 4-9.
1912. Notes on Tertiary deposits of the Big Horn basin. Bull. Amer. Mus. Nat. Hist., vol. 31, art. 5, pp. 57-67, figs. 1-2, pls. 5-6.

Thorpe, Malcolm R.
1934. *Meniscotherium robustum* sp. nov., and a discussion of *Hyracops socialis* Marsh. Amer. Journ. Sci., vol. 27, pp. 401-409, figs. 1-6.

Troxell, Edward L.
1923a. The Eocene rodents *Sciuravus* and *Tillomys*. Amer. Journ. Sci., vol. 5, pp. 383-396, figs. 1-23.
1923b. A new marsupial. Amer. Journ. Sci., vol. 5, pp. 507-510, figs. 1-4.

Van Houten, Franklyn B.
1945. Review of latest Paleocene and early Eocene mammalian faunas. Journ. Paleont., vol. 19, No. 5, pp. 421-461, 1 fig., 4 tables.

Veatch, Arthur C.
1907. Geography and geology of a portion of southwestern Wyoming. U. S. Geol. Surv. Prof. Pap. No. 56, pp. i-vi, 1-178, figs. 1-9, pls. 1-26.

Weber, Max.
1904. Die Säugetiere, pp. i-xi, 1-866, figs. 1-567. Jena.

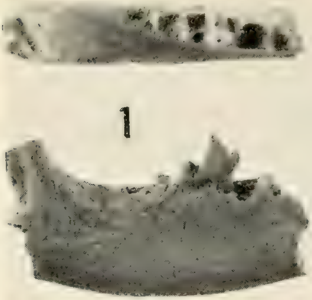
White, Theodore E.
1952. Preliminary analysis of the vertebrate fossil fauna of the Boysen Reservoir area. Proc. U. S. Nat. Mus., vol. 102, pp. 185-207, figs. 75-79, 1 map.

Wilson, Robert W.
1938. Review of some rodent genera from the Bridger Eocene. Amer. Journ. Sci., vol. 35, pp. 123-137, figs. 1-4.
1949. Early Tertiary rodents of North America. Carnegie Inst. Washington Publ. 584, pp. 67-164, figs. 1-13.

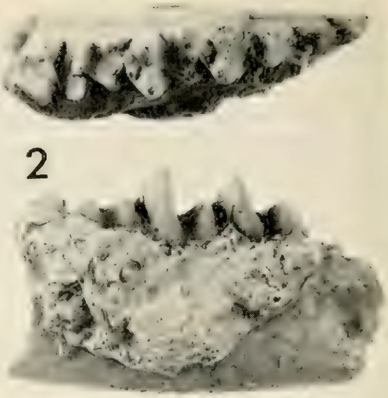
Wood, Horace E., 2d, et al.
1941. Nomenclature and correlation of the North American Tertiary. Bull. Geol. Soc. Amer., vol. 52, pp. 1-48, pl. 1.

Wortman, Jacob L.
1903. Studies of Eocene Mammalia in the Marsh collection, Peabody Museum. Part II. Primates. Suborder Cheiromyoidea. Amer. Journ. Sci., vol. 16, pp. 345-368, figs. 105-119, pls. 11-12.

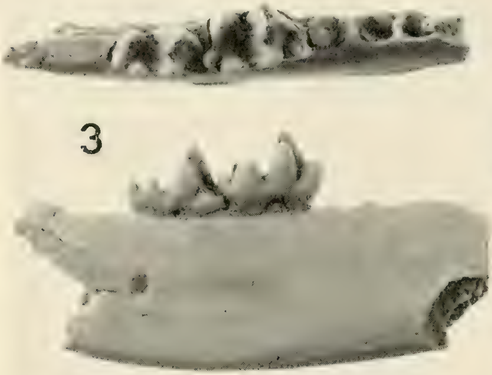
PLATES



1

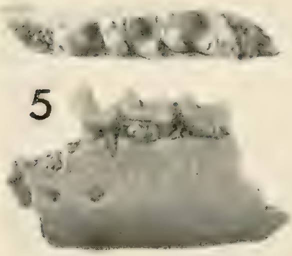


2

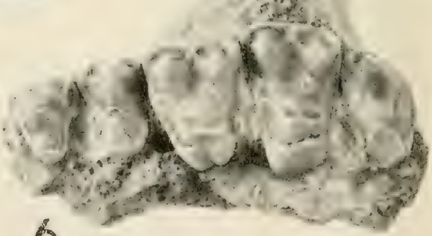


3

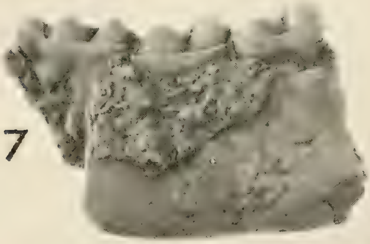
4



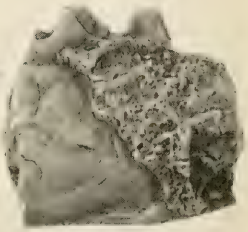
5



6



7



8

MARSUPIALS, INSECTIVORE, AND PRIMATES FROM THE KNIGHT LOWER EOCENE

Plate 1

Fig. 1. *Peratherium chesteri,* new species: Right ramus of mandible (U.S.N.M. No. 19199), type specimen, occlusal and lateral views. Approximately six times natural size.

Fig. 2. *Diacodon pineyensis,* new species: Left ramus of mandible (U.S.N.M. No. 19204), type specimen, occlusal and lateral views. Approximately four times natural size.

Figs. 3 and 4. *Peratherium edwardi,* new species: 3, Left ramus of mandible (U.S.N.M. No. 19200), type specimen, occlusal and lingual views; 4, left maxilla (U.S.N.M. No. 19206), occlusal view. Approximately five times natural size.

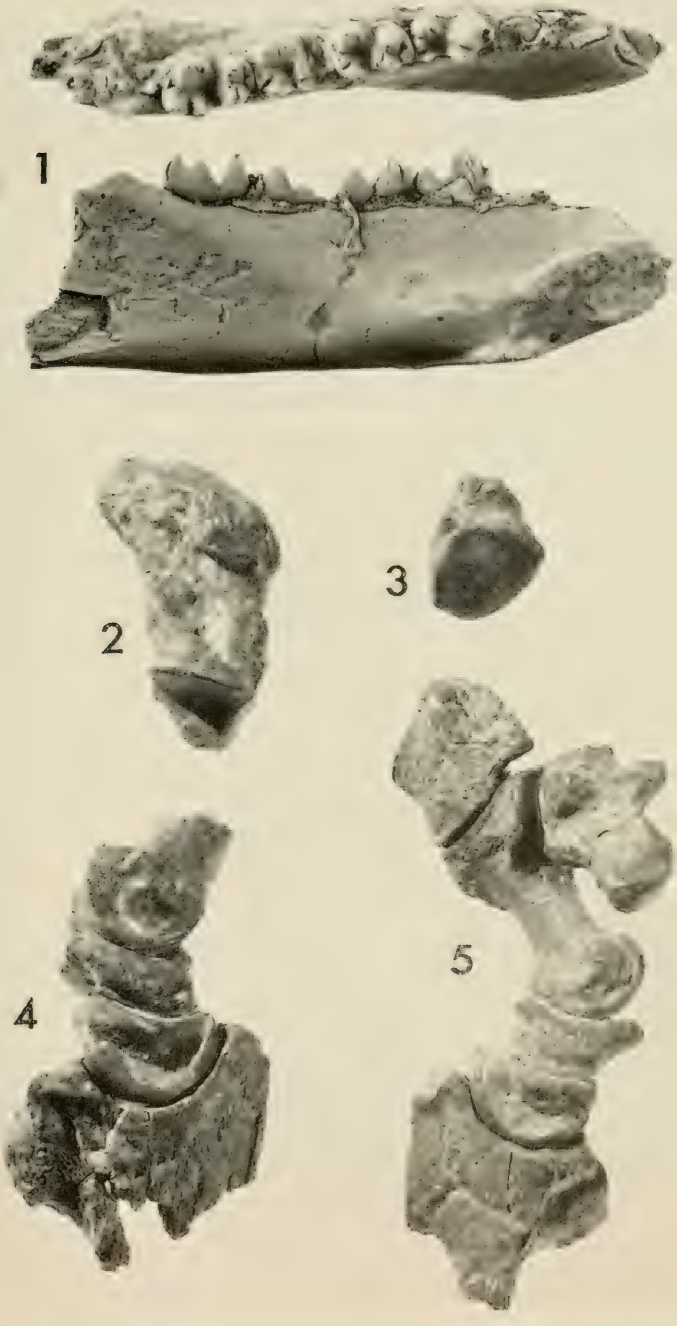
Fig. 5. *Paratetonius? sublettensis,* new species: Left ramus of mandible (U.S.N.M. No. 19205), type specimen, occlusal and lateral views. Approximately five times natural size.

Figs. 6-8. *Notharctus limosus,* new species: 6, Left maxilla (U.S.N.M. No. 19293), occlusal view; 7, right ramus of mandible (U.S.N.M. No. 19294), type specimen, lateral view; 8, left ramus of mandible (U.S.N.M. No. 19294), type specimen, lingual view. Approximately three times natural size.

PLATE 2

FIG. 1. *Cynodontomys knightensis,* new species: Left ramus of mandible (U.S.N.M. No. 19314), type specimen, occlusal and lingual views. Approximately three times natural size.

FIGS. 2-5. Undetermined stylinodont: Fore foot (U.S.N.M. No. 18425); 2, pisiform, lateral view; 3, scaphoid, proximal view; 4, 3d(?) digit, inner view; 5, fourth digit with unciform and fifth metacarpal, lateral view. Natural size.



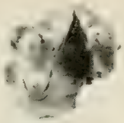
INSECTIVORE AND TAENIONDONT FROM THE KNIGHT LOWER EOCENE

TAENIODONT FOOT FROM THE KNIGHT LOWER EOCENE

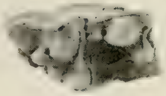
Articulated right hind foot of undetermined stylinodont (U.S.N.M. No. 18425), anteromedial view. Internal cuneiform and distal phalanx of 2d digit partially restored from left foot. A portion of the proximal extremity of second metatarsal not represented. Approximately four-fifths natural siz.

TAENIODONT FOOT FROM THE KNIGHT LOWER EOCENE

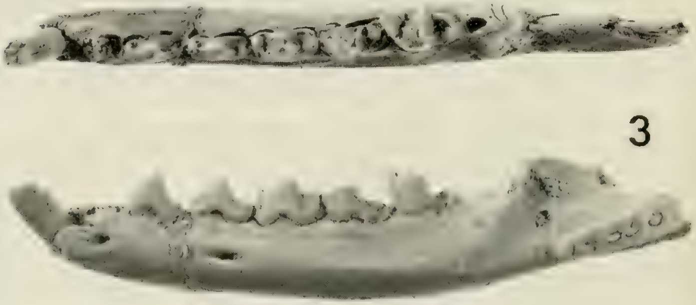
Articulated right hind foot of undetermined stylinodont (U.S.N.M. No. 18425), anterolateral view. Fifth metatarsal and distal phalanx of second digit partially restored from left foot. Approximately four-fifths natural size.



1



2



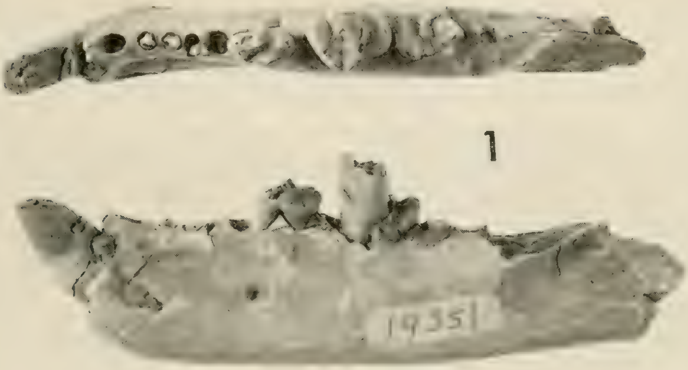
3

4

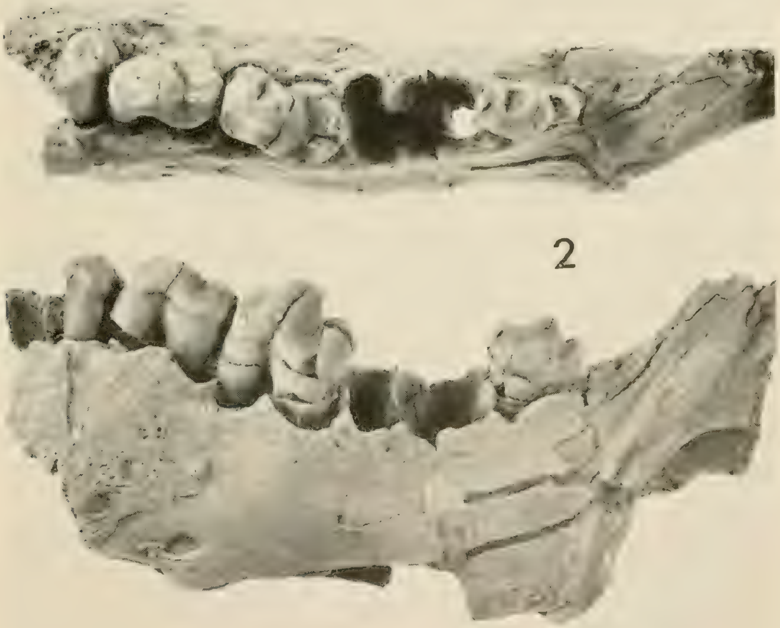
CREODONTS FROM THE KNIGHT LOWER EOCENE

FIGS. 1-3. *Prolimnocyon elisabethae,* new species: 1, Left maxilla (U.S.N.M. No. 19348), occlusal view of M^1 and M^2; 2, right maxilla (U.S.N.M. No. 19348), occlusal view of P^4 and M^1; 3, left ramus mandible (U.S.N.M. No. 19350), type specimen, occlusal and lateral views. Approximately one and one-half natural size.

FIG. 4. *Vulpavus asius,* new species: Left ramus of mandible (U.S.N.M. No. 19337), type specimen, occlusal and lateral views. Approximately one and one-half natural size.



1



2

CREODONTS FROM THE KNIGHT LOWER EOCENE

FIG. 1. *Uintacyon asodes,* new species: Left ramus of mandible (U.S.N.M. No. 19351), type specimen, occlusal and lateral views. Approximately one and one-half natural size.

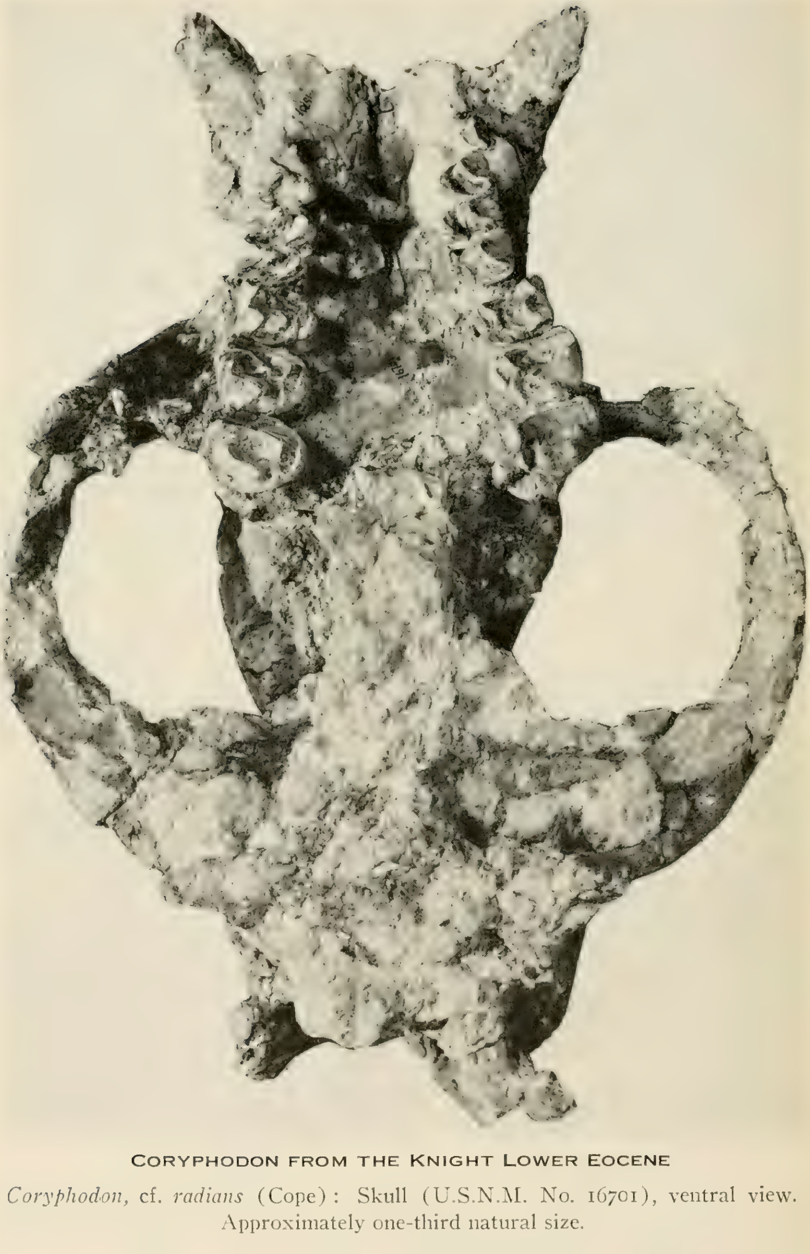
FIG. 2. *Ambloctonus major* Denison: Left ramus of mandible (P. U. No. 14720), occlusal and lateral views. Natural size.

MENISCOTHERIUM FROM THE KNIGHT LOWER EOCENE

Meniscotherium robustum Thorpe: Skull and mandible (U.S.N.M. No. 18283), dorsal and lateral views. Upper, approximately three-fourths natural size; lower, two-thirds.

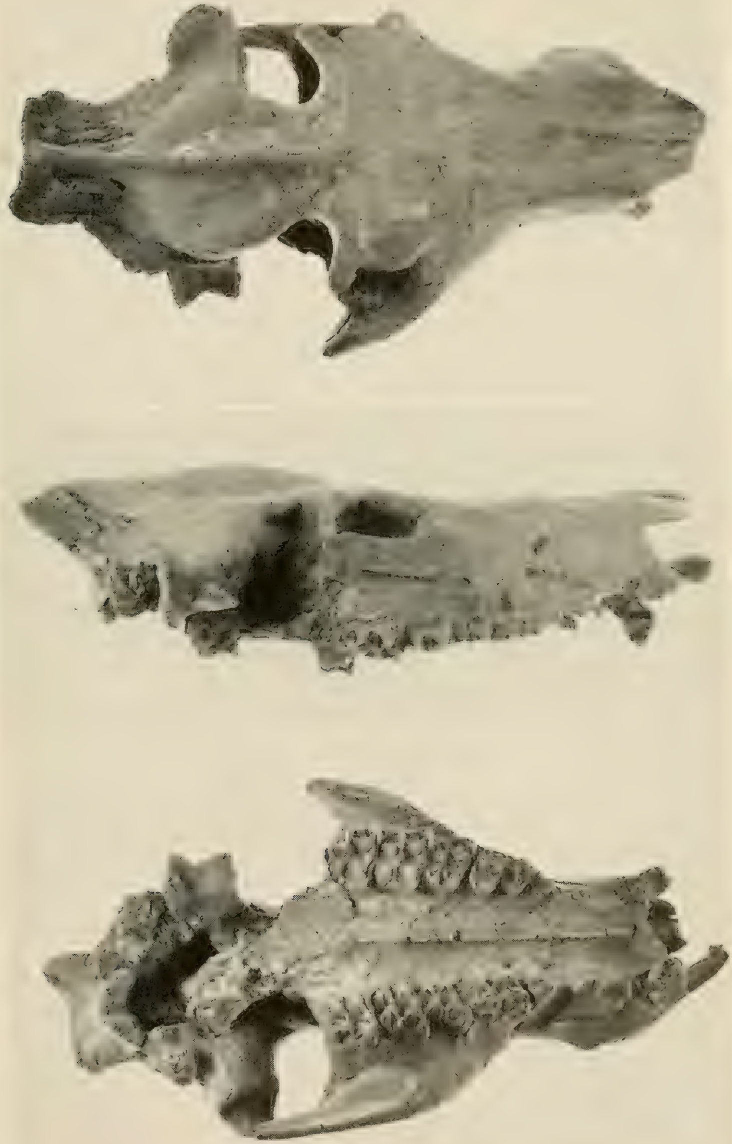
MENISCOTHERIUM FROM THE KNIGHT LOWER EOCENE

Meniscotherium robustum Thorpe: Above, skull and mandible (U.S.N.M. No. 19505), lateral view; below, skull (U.S.N.M. No. 18260), ventral view. Approximately three-fourths natural size.



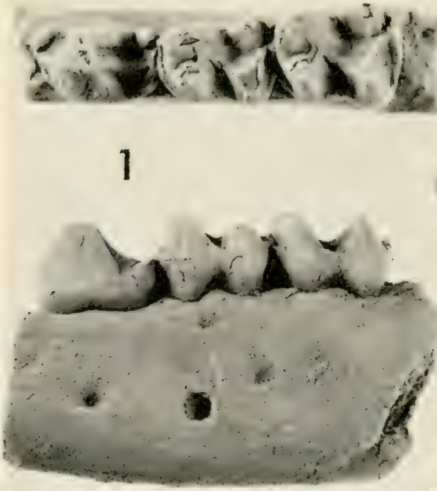
CORYPHODON FROM THE KNIGHT LOWER EOCENE

Coryphodon, cf. *radians* (Cope): Skull (U.S.N.M. No. 16701), ventral view. Approximately one-third natural size.



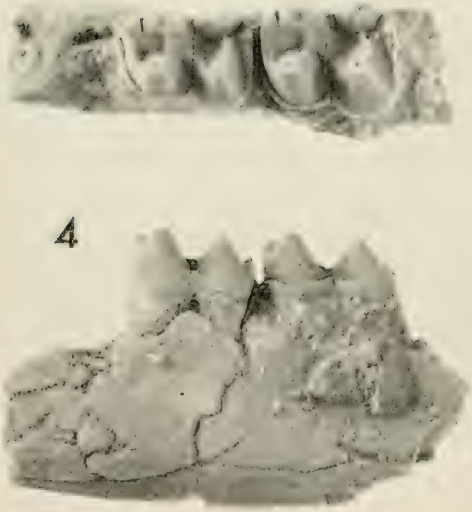
LAMBDOTHERIUM FROM THE KNIGHT LOWER EOCENE

Lambdotherium popoagicum Cope: Skull (U.S.N.M. No. 19761), dorsal, lateral and ventral views. Approximately one-half natural size.

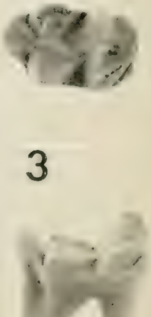


1

2



4



3

Artiodactyles from the Knight Lower Eocene

PLATE 11

FIGS. 1-3. *Hexacodus pelodes,* new genus and species: 1, Left ramus of mandible with P_4—M_2 (U.S.N.M. No. 19215), type specimen, occlusal and lateral views; 2, right ramus of mandible with M_3 (U.S.N.M. No. 19217), occlusal and lateral views; 3, right M_3 (U.S.N.M. No. 19219), occlusal and lateral views. Approximately four times natural size.

FIG. 4. *Hexacodus uintensis,* new species: Left ramus of mandible with M_1-M_2 (P.U. No. 16175), type specimen, occlusal and lateral views. Approximately four times natural size.