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THE LIZARD GENUS *IGUANA* IN THE LESSER ANTILLES

JAMES D. LAZELL, JR.*

ABSTRACT. All Lesser Antillean material available of *Iguana iguana* and *Iguana delicatissima* has been examined and compared, within the islands, and to material from all over the range of the genus. The two species are best distinguished by the presence and size of the subtympanic plate. Both species are monotypic. The name *"rhinolopha"* applies to a polytopic, polyphyletic grade. *I. delicatissima* occurs only in the Lesser Antilles; *I. iguana* ranges past it, northward to the Virgin Islands. Clines in variation in *I. iguana* indicate this species is native to the islands where it now occurs; it was not introduced, as suggested by previous authors. Both species are abundantly sympatric in Les Iles des Saintes; there is no evidence that one displaces the other. A large body of anecdotal information on the life styles of iguanas has been condensed from field notes spanning nearly ten years. Habitat destruction by man directly threatens many populations of both species. Immediate steps to protect them on islands like Antigua and St. Croix should be taken.

> *The iguana is a sort of quadruped serpent, very frightful to look at but very good to eat. . . . There are few men who have seen it alive who dare to eat it, except those in that land who are used to that fright and even greater ones.* Oviedo (1526)

During nearly a decade of herpetological investigation of the Lesser Antilles, I collected many specimens of and data on iguanas. All of the currently recognized forms occur there. All of my specimens are in the Museum of Comparative Zoology (MCZ), which now has the bulk of the museum specimens of the Lesser Antillean endemic, *Iguana delicatissima*. In addition, I have examined specimens of the Albert Schwartz Field Series (ASFS) and the Philadelphia Academy of Natural Sciences (PANS). I am indebted to the curators of these collections.

IGUANA LAURENTI

Iguana Laurenti (1768: 47).
Hypsilophus Wagler (1830: 147).
Amblyrhynchus Wagler (1830: 148) (*non* Bell, 1825).
Type-species.—Lacerta iguana Linnaeus (1758), by tautonymy.

Definition. Iguanid lizards with femoral pores; a pendulous, longitudinal dewlap; a dorsal crest consisting of single, elongate scales; ilial shaft broad, hardly tapering, posteriorly blunt, inclining smoothly anteriorly to form the dorsal surface of a heavy anterior iliac process; a large secondary coracoid fenestra; basisphenoid greatly expanded laterally behind basipterygoid processes; a low finlike process above neural arch of no more than six anterior caudal vertebrae.

Remarks. Savage (1958) distinguished *Iguana, Cyclura, Brachylophus, Ctenosaura, Conolophus, Amblyrhynchus, Dipsosaurus,* and *Sauromalus* from other New World iguanid lizards, and referred to them informally as "iguanines." This is nearly the same as Boulenger's (1890) "iguanina."

In *Dipsosaurus* and *Sauromalus* the ilial shaft tapers abruptly posteriorly and the

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* Massachusetts Audubon Society, Lincoln, Mass. 01773

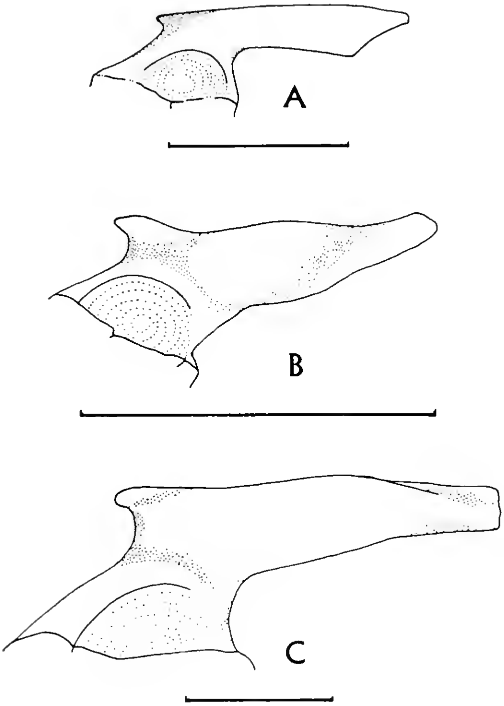

Figure 1. The ilium in three kinds of Iguanidae: (A) *Sauromalus obesus*, UIMNH 33236; (B) *Dipsosaura dorsalis*, UIMNH 33235; and (C) *Iguana delicatissima*, MCZ 82305. The line equals one centimeter in each example.

anterior iliac process is rather weakly developed (see Fig. 1).

In *Ctenosaura, Conolophus,* and *Amblyrhynchus,* the basisphenoid is constricted behind the basipterygoid processes (see Etheridge, 1964: 68, for details and quantification).

Brachylophus and *Cyclura* are very close to *Iguana.* Etheridge (*in litt.*) has provided the following distinctions: *Brachylophus* has no secondary coracoid fenestra; *Cyclura* has high, finlike processes above the neural arches of all the caudal vertebrae. I question the value of these generic distinctions.

Boulenger (1885) recognized two species of *Iguana: tuberculata* and *delicatissima,* both of Laurenti (1768); he also recognized *rhinolopha* Wiegmann (1834) as a variety of *tuberculata.* Dunn (1934) essentially agreed. He placed *Iguana iguana* (=*tuberculata*) under its correct name, maintained *I. delicatissima* as a distinct species, and *I. i. rhinolopha* as a subspecies of *I. iguana.* Dunn's remarks on the distributions of the three forms are confused and contradictory, but his classification has remained standard; there are only two species in the genus.

The allocation of each of the names is not clear from the descriptions given by Linnaeus (1758) and Laurenti (1768), respectively, but Boulenger's (1885) allocations have never been challenged to my knowledge, and are accepted here.

The type locality for the two species given by both their authors is *Indiis;* this is properly translated as "The Indies" (not "India," *cf.* Cuvier, 1829), and is thus quite correct. Both species form a conspicuous part of the fauna of the Lesser Antilles. The two species are extremely similar (see *Comparisons,* below). Many supposed distinctions between them have been noted by various authors, but only one external character—the presence or comparative size of the subtympanic plate—consistently separates the two species when large numbers of both are compared. Dunn (1934) provides photographs of the sides of the heads of two examples which show clearly the magnitude of the distinction in typical specimens. Two less typical examples are shown in Figure 2.

Not only are the two species very similar in morphological detail, but both occupy a wide range of habitats, from wet forest to the most arid and desolate cays, and both seem basically identical in diet and habits. It should not seem remarkable, considering their similarity, that the two species occupy nearly mutually exclusive ranges, and are definitely known to occur together only in the Guadeloupéen Archipelago. However, when one considers the nature of their sympatry in detail, against the background of what we know and theorize about niche segregation and inter-

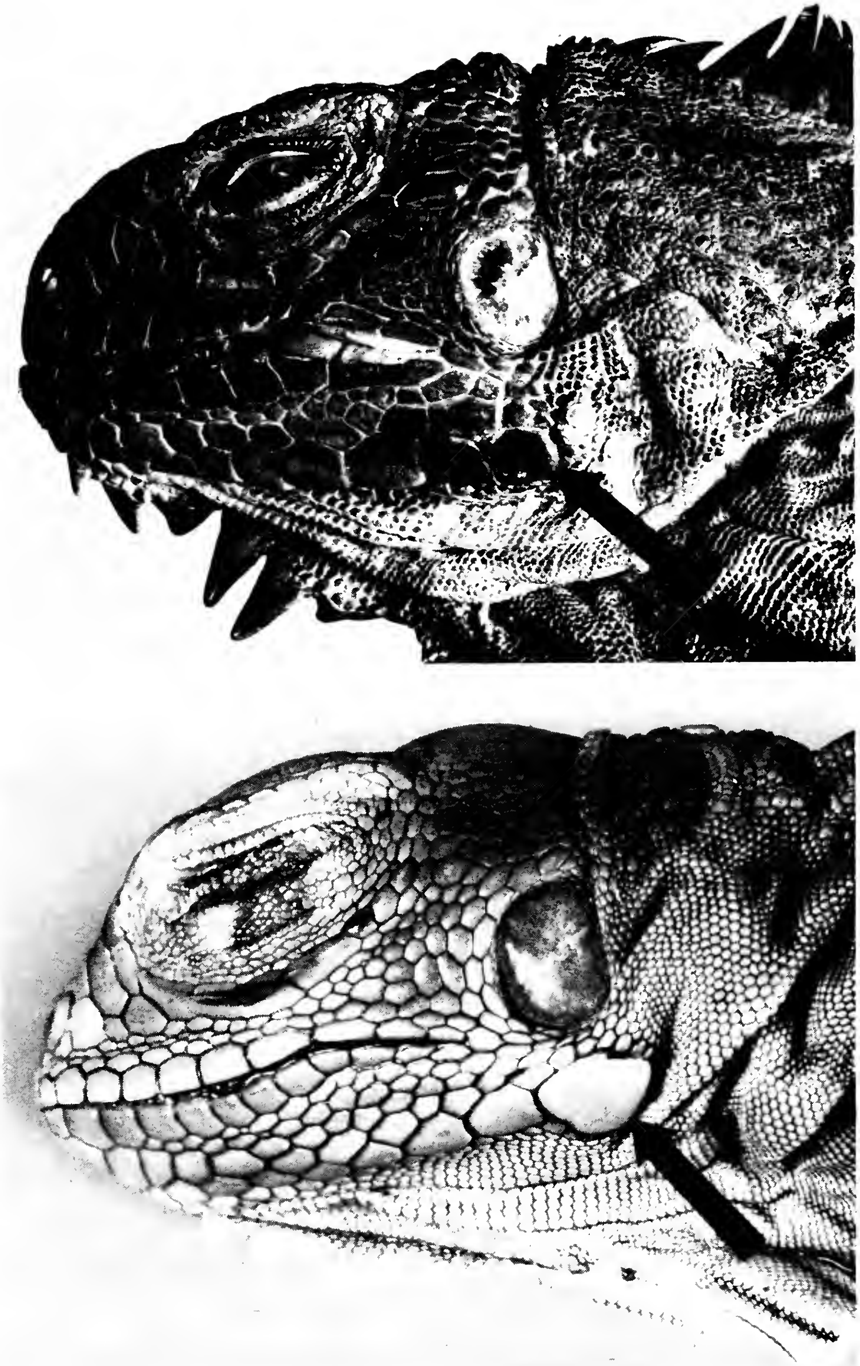

Figure 2. Heads of two species of *Iguana*: above, *I. delicatissima*, MCZ 10969, Terre de Haut, Les Iles des Saintes; below, *I. iguana*, MCZ 82908, Grande Anse, St. Lucia. An arrow indicates the subtympanic plate. Note also the gular spikes and tubercular nape scales of each specimen. Photos by Ross Harris.

species competition, it becomes strange indeed.

The Guadeloupéen Archipelago is composed of three banks of islands. The largest, the Guadeloupe Bank, harbors both species. *I. iguana* occurs along the extremely dry leeward coast of the island of La Guadeloupe proper, and is especially abundant on the adjacent, arid little Iles de Pigeon. *I. delicatissima* occurs in the Bois Eusebe of eastern Grande Terre, and is especially abundant on the adjacent island of La Desirade; this area is only slightly less dry than the area occupied by *I. iguana.* The many other small islands of that bank, like Ilet-a-Kahouanne, Ilet-a-Fajou, and Les Iles de la Petite Terre, simply have no iguanas. Similarly, the Marie Galante Bank, the second largest, has never been known to support any iguanas.

The third bank is the smallest, and has five small islets and a few rock cays on it. It has a seemingly depauperate reptile fauna, in keeping with the small size of its land areas. It lacks teiid lizards, boid and viperid snakes, and has but one colubrid snake (*Alsophis*); it shares the Guadeloupéen *Anolis marmoratus* (and has two races of that species); it has the usual complement of geckos, and one skink. Nevertheless, to this small bank of cays, known as Les Iles des Saintes, must go undisputed the title of the *Iguana* capitol of the world.

Les Iles des Saintes are rather dry; what little ecological diversity they have is totally overshadowed by the larger islands immediately to the north and south, La Guadeloupe and Dominica. Les Iles des Saintes are infested with dogs, cats, pigs, goats, and people. The people not only eat iguanas, but slaughter them in large numbers, crudely stuff them, and sell them to the tourists in the cities of the Guadeloupéen mainland. For all that, Les Iles des Saintes are infested with iguanas, too. Les Iles des Saintes have both species of iguanas. They have the biggest, the smallest, the most interesting, and by far the most iguanas I have ever seen.

Iguanas of either species may, seemingly, be amazingly wild and wary or spectacularly tame and unconcerned; I have been unable to correlate either extreme with habitat, hunting pressures, time of day, or anything else. Perhaps the most arduous day of my life was spent on the tiny Iles de Pigeon: uninhabited, iguana-infested cays off the leeward coast of La Guadeloupe. Just securing a dead specimen of *I. iguana* with a rifle there was an ordeal.

In the town of Terre de Haut, on the island of Terre de Haut, Les Iles des Saintes, I have walked right up to an *Iguana iguana* and, while whistling, grabbed it with my bare hands.

On the uninhabited Ile Fourchue, between St. Martin and St. Barts, I was merely sitting on a rock observing the antics of a dozen or more *I. delicatissima,* when a large female walked up to me, bobbed several times, and, eliciting no response from me, clambered up my leg to scrutinize me more closely. She was rewarded with the catalogue entry of MCZ 75831.

The first *Iguana* ever collected on the Antigua Bank is a large female *delicatissima,* MCZ 82308, that I succeeded in catching bare-handed. It was the only one of a dozen seen that day that I could closely approach.

In the extremely precipitous terrain between Grande Riviere and Cap St. Martin, on the north coast of Martinique, I have seen many *I. delicatissima.* I never succeeded in getting a specimen, however, owing to the very shy nature of the animals there, and the habitat. Even if I had been able to shoot one, the dense vegetation and sheer cliffs would have negated my ability to retrieve the carcass.

The trick of whistling at large iguanines has long been known; Lewis (*in* Grant, 1940), for example, mentions taking *Cyclura* with this aid. Both species of *Iguana* often fall for this; usually a con-

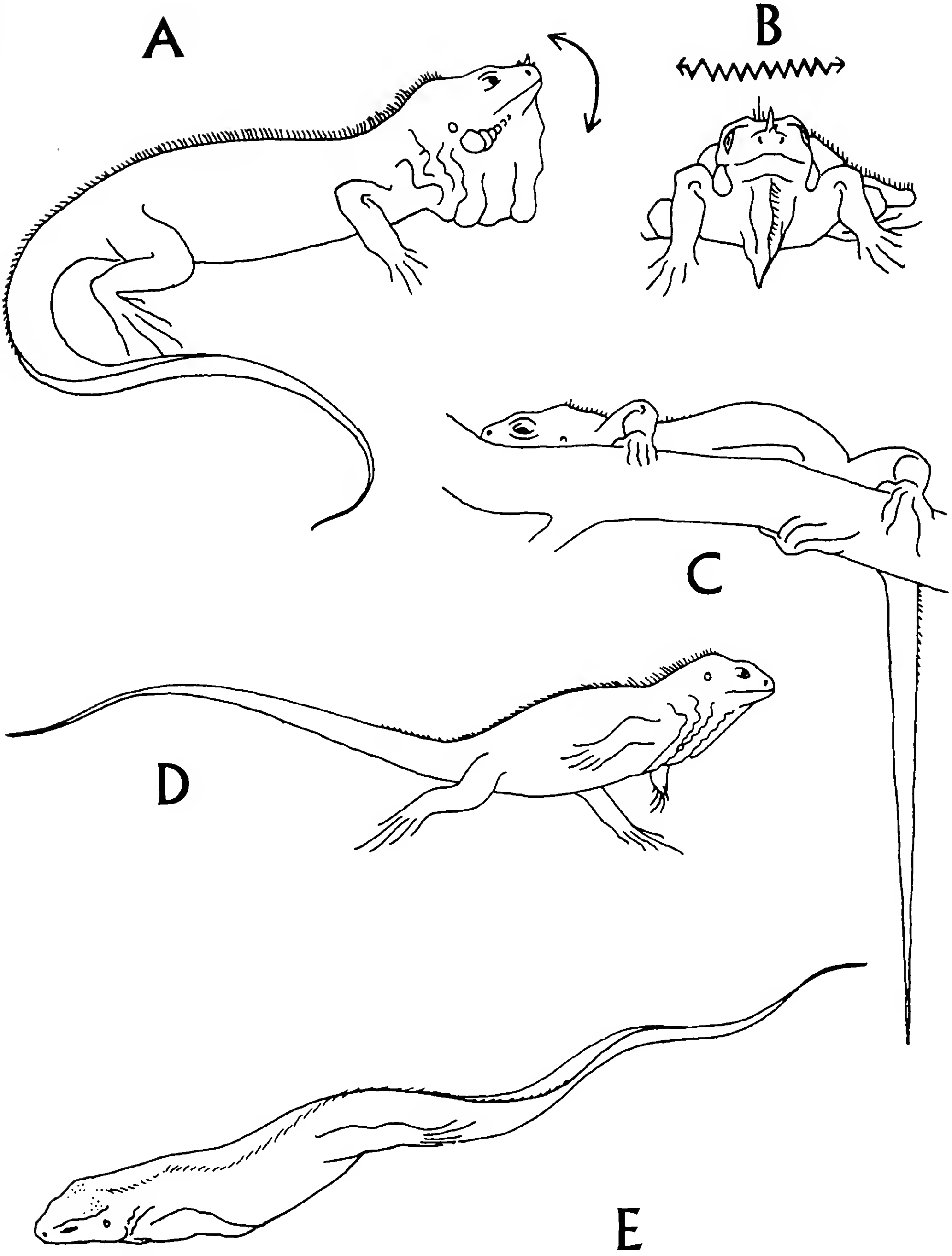

Figure 3. Field sketches made of *Iguana*: *I. iguana*, (A) head bobbing and (B) subsequent dewlap shaking; an apparent male, Millikins Bay, St. Vincent. *I. delicatissima*, (C) in tree, Gaynor's Gut, Antigua; (D) bipedal running, and (E) swimming, both at Woodford Hill, Dominica.

tinuous, undulating whistle works best, but iguanid tastes differ, and one *delicatissima* at Woodford Hill, Dominica, was on the verge of escape before I brought him to rapt attention by piping away like a frog.

Like many lizards, iguanas may be readily noosed on many occasions, and most of my Lesser Antillean material has been collected this way. When the animals are difficult to approach, the .22 rifle becomes the collector's chief tool. Shooting iguanas is no easy matter, however, and considerable care must be taken to avoid fruitless wounding of animals. I have seen an iguana with half its head blown away by a .30–06 slug run at least a hundred yards and disappear. Iguanas should always be shot in the shoulder; this immobilizes the forelegs, and, though it rarely kills them outright, prevents their running away. Unless an iguana can get up on its hind legs—after running quadrupedally for a short distance—it cannot outdistance a human pursuer.

Both species of *Iguana* seem to be similar in general behavior. In Figure 3 I show iguanas in characteristic poses and attitudes as I have sketched them in the field. I spent two days observing a large colony of *Iguana iguana* at Millikins Bay (Prospect), St. Vincent, and another two days observing a large colony of *Iguana delicatissima* on the Ile Fourchue, near St. Barts; four days were spent observing *I. iguana* on Saba, and six I. *delicatissima* were maintained and fed in a large enclosure at Woodford Hill, Dominica. Other field observations have all been made while I was actually attempting to collect specimens. Iguanas sleep in trees or rock crevices; early in the morning they emerge, and generally bask in the sun for an hour or so. The remainder of their waking hours are principally spent in search of food. Both when emerging from sleep, and when searching for food, adults of both sexes often go through some head bobbing when they encounter each other. I have never observed this to lead to any sort of combat, and only rarely does one individual even change course after such an encounter. I have never observed copulation, or even definite courtship, in iguanas, but I have not observed either species between October and January, or in April and May.

Head bobbing serves to extend the dewlap; I have seen some iguanas (*e.g.*, MCZ 79747, Old Sandy Bay, St. Vincent; a young *I. iguana*) that were capable of extending the dewlap independently, in the manner of *Anolis*. When iguanas are basking in the sun, they may pile up on top of each other in great heaps, as pond turtles do in the United States. Bogert (1959) thought iguanas did not position themselves to thermoregulate. McGinnis and Brown (1966) have shown that they, like most other diurnal lizards, definitely do; thermoregulation by position is apparent in captive and wild specimens of both species (personal observations).

Iguanas display a quiet, determined arboreality. They are most awkward in trees, except when resting motionless, and frequently fall down; they seem to persist in climbing, provided there are trees around, even so. An iguana climbing around in a tree looks quite as much at home there as would the average dog.

Iguanas are graceful at only two times: when running, and when swimming. Svihla and Svihla (1952) discuss bipedal running in *I. iguana*, and Neill (1958) and Tercafs (1961) note the swimming ability of this species. Both species are similar in these respects. It takes an iguana a few yards of quadrupedal running before it can push itself up off the ground with its front legs and begin to really run. Unless a large open area is available (like one of the cleared fields at Woodford Hill, Dominica) little observation on the bipedal running of iguanas can be made—they are too soon gone. Across a large expanse, however, they can be seen well as they sprint along; their forelegs are usually clapped against the chest, and the tail is curved upward for about its first third, then trails behind under the control of wind and gravity. Young iguanas, especially, hold their forelegs up at right angles to the body when running. This gives them the bizarre appearance of clasping the handlebars of an invisible bicycle as they zoom along. When swimming, iguanas flatten their limbs along the body and tail base. All speed is achieved by undulations of the tail, and this is considerable. Both species of iguanas swim well and frequently; they commonly escape pursuit by diving into the sea or other bodies of water.

Iguanas of both species are quite good to eat. Irvine (1960) discusses this point. My personal experience is that *Iguana iguana* is sometimes a bit tough and stringy, and individuals in coastal areas sometimes have a fairly strong flavor. *Iguana delicatissima* are, on the other hand, extremely tasty and tender, wherever I have collected them.

Underwood (1962: 65–66) reports that "there is some power of colour change." I have noticed that the general vicinity of a bullet wound, in both species of iguanas, will darken in minutes—apparently from melanophore expansion. Strong formalin preservation can turn a green iguana dark and muddy, quite as it does with those anoles that show a marked ability for color change; this implies, perhaps, a similar color change mechanism in both genera. In captivity, *I. iguana* changes from darker to lighter in response to temperature; I have not been able to induce any change by other methods, such as light, handling, feeding, or confrontation with other individuals.

Although many people in the Lesser Antilles recognize that there are two forms of *Iguana*, if they live in an area where both occur, or have ever seen both species, no distinction between them is made in the vernacular. The common name for both species used by English-speaking peoples is "iguana" or "guana"; French- and Creole-speaking peoples use the appelation "lezard" or "lezard iguane." Small lizards, like anoles ("Z'anolis") or geckos ("mabuyas") are never confused with "lezards" by Creole-speaking peoples, and the metropolitan Frenchman who refers to any small species of lizard as a "lezard" simply does not know what he is talking about, from the native point of view.

Morphological comparison of the two species and discussion of both forms follows the species accounts. The type-species of the type-genus of the family Iguanidae is:

IGUANA IGUANA (LINNAEUS, 1758)

Lacerta iguana Linnaeus (1758: 206).
Iguana tuberculata Laurenti (1768: 49).
Iguana caerulea Daudin (1805: 286).
Iguana sapidissima Merrem (1820: 47).
Iguana viridis Spix (1825: 6).
Iguana squamosa Spix (1825: 7).
Iguana coerulea Spix (1825: 7).
Iguana emarginata Spix (1825: 7).
Iguana lophryoides Spix (1825: 8).
Iguana rhinolopha Wiegmann (1834: 44).
Iguana Hernandesii Jan (1857: 58): *nomen nudum fide* Smith and Taylor (1950).

Type. None ever designated. However, because no real confusion over the identity of the two species of *Iguana* has existed since Boulenger (1885), I do not regard it necessary to designate a neotype.

Type locality. Indiis (= The Indies); here restricted to the island of Terre de Haut, Les Iles des Saintes, Departement de La Guadeloupe, French West Indies. The species is extremely abundant on this island (see above, *Remarks*).

Diagnosis. An *Iguana* possessing a large scale, the subtympanic plate, separated by not more than 12 small scales from the ventral border of the tympanum, which has a maximum diameter greater than 80 percent of the maximum diameter of the tympanum.

Description. In my study of *Iguana iguana*, I have attempted not only to analyze variation in characters previously used (*e.g.*, dorsal crest scales, femoral pores; Boulenger, 1885), but also other

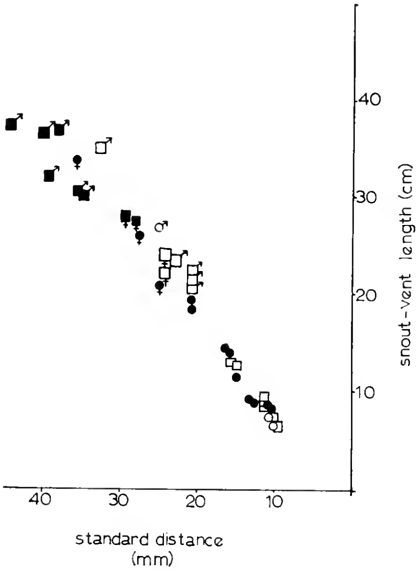

Figure 4. Standard distance vs. snout–vent length in *Iguana iguana* from four localities; open circles: Terre de Haut, Les Iles des Saintes; solid circles: Polvon, Nicaragua; open squares: Santarém, Brasil; solid squares: The Swan Islands. Sex is indicated where determinable.

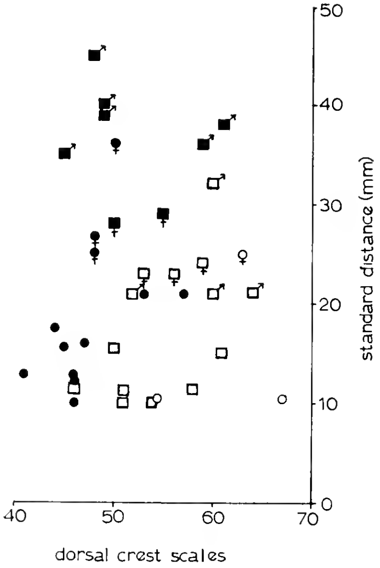

Figure 5. Number of dorsal crest scales vs. standard distance in *Iguana iguana* from four localities; open circles: Terre de Haut, Les Iles des Saintes; solid circles: Polvon, Nicaragua; open squares: Santarém, Brasil; solid squares: The Swan Islands. Sex is indicated where determinable.

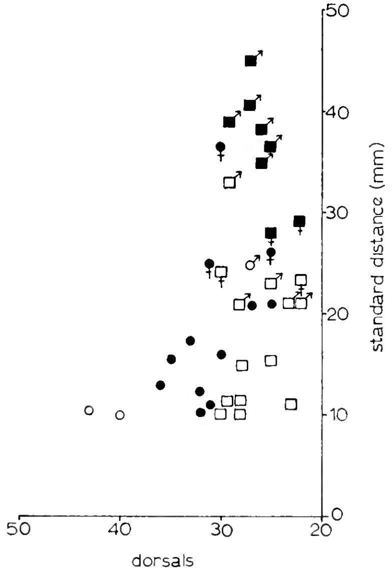

Figure 6. Number of dorsal scales in the standard distance at midbody vs. the standard distance in four populations of *Iguana iguana*. Open circles: Terre de Haut, Les Isles des Saintes; solid circles: Polvon, Nicaragua; open squares: Santarém, Brasil; solid squares: The Swan Islands. Sex is indicated where determinable.

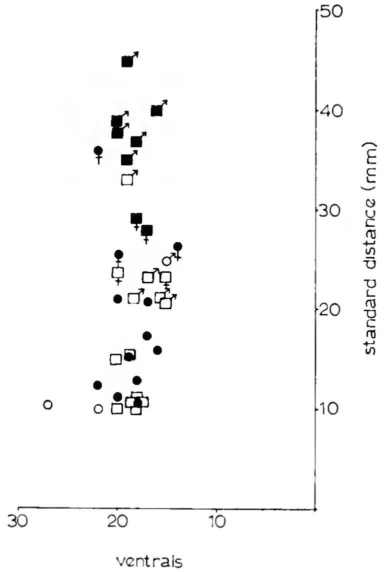

Figure 7. Number of ventral scales in the standard distance vs. the standard distance in four populations of *Iguana iguana*. Open circles: Terre de Haut, Les Iles des Saintes; solid circles: Polvon, Nicaragua; open squares: Santarém, Brasil; solid squares: The Swan Islands. Sex is indicated where determinable.

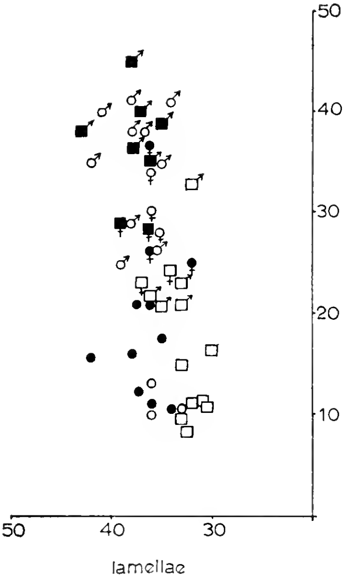

Figure 8. Subdigital lamellae under the fourth toe vs. the standard distance in four populations of *Iguana iguana*. Open circles: Terre de Haut, Les Iles des Saintes; solid circles: Polvon, Nicaragua; open squares: Santarém, Brasil; solid squares: The Swan Islands. Sex is indicated where determinable.

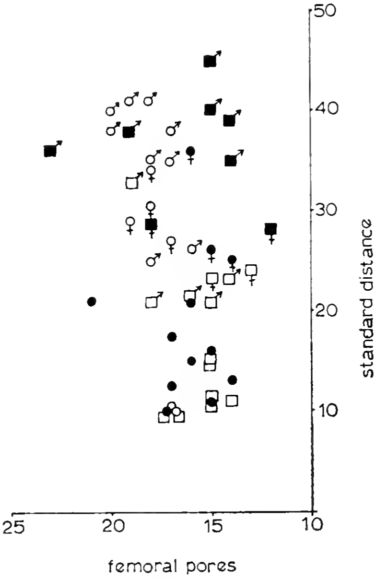

Figure 9. Number of femoral pores vs. the standard distance in four populations of *Iguana iguana*. Open circles: Terre de Haut, Les Iles des Saintes; solid circles: Polvon, Nicaragua; open squares: Santarém, Brasil; solid squares: The Swan Islands. Sex is indicated where determinable.

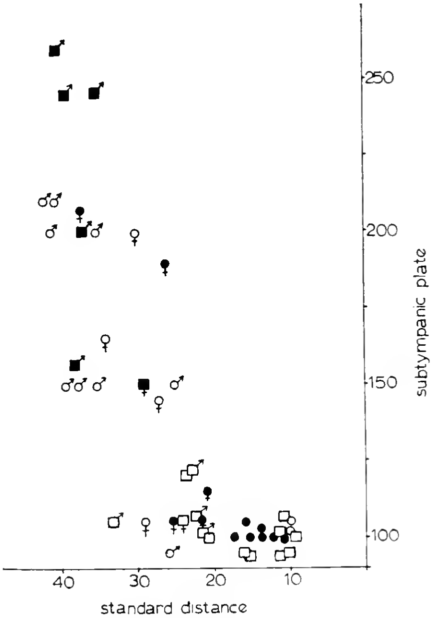

Figure 10. Diameter of the subtympanic plate as percent of the diameter of the tympanum vs. standard distance in four populations of *Iguana iguana*. Open circles: Terre de Haut, Les Isles des Saintes; solid circles: Polvon, Nicaragua; open squares: Santarém, Brasil; solid squares: The Swan Islands. Sex indicated where determinable.

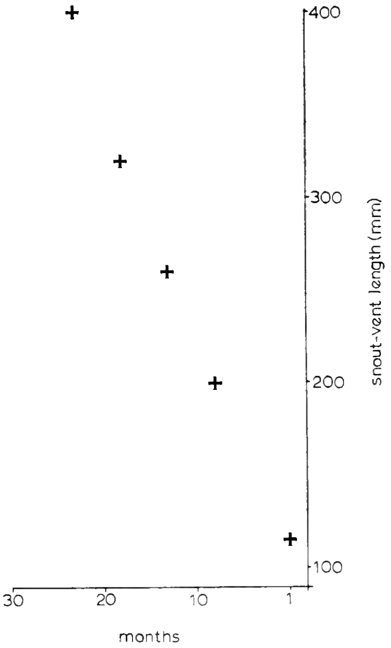

Figure 11. Growth rate in a captive *Iguana iguana*. Measurements were made between the tenth and fifteenth of the following months: December, 1965; August, 1966; January, 1967; June, 1967; and March, 1968.

meristic characters that might have shown geographic variation or distinctions between this species and *Iguana delicatissima.* Unfortunately, I have been unable to find anything new of importance in this respect. The raw data for meristic characters are presented in the form of graphs (Figs. 4–10): four series of *I. iguana* from widely separated geographic areas (Terre de Haut, Les Iles des Saintes; Polvon, Nicaragua; Santarém, Brasil; and the Swan Islands) have been compared to each other; all specimens of *I. iguana* have been compared to all *I. delicatissima* (see *Comparisons* and Table 1, below).

I have examined 139 specimens of this species. Unfortunately, not all specimens can be used for every character. For example, many collectors skin large specimens; I cannot determine snout-vent length, number of dorsal crest scales, or comparative dorsal or ventral scale size in these specimens. In some parts of Central America, iguanas are secured by a method of tying the toes (see Ditmars, 1946: 67–68), which mutilates them to the extent that subdigital lamellae cannot be counted. In the graphs (Figs. 4–10), the number of specimens can be readily counted.

Iguanas range from less than 70 mm to more than 400 mm, snout to vent. Sex could be determined readily in specimens over 200 mm snout–vent length, or those with a standard distance* over 21 mm. In males, the size of the femoral pores (not the number) is two to four times greater than in females of equivalent size. Sex characters, like the hemipenes, testes, and ovaries, can be checked without undue damage to the specimen, and convince me that the use of comparative femoral pore size is valid with skinned or gutted individuals of large size. In specimens below 21 mm in standard distance determination of sex is difficult, and only a few individuals were definitely determined. No sexual dimorphism was found in any of the meristic characters considered here; sex is indicated on all graphs where determinable.

Variation in seven meristic characters which does not correspond to geography is shown in Table 1.

Head-body proportions. The standard distance varies from 9 to 16 percent of the total length. Variation in this character is largely ontogenetic. In juveniles of less than 150 mm the standard distance is normally between 12 and 16 percent of the snout–vent length. With age, the body becomes proportionally longer, so that in old adults, the standard distance is between 9 and 12 percent of the snout–vent length. See Figure 4 and Table 1.

The standard distance is used to measure scale size, as in dorsals or ventrals counted in the standard distance at midbody. Since scale size increases proportionately with age, a systematic error is introduced (see below). Nevertheless, when specimens of similar size of both species of *Iguana* are compared, no difference in scale size can be discerned, and thus the differing proportions of juveniles and adults are of no taxonomic import. Around-the-body counts were made on all *I. delicatissima,* and these counts were compared to counts from *I. iguana* of similar size. No distinction was apparent.

Dorsal crest. Dorsal crest scales were counted on specimens from their beginning on the nape to the level of the posterior end of the ilium. With respect to this character, *I. iguana* is extremely variable. There may be from 34 to 73 crest scales; the individual with the lowest count, MCZ 61119, whose parents were collected at Plymouth, Montserrat, has from two to five crest scales fused at four points along its back, and is thus anomalous. A specimen with 40 crest scales, one of MCZ 2309 from San Pablo Station, Panama Railroad, Panama, does not show fusion, and thus has the lowest normal count. The highest

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* Standard distance is the distance from the center of the eye to the tip of the snout.

Table 1. Meristic characters in the two species of *Iguana*. None of these are useful in separating the species; see text.

	I. iguana (139)	*I. delicatissima* (29)
Standard distance as percent of snout–vent length	9–16	9.5–13.5
Crest scales	34–73 (av. 54)	53–62 (av. 59)
Dorsals in standard distance	21–43 (av. 29)	27–38 (av. 31)
Ventrals in standard distance	14–27 (av. 19)	14–25 (av. 20)
Femoral pores	9–23 (av. 17)	16–25 (av. 20)
Lamellae	29–45 (av. 34)	31–39 (av. 35)
Gular spikes	7–22	4–10

count, 73, is from MCZ 13338 from Milford Bay, Tobago. I am unable to correlate variation in this character with age, sex, or geography. See Figure 5.

Dorsal scale size. As stated above, dorsal scales are counted in the standard distance at midbody. The highest count, as might be expected, is from a small specimen, MCZ 10626 from Terre de Haut, Les Iles des Saintes. This individual has 43 dorsals in the standard distance. The lowest counts, however, do not come from remarkably large animals. MCZ 35604, from Water Island near St. Thomas has 21 dorsals in this distance, and another individual from the same locality, MCZ 12144, has 22; these individuals measure 285 mm and 181 mm, snout-to-vent length, respectively. An individual from Saboga Island, Panama, MCZ 9912, has 22 dorsals in this distance and measures 212 mm, snout to vent. I am unable to correlate variation in this character with sex or geography. See Figure 6.

Ventral scale size. The number of ventrals measured in the standard distance is less variable than the number of dorsals. The individual with the highest dorsal count, MCZ 10626 from Terre de Haut, has 27 ventrals in this distance, which is the highest ventral count. As with dorsal scales, the lowest counts do not come from the largest individuals, and MCZ 75832 from the Windward Side, Saba, and MCZ 2555 from Montenegro, Brasil, both have but 14 ventrals in this distance. They are 275 and 272 mm snout to vent, respectively. I am unable to correlate variation in this character with sex or geography. See Figure 7.

Lamellae. Lamellae counts vary from 34 to 42 in a series of 12 specimens from Polvon, Nicaragua, from 33 to 42 in 15 specimens from Terre de Haut, Les Iles des Saintes, and from 30 to 37 in 14 specimens from Santarém, Brasil. For the species as a whole, the variation is from 29 to 43. The highest count is from MCZ 32547 from the Swan Islands; the lowest (29) is from MCZ 35604 from Water Island near St. Thomas. I am unable to correlate variation in this character with age, sex, or geography. See Figure 8.

Femoral pores. Femoral pores have been cited by several authors (*e.g.*, Boulenger, 1885, and Underwood, 1962) as a distinction between the two species of *Iguana*. Variation in femoral pores in *I. iguana* is from 9 (MCZ 49937, 5 km below Choluteca, Tegucigalpa, Honduras) to 23 (MCZ 32546 from the Swan Islands); this high extreme is from a specimen with two rows of pores, 19 above and 4 below. The highest single row count is 22 (MCZ 15375, Paso Agres, Costa Rica). In the series of 12 specimens from Polvon, Nicaragua, femoral pores vary from 16 to 20. In the 14 specimens from Santarém, Brasil, they vary from 13 to 20. A specimen from Iles

Bay, Montserrat (MCZ 82310), has 10 femoral pores, and one from Old Sandy Bay, St. Vincent (MCZ 79747), has 21. Thus, even within the Lesser Antilles, femoral pores cannot be used to distinguish the two species.

Femoral pores are usually in a single row in this species. However, MCZ 82309 from the Ilet de Pigeon du Nord, off La Guadeloupe, has 19 pores in the principal row and two in a supernumerary row. As mentioned above, MCZ 32546 has 19 in the primary row and four in a supernumerary row. Another specimen from the Swan Islands, MCZ 32547, has 17 in the primary row and two below this. One specimen, MCZ 79749, from Dougaldston, Grenada, has staggered femoral pores. In no case is the arrangement of femoral pores as varied as in some *I. delicatissima* and some *Cyclura* (*e.g., cornuta,* Cochran, 1941). Variation in number of femoral pores does not correlate with age, sex, or geography. See Figure 9.

Gular spikes. I have been unable to find a satisfactory method for counting gular spikes. The spikes, though large and obvious in all specimens on the anterior part of the dewlap, usually grade into small scales both on the chin and posteriorly on the dewlap. Certainly, there are usually fewer large spikes in *delicatissima* than in this species, but the number of enlarged spikes counted by me overlaps greatly, and different counts are possible on the same specimen. Therefore, the range given in Table 1 does not reflect particular specimens, but rather the range of possible counts; for this reason, variation in this character is not amenable to graphing.

The following characters are helpful in distinguishing the two species, or show geographic variation in *Iguana iguana.*

Subtympanic plate. In *I. iguana* there is a large subcircular plate or scale separated by 4 to 12 scales from the ventral edge of the tympanum. In the vast majority of specimens, the greatest diameter of this scale is equal to or greater than the greatest diameter of the tympanum. In some individuals, especially old males, its diameter may exceed by three times the diameter of the tympanum (*e.g.,* MCZ 21695, from the Swan Islands; this specimen is not graphed). However, there are exceptions, especially in subadult individuals. In MCZ 79056 from Bequia, Grenadines, measuring 132 mm snout to vent, the greatest diameter of the subtympanic plate is slightly more than 85 percent of the diameter of the tympanum, and it is similarly small in one of MCZ 2729, measuring 95 mm, from Acapulco, Mexico. In another individual, MCZ 83121 from Guayaquil, Ecuador, measuring 113 mm, it is about 90 percent of the diameter of the tympanum. A specimen from Terre de Haut, Les Iles des Saintes, MCZ 10972, has been skinned, but was probably in excess of 250 mm, snout–vent length; its subtympanic plate has a greatest diameter of only about 95 percent of the greatest diameter of the tympanum. See Figure 10.

Dunn (1934) mentions the enlarged sublabials of *delicatissima* as a distinction between the two species, apparently basing this on the assumption that only a single subtympanic plate is enlarged in *I. iguana.* However, in many specimens of *I. iguana* the sublabial scales may be greatly enlarged, and in one specimen (MCZ 3304 from Para, Brasil) the scale anterior and adjacent to the subtympanic plate is the largest in the series.

Ventral keeling. The ventrals in *Iguana iguana* vary from smooth to tectiform. This variation is individual, not geographic, as revealed by examination of large series, like the 12 specimens from Polvon, Nicaragua, or the 15 specimens from Terre de Haut, Les Iles des Saintes. This character has not been quantified.

Tubercular nape scales. The presence of much enlarged, tectiform, swollen, or tubercular scales of the nape has been cited (Boulenger, 1885; Cuvier, 1829; etc.) as a distinction between the two species of

Iguana. In many specimens of *I. iguana* these scales are so prominent that they considerably distort and fold the skin of the nape, and produce an almost pathological appearance. Nape scales of this sort are especially well developed in animals from the northern Lesser Antilles and Virgin Islands (*e.g.*, MCZ 75832–3 from The Windward Side, Saba, MCZ 69111 from the east end of St. Croix, and MCZ 35604–5 from Water Island near St. Thomas). In some Central American individuals, such as one of MCZ 5455 from Polvon, Nicaragua, nape scales may be similarly developed. In the largest of MCZ 2729 from Acapulco, MCZ 73904 from Ciudad Carmen, Campeche, Mexico, and MCZ 9912 from Saboga Island, Panama, the nape scales are swollen to the point of being spikes. Several specimens from the Swan Islands (MCZ 32547–8 and 21698) have a few spikelike nape scales.

In many specimens of *I. iguana*, however, the nape scales are not well developed. Some specimens from Terre de Haut, Les Iles des Saintes (MCZ 10978, 10980, 10984) show little development of tubercular nape scales. Another Lesser Antillean individual, MCZ 79750 from Sandy Island, northeast of Grenada, and one from Milford Bay, Tobago (MCZ 13338), show equally poor development of these scales. Nape scales are but slightly evident in MCZ 2598 from Januaria, Rio San Francisco, Brasil. Two untagged specimens (bottled with MCZ 2811, etc.) from Santarém, Brasil, have very few and but slightly enlarged tubercular nape scales.

A specimen from Marajo Island, Brasil (MCZ 24390), was originally identified as *I. delicatissima*, presumably because of the virtual lack of nape scales. A specimen from Puty, Rio Puty, Brasil, MCZ 2905, is the extreme in variation in this character observed. It is certainly an *Iguana iguana*, but it has no tubercular nape scales.

Variation in this character has not been quantified.

Snout squamation. The enlargement and alignment of median scales on the snout has been cited (Dunn, 1934) as the only distinguishing feature of the race *rhinolopha* Wiegmann (1834). Ray (1964) questioned this distinction; even within the range outlined by Dunn (1934), the character is inconsistent. For example, one of MCZ 5455 from Polvon, Nicaragua, has neither an aligned median scale series nor raised scales on the snout. Similarly, one of MCZ 2729 from Acapulco, Mexico, shows no evidence of the "*rhinolopha*" condition. In MCZ 1157 from Villa Bella, Brasil, as well as MCZ 2629 and one of MCZ 2779 from Santarém, Brasil, there is one medial, swollen snout scale; MCZ 2905 from Puty, Rio Puty, Brasil, and MCZ 24390 from Marajo Island, Brasil, are indistinguishable from typical Central American or Mexican animals of the same size with respect to their snout squamation. In the Lesser Antilles, the "*rhinolopha*" grade is well developed in specimens from Grenada to St. Lucia. Boulenger (1885) records "*rhinolopha*" from St. Lucia, and fresh material (which I collected: MCZ 82908 from Grande Anse), confirms his identification. For some reason, Underwood (1962: 156) gives the subspecific designation *I. i. iguana* to St. Lucian animals. Apparently, no specimens not of the "*rhinolopha*" grade have ever been taken on St. Lucia. Similarly, MCZ 6094(2), Grenada, MCZ 79749, Dougaldston, Grenada, MCZ 79748, True Blue, Grenada, and MCZ 79747, Old Sandy Bay, St. Vincent, are of the "*rhinolopha*" grade. Dunn (1934) reports "*I. i. iguana*" from Grenada; this presumably means that he saw material lacking hornlike, medial snout scales. I have seen no specimens from Grenada that lacked these scales. Excellent examples of the "*rhinolopha*" condition from Bequia, Grenadines (MCZ 79056–8), may be compared to MCZ 27901–3 of similar size, from Tapanatepec, Oaxaca, Mexico. Because the "*rhinolopha*" condition is often inconsistent where it occurs, and because it occurs polytopically in the

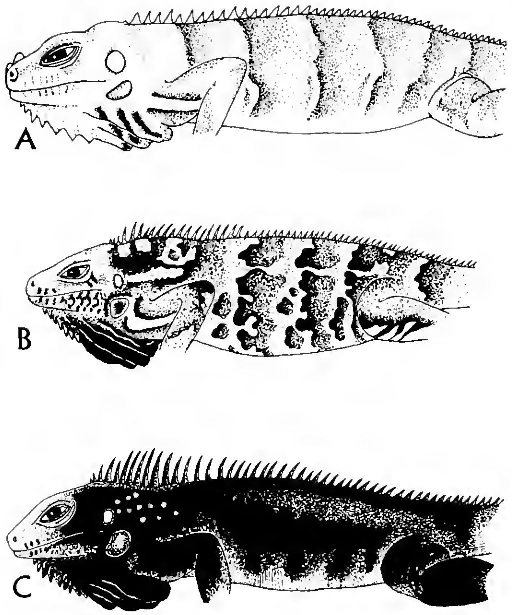

Figure 12. Some color patterns of *Iguana iguana*: A, banded (MCZ 79057, Bequia, Grenadines); B, carpet (MCZ 82310, Iles Bay, Monserrat); C, melanic (MCZ 75833, The Windward Side, Saba).

range of *I. iguana*, I do not recognize it as a subspecies.

Occipital scales. The relative convexity of the occipital scales is mentioned by Boulenger (1885) as a difference between the two species. There certainly is an average difference: in *Iguana iguana* the occipitals are normally much less convex and swollen than in *I. delicatissima*. However, in juveniles the distinction is frequently not apparent, and in some adults of *I. iguana*, for example MCZ 73904 Ciudad Carmen, Campeche, Mexico, the occipitals are quite as convex as in any *I. delicatissima* examined by me.

Shoulder stripe. A light stripe, often bordered by dark pigment, arises on the shoulder and extends onto the anterior surface of the forearm in many individuals of *Iguana iguana*, regardless of age or sex. I have seen this marking in only three specimens of *I. delicatissima* (see below).

Coloration and pattern. Typically *I. iguana* is a green lizard, varying from olive green to brilliant "arsenic" green. The commonest pattern is one of dark, transverse bands on the dorsum (sometimes extending boldly onto the venter, in the northern and western parts of the species range), frequently set off by whitish streaks. However, many individuals differ widely in appearance. Some may be grey, grey-brown, or reddish in ground color; in others speckling may overlie and obscure the bands. Speckling is evident in two of MCZ 5455 from Polvon, Nicaragua, and in MCZ 10972, 10977, 10980, and 10983–4 from Terre de Haut, Les Iles des Saintes. Frequently the simple banding may be scalloped and interrupted in such a way as to form an ornate arrangement which I refer to as "carpet pattern" (see Fig. 12). Carpet patterns are well developed in some specimens from Peru (*e.g.*, MCZ 45874, Pucallpa, and MCZ 45875, Rio Ucayali near Cumaria, Loreto, Peru) and Brasil (MCZ untagged, bottled with MCZ 2811, etc., Santarém). Carpet patterns are also conspicuous in the northern Lesser Antilles: MCZ 82310 from Iles Bay, Montserrat, MCZ 75832 from The Windward Side, Saba, and MCZ 35605 from Water Island near St. Thomas (Virgin Islands), are excellent examples.

Another deviation from the banded norm is uniform coloration. Because method of preservation (*e.g.*, strong formalin) may obliterate color pattern, I am able to state with assurance only that the following specimens, seen alive by me, were unpatterned in life: MCZ 82309 from Ilet de Pigeon du Nord, off La Guadeloupe (a grey individual), and MCZ 79747 from Old Sandy Bay, St. Vincent (a green individual). However, MCZ 10976 from Terre de Haut, Les Iles des Saintes, is the only one in a series of 13 specimens, all presumably preserved under similar conditions, which shows no trace of a pattern on the body. I have seen patternless individuals in the field on Terre de Haut and the Iles de Pigeon, off Guadeloupe.

Melanism has been reported in some populations of *Iguana iguana* (*e.g.,* Roze, 1956, on Los Roques, off the coast of Venezuela). There is a perceivable increase in melanic individuals proceeding northward from Montserrat to St. Croix; this geographic variation presumably includes the Virgin Island populations as well. On Saba about 20 percent of adult males are entirely melanic (personal observation). One preserved specimen (MCZ 69111) and two of four seen in the field in St. Croix were melanic; melanism is only weakly developed in the one individual showing any at all (MCZ 82310, Iles Bay) that I have seen from Montserrat. In melanic individuals the face, snout, and sometimes the sides are usually purple or maroon.

The dewlap is typically green in *I. iguana.* As with other characters, however, there is much variation; in three individuals from Bequia, Grenadines, it may be nearly plain green (MCZ 79056), reddish or orange (MCZ 79056), or green streaked with black (MCZ 79057). In melanic individuals (*e.g.,* MCZ 35604, Water Island near St. Thomas) it is quite black.

Lesser Antillean *I. iguana* may be usefully divided into three groups of populations which differ from each other, and other extralimital populations, in the manner in which they combine average differences, extremes of variation, and unusual characteristics. These are nontaxonomic groups; the variation in *I. iguana* is, even when geographic in orientation, polytopic and discordant; the average differences between populations fall far short of taxonomic significance.

The *I. iguana* populations of the northern Lesser Antilles, from St. Croix, Saba, and Montserrat, may be characterized by the following: (1) the tubercular nape scales and dorsal crest spikes may be developed to an extreme matched only by some individuals from Mexico, Central America, and the Swan Islands; (2) there is a high incidence (10–30 percent) of carpet-patterned individuals (carpet-patterns also occur in Peru and Brasil but seem to be rare or nonexistent elsewhere in the species range); (3) there is an increasing incidence of melanic individuals, proceeding northward from Montserrat to St. Croix. Concordantly, the melanic individuals show an increasingly greater extent of obliterative blackness; (4) these animals have flat, irregular snout scales. From a consideration of the material at hand, Puerto Rico Bank populations should be included within this group; I have not seen Puerto Rico Bank animals alive and in the field; I cannot report with assurance on the relative numbers of carpet-patterned or melanic individuals in these populations.

The *I. iguana* of the Guadeloupéen Archipelago (La Guadeloupe and the coastal Iles de Pigeon ou Goyave, plus the low, dry "crescent" of Les Iles des Saintes) may be characterized as follows: (1) the tubercular nape scales may be very weakly developed, as in some individuals from Brasil and the southern Lesser Antilles; (2) there is a high incidence of unpatterned (but not melanic) individuals; (3) there is an independent, high incidence of grey (but not melanic) individuals, and the combination of grey, unpatterned animals occurs; (4) these animals have irregular, though rarely swollen, snout scales.

The southern Lesser Antillean populations, from St. Lucia, St. Vincent, the Grenadines, and Grenada, may be characterized as follows: (1) the tubercular nape scales may be weakly developed as above; (2) most individuals are either green or grey with laterodorsal bands, as is normally the case in eastern South America; (3) the enlarged, median, hornlike snout scales, characteristic of the "*rhinolopha*" grade, are strongly developed (this is also the case in Mexico and northern Central America, and, to a lesser extent, in Brasil and the Swan Islands).

In this species as a whole the following points on variation may be discerned:

(1) There is an average increase in the development of tubercular nape scales and the length of dorsal crest spikes, as one proceeds northward in the range of the species. (2) Banding, when present, tends to be more lateroventral as one proceeds westward and northward, and more laterodorsal as one proceeds eastward and southward, in the range of the species. (3) Snout squamation of the "*rhinolopha*" grade may be strongly developed over widely separated, large geographic areas: the southern Lesser Antilles, and northern Central America and Mexico; this type of snout squamation may be weakly or inconsistently developed elsewhere, *e.g.*, Brasil and the Swan Islands. (4) Melanism (northern Lesser Antilles and some of the Venezuelan coastal islands), carpet patterns (northern Lesser Antilles, Peru, and Brasil), and lack of dorsal pattern (Guadeloupéen Archipelago, St. Vincent, and doubtlessly elsewhere), appear polytopically scattered, and involve varying percentages of individuals, in a number of populations.

As revealed by examination of large series from widely separated localities (Terre de Haut, Les Iles des Saintes; Polvon, Nicaragua; Santarém, Brasil; and the Swan Islands), variation in other characters is far more individual than geographic.

Size. The smallest specimen examined, MCZ 71834 from Terre de Haut, Terre de Haut, Les Iles des Saintes, measures 68 mm, snout–vent length. This specimen, like the majority of others I have examined under 85 mm snout to vent, shows a definite yolk sac scar (area of bare skin), and may thus be thought of as a hatchling. Native opinion in St. Lucia and Terre de Haut, Les Iles des Saintes, has it that the young of this species hatch in March, April, and May; the specimens I collected between June and early September that are under 80 mm snout to vent (*e.g.*, MCZ 79750, Sandy Island NE of Grenada; MCZ 71834, Terre de Haut, Les Iles des Saintes; and MCZ 82908, Grande Anse, St. Lucia), indicate that this is probably true (see also *Population structure and ecology*, below).

The largest specimen examined is MCZ 2095, from Manaos, Rio Madeira, Brasil; this adult male measures 445 mm, snout–vent length; the tail is truncated. Most authors (*e.g.*, Ditmars, 1946) give the size of large *Iguana iguana* as about six feet; this is certainly not an exaggeration. Most collectors tend to take the smallest specimens they can of animals as large as *I. iguana*, because the difficulties of preservation and storage are, especially in the field, severe with huge beasts; I have certainly never tried to collect very large specimens, for these reasons. The largest *I. iguana* (and the largest living lizard, outside of captive *Varanus*) I have seen resided at the garbage dump at the southern end of the town of Terre de Haut, Les Iles des Saintes, from at least August, 1961, to August, 1964. It seemed so much larger than MCZ 2095 that I would not care to estimate here how big it was. This animal may be recognized by a rather H-shaped, blackened scar on its left side, and, of course, by its size, should anyone care to go and measure it; I expect it is still there.

An *Iguana iguana* was purchased on 10 December 1965 in a pet store in Cranston, Rhode Island. The specimen measured, when purchased, 115 mm snout to vent. On 10 August 1966 the specimen was 200 mm snout to vent, and appeared to be a male. By March 1968, this specimen had exceeded 400 mm, and was a large, vigorous adult male. Growth rate is graphed in Figure 11.

Population structure and ecology. In the Lesser Antilles *Iguana iguana* seems to be rather "clumped," or colonial, at the east end of St. Croix, in southern Montserrat, on the Iles de Pigeon ou Goyave and the low, dry, "crescent" of Les Iles des Saintes, at the south tip of Maria Island (off St. Lucia), along the south coast of St. Vincent, and in the Grenadines. These areas are all of xeric conditions. On Saba, in central Montserrat, along the leeward coast of La Guadeloupe, along the windward coast of St. Lucia, along both windward and leeward coasts of St. Vincent, and throughout mainland Grenada this species is apparently more or less infradispersed. These areas, with the exception of the leeward coast of La Guadeloupe and the southern coast of Grenada, are of mesic conditions.

I have not collected gravid females of *Iguana iguana* in the Lesser Antilles; native opinion has it that this species lays its eggs in December, January, and February. Underwood (1962: 66) says, "a specimen of *I. iguana* laid 17 eggs which hatched in 14 weeks." No dates are given; however, 14 weeks fits well with the above laying dates, if the information on hatching dates (see *Size* above) is correct. A specimen from Turbo, Isthmus of Darien, Panama, the largest female examined (420 mm), contains 43 eggs of 35–40-mm diameter; there is no date of collection.

Swanson (1950), in his notes on Panamanian *I. iguana,* gives times when young are seen in June and July, and judges that eggs are laid in February or early March. Correspondingly, he estimates that eggs require three months to hatch; given a three-and-a-half month (= 14 to 15 weeks) incubation period, our laying dates would nearly coincide. He notes a female with eggs 25 mm in diameter in late January; these are, I believe, within a month of being ready to be laid. Swanson also notes a female with 72 eggs, from 3 to 6 mm in diameter; this number would, in my opinion, be astronomical for a single clutch, and I agree with Swanson that more than one clutch was potentially represented. Hirth (1963a) records clutches averaging 36 eggs laid in March and early April. Hirth (1963b) also gives the optimal temperature for this species as above 30° C., and states that eggs take three months to hatch. Licht and Moberly (1965) note a 1200-gram female that laid 41 eggs on 6 March 1964; eggs kept at 30° C. hatched in 73 days, on 18 May.

Duellman (1954) records *I. iguana* at 2600 feet (*ca.* 800 meters) in Michoacan, Mexico, and I have seen this species at approximately the same elevation in remnant montane rain forest on The Mountain, Saba. On Les Iles des Saintes, the Iles de Pigeon, the leeward coast of La Guadeloupe, and some of the Grenadines (*e.g.,* Kick-'em-Jenny) *Iguana iguana* occupies as xeric habitats as are available in the Lesser Antilles.

Ticks of the genus *Amblyomma* infest many specimens from Mexico, and Central and South America. A specimen from Bequia, Grenadines (MCZ 79058), supported ticks of the genus *Aponomma.* The intestines and liver of *Iguana iguana* are sometimes infested with nematodes (Hill, 1954). Leussink (1958) reports these nematodes to be of the genus *Ozolaimus.*

Iguana iguana feed on a wide variety of animal and vegetable matter (see, for example, Ditmars, 1946). In the Lesser Antilles I have observed them eating bird eggs, mangoes, and prickly pear fruits. Loftin and Tyson (1965) record *Iguana iguana* feeding on carrion.

Distribution. Iguana iguana occurs from about 24°30′ north latitude (Costa Rica Village, Sinaloa, Mexico; Smith and Van Gelder, 1955), on the Pacific Coast, and about 21°30′ north latitude (Laguna de Tamiahua, Veracruz, Mexico; Smith and Burger, 1951), on the Atlantic Coast, southward at least to the Tropic of Capricorn (Gran Chaco, Paraguay; Hellmich, 1960). The species is conspicuously absent from the Tres Marias islands, off the Pacific coast of Mexico (Zweifel, 1960); it occurs in the Archipiélago de las Perlas, off the Pacific coast of Panama (*e.g.,* MCZ 9912, Saboga Island), and on Gorgona Island (MCZ 6992), off the Pacific coast of Colombia.

The species occurs on the Isla Cozumel, Quintana Roo, Mexico (Smith and Taylor, 1950), the Swan Islands (MCZ 32546–8, 21695–8, and 73905), the islands of the Gulf of Honduras (*e.g.,* MCZ 61120, 66354, Half Moon Cay), the Corn Islands (*e.g.*, MCZ 26967), and on Old Providence and St. Andrew (= Providencia and San Andres; Dunn and Saxe, 1950).

On the coastal South American islands of the Caribbean, Hummelinck (1940) records *Iguana iguana* by sight or by specimens from Margarita, Los Testigos, Los Frailes, Los Hermanos, La Blanquilla, La Tortuga, Isla Orchilla, Los Roques, Isla Aves, Bonaire, Klein Bonaire, Curaçao, and Aruba. The species is common, at least locally, in both Trinidad and Tobago (Underwood, 1962; MCZ 6095 and MCZ 13338–9).

On the Grenada Bank *Iguana iguana* occurs virtually throughout coastal Grenada and on most of the adjacent cays; it is not reported from Bird Island (= "Mouchie Carré") or Marquis Island, and is said to have been extirpated on Glover Island. There may be some islands of the Grenadines from which the species is genuinely absent; I have encountered *I. iguana* on the Isle-a-Caille, the Isle-a-Ronde, Kick-'em-Jenny, Mabouya Cay, Carriacou, Petite St. Vincent, Frigate Island (south of Union), Union Island, Tobago Cays, Cannouan, Savan Island, Petite Mustique, Mustique, Battowia, Quatre, and Bequia.

On the St. Vincent Bank, *Iguana iguana* occurs virtually throughout the lowlands of St. Vincent, and on all of the coastal cays that support trees.

On the St. Lucia Bank, this species occurs on the southern tip of Maria Island (the larger), off the southeast coast of St. Lucia, and on the northern windward coast (*e.g.*, Grande Anse) of St. Lucia proper. I have not heard of the species occurring elsewhere on this bank in recent years, but there are old rumors of iguanas on Pigeon Island.

The specimen of *Iguana iguana* cited by Boulenger (1885) as coming from Dominica constitutes an unconfirmed record (see *Distribution, I. delicatissima*, and *Discussion*, below).

In Les Iles des Saintes, *Iguana iguana* is abundant on La Coche, Grande Ilet, central and eastern Terre de Haut, and the Ilet-a-Cabrit. This area forms a low, dry "crescent" around the wetter, western end of Terre de Haut, and lies largely to the east of the comparatively moist island of Terre de Bas.

On the Guadeloupe Bank this species seems restricted to the Iles de Pigeon ou Goyave and the adjacent, arid, leeward coast of La Guadeloupe proper. Iguanas are said to occur on the windward coast of La Guadeloupe (*e.g.*, Bois Debut), but I have been unable to ascertain the species.

In the northern Lesser Antilles, *Iguana iguana* is locally abundant in southern Montserrat and occurs all over the lowlands of that island; on Saba this species is everywhere common; on St. Croix the species is locally abundant in the East End district, but is not reported to occur on any of the small cays of the St. Croix Bank.

Iguana iguana occurs on many of the Virgin Islands of the Puerto Rico Bank (Dunn, 1934).

Iguana iguana is extinct on Barbados, and may not have occurred there in post-Columbian times (Ray, 1964). There is no evidence that any of the Lesser Antillean populations are the result of human introduction, and considerable evidence against this theory (see *Discussion*, below).

The widest ranging, most variable, and probably the largest species of iguana is *Iguana iguana*. However, the most delicious iguana is:

IGUANA DELICATISSIMA LAURENTI (1768)

Iguana delicatissima Laurenti (1768: 48).
Iguana nudicollis Cuvier (1829: 45).
Amblyrhynchus delicatissimus, Wagler (1830: 148).
Iguana iguana reverti Hoffstetter (1940: 269).

Type. None ever designated; Laurenti (1768) notes material deposited in the Museum of Turin, Italy, but no longer known to exist. For the same reasons given under *Iguana iguana,* I do not regard it necessary to designate a neotype.

Type locality. Indiis (= The Indies); here restricted to the island of Terre de Bas, Les Iles des Saintes, Departement de La Guadeloupe, French West Indies. The species is here abundant; see *Remarks,* above.

Diagnosis. An *Iguana* with no large scale, separated by 12 or fewer small scales from the border of the tympanum, that has a greatest diameter more than 80 percent of the greatest diameter of the tympanum.

Description. I have examined 29 specimens of this species. Of these, eight were skinned and could not be used for some characters; three were too small to definitely sex. Sexual dimorphism is apparent not only in primary sex characters, but also in size (not number) of femoral pores, as in *Iguana iguana.*

Iguana delicatissima is probably genuinely less variable than *I. iguana.* This is presumably because it occupies a much smaller range, but may possibly also be an artifact resulting from the fact that I have many fewer specimens of this species to examine. Variation in seven meristic characters is shown in Table 1. It is apparent that while average differences exist between the two species in some of these characters, none of them will separate the forms. The following characters are worthy of closer consideration.

Dorsal crest. Dorsal crest scales are counted as in *I. iguana.* Although the variation in *I. delicatissima* is completely included within that of *I. iguana,* there is a difference that is frequently noticeable in young individuals: juveniles of *I. delicatissima* typically have their dorsal crest scales in contact, whereas those of *I. iguana* are usually separated from each other by ordinary dorsal scales. This difference weakens with age, owing to the enlargement of the crest scales, and is not helpful when one is dealing with adults.

Ventral keeling. In *Iguana delicatissima* the ventrals are always at least tectiform and may be sharply keeled. Variation in this character is individual, rather than geographic. MCZ 57849 and 60823–4 from Woodford Hill, Dominica, show this variation clearly.

Femoral pores. The number of femoral pores averages higher in *I. delicatissima* than in *I. iguana.* The highest count is from MCZ 60823, Woodford Hill, Dominica, which has 19 pores in the primary row and 6 in a secondary row, for a total of 25. The highest count for a specimen with a single row of femoral pores is 22 (MCZ 10969, Terre de Haut, Les Iles des Saintes). The lowest count (16) comes from MCZ 10699, which has been erroneously recorded as having been collected in the Cayman Islands (see *Discussion,* below). However, MCZ 16157, from Anguilla, and MCZ 60824, from Woodford Hill, Dominica, have but 18 femoral pores. Double rows of femoral pores are present in MCZ 82306 from between Terre de Bas and Pointe du Gouvernail, Terre de Bas, Les Iles des Saintes. The femoral pores of MCZ 60824 from Woodford Hill, Dominica, are irregularly staggered. Cochran (1941) reports multiple femoral pore rows in *Cyclura cornuta,* and the condition probably occurs in other species of *Cyclura.*

Tubercular nape scales. Large, tubercular nape scales are not usually present in *Iguana delicatissima,* but MCZ 10969 from Terre de Haut, Les Iles des Saintes, has them strikingly developed, and they are also developed, though to a lesser extent, in MCZ 60824 from Woodford Hill, Dominica, MCZ 82307 from L'Anse des Galets, Desirade, and MCZ 16155 from St. Eustatius.

Subtympanic plate. In all specimens of *Iguana delicatissima* examined but one, MCZ 10969 from Terre de Haut, Les Iles des Saintes, there was no large scale at a distance of 12, or less, small scales from the border of the tympanum. MCZ 10969, which comes closest to *Iguana iguana* in this character, is shown in Figure 2.

Snout squamation. The snout scales of

I. delicatissima are typically flat and unaligned. However, MCZ 6098 from St. Barts has aligned, though flat, median snout scales, and MCZ 82308 from Gaynor's Gut, Antigua, has swollen, though irregularly arranged, snout scales.

Occipitals. The occipital scales of adult *Iguana delicatissima* are typically very convex and may even be bluntly spikelike. Such occipital scales are particularly well developed in adult males (*e.g.*, MCZ 82305 from between Terre de Bas and Pointe du Gouvernail, Terre de Bas, Les Iles des Saintes; MCZ 16154 from St. Eustatius; and MCZ 16156 from Anguilla). In very large adult females, such as MCZ 82308 from Gaynor's Gut, Antigua, the terrain of the top of the head may be equally precipitous.

Shoulder stripe. Two juveniles, MCZ 6098 from St. Barts and MCZ 74345 from the Ile Fourchue near St. Barts, have well-developed shoulder stripes. The only adult specimen examined with a well-defined shoulder stripe is MCZ 10969 from Terre de Haut, Les Iles des Saintes.

Coloration and pattern. Most *I. delicatissima* are uniform in body color. However, MCZ 10969 from Terre de Haut, Les Iles des Saintes, has light, vertical streaks on the sides. A specimen from Picard Estate, Dominica (JDL 272), has light-bordered dark markings on the sides that approach the ornateness of a "carpet pattern" (see *I. iguana*), but are far less bold. Juveniles, like MCZ 74345, MCZ 6098, and PANS 8083, show a pattern consisting of a double row of light spots along the side of the body and a similar double row of light streaks along the sides of the tail.

All of the young individuals of *Iguana delicatissima* seen were bright apple green; with advancing age, the color darkens, and old adults, especially males, may be dark slate (*e.g.*, MCZ 82305 from between Terre de Bas and Pointe du Gouvernail, Terre de Bas, Les Iles des Saintes). Some females (*e.g.*, MCZ 75831 from the Ile Fourchue) may be slate-colored, too. There appears to be some geographic variation in the manner of the shift from green to grey. In Martinique and Dominica I have seen very large, but never grey individuals. To the north, in Les Iles des Saintes, La Desirade, and St. Eustatius the transition is gradual, and takes place between approximately 275 and 300 mm snout–vent length. It seems to affect mostly males. In Antigua the transition from green to grey is apparently quite abrupt at approximately the same size as above; I have seen about a dozen individuals in the field, but never one of intermediate color. However, in Antigua, females may also be exempt from greying, as MCZ 82308 from Gaynor's Gut was bright blue-green in life. On the Anguilla Bank, where *delicatissima* is frequently extremely abundant, I have observed very few greying individuals, and there seems to be an abrupt shift in both sexes from green to grey or grey-brown at about 300 mm, snout–vent length. Boulenger (1885) remarks on the yellowish head color of adult *I. delicatissima.* This color is the result of fading after preservation. In all adults seen, whether green or grey, the head was distinctly bluish, though in slate-colored individuals lighter than the remainder of the body.

The dewlap of *I. delicatissima* varies from green to slate grey in close correspondence with the dorsal coloration. I have never seen an individual with markings on the dewlap.

The only geographically correlated variation in *I. delicatissima* I have discerned is the ontogenetic shift from green to grey. This may be summarized by saying that as one proceeds northward in the range of this species there is a tendency, beginning in males, for large adults to turn grey; in the northern part of the range (Anguilla Bank) both sexes become abruptly grey on attaining large size; in the southern part of the range (Martinique and Dominica) even very large, old males may be quite bright green.

Size. The smallest individual examined, PANS 8083, bears the datum "West

Indies," and measures 93 mm, snout–vent length. In this specimen the yolk sac scar is quite obliterated. I have seen no hatchlings of this species; native opinion on Dominica and Terre de Bas, Les Iles des Saintes, has it that the young of this species hatch in December, January, and February. The smallest individuals seen, in June, July, and August, look approximately the right size to have hatched about six months previously.

The largest museum specimen examined is a female from Antigua, MCZ 82308, measuring 346 mm snout to vent; this is as large as any female I have ever seen. A male from Anguilla, MCZ 16156, measures 345 mm snout to vent; this is far from the largest individual I have seen. Each of these specimens has a total length of about four feet. A male from Melville Hall, Dominica, collected in July, 1958, was over five feet in total length. Unfortunately, in 1958 I was collecting iguanas only for the Philadelphia Zoological Garden, and was unaware that there was anything remarkable about a five-foot *Iguana delicatissima* on Dominica; because juveniles survive best in captivity, this individual was prepared *par fumée* by Mrs. C. A. Winston, of Woodford Hill, and the Winston family and I ate it. I have seen specimens in the field on Terre de Bas that certainly seemed to be even larger than this one.

As in *I. iguana,* collectors have a bias for smaller individuals; the same problems of preservation and storage mentioned previously apply to this species, too.

Population structure and ecology. As in *Iguana iguana, I. delicatissima* may be either infradispersed or strikingly clumped. The same remarks made for *I. iguana* concerning habitat seem to hold for *I. delicatissima:* in the driest parts of the range (*e.g.,* the Anguilla Bank) colonies are the general rule; in wet areas (*e.g.,* windward Dominica), infradispersion seems to be more normal.

Native opinion, as discussed above, has it that *I. delicatissima* hatch from December to February; the size of young seen and collected between June and August indicates that this is probably true.

Eggs are probably usually laid from August to October. A female from the Ile Fourchue collected on 12 July (MCZ 75831) contains 17 eggs with an average diameter of about 25 mm; MCZ 82308, collected at Gaynor's Gut, Antigua, on 27 August contains 18 eggs with diameters from 6 to 17 mm. I dug up a clutch of 22 eggs at Woodford Hill, Dominica, in late August, 1959; they were oblong, and about 35 mm in length. This clutch was laid in sand under sea grape (*Cocoloba*) at a depth of about ten centimeters.

Population structure of the two species of *Iguana* in the Lesser Antilles seems basically identical.

Iguana delicatissima occupies wet, lowland forest in Martinique and Dominica; the conditions elsewhere in its range vary from moderately xeric forest (*e.g.,* Terre de Bas, Les Iles des Saintes) to arid, cactus-and-rock areas like the Ile Fourchue, on the Anguilla Bank. I have never encountered the species above 300-meters elevation, despite many weeks of collecting in highland areas.

I have found ticks on only one specimen of *Iguana delicatissima*: ASFS 11445, from Layou, Dominica. Dr. G. M. Kohls (Rocky Mountain Laboratory) reports (*in litt.*) that these are an unknown species of *Amblyomma.* Leussink (1958) reports nematodes of the genus *Ozolaimus* from specimens taken on St. Barts and St. Eustatius; Leussink called all his specimens *I. iguana,* but Dr. C. E. Ray (USNM) got Leussink to check and reports (*in litt.*) that these specimens are, in fact, *I. delicatissima.*

The diet of *I. delicatissima* is like that of the omnivorous *I. iguana.* I have seen wild specimens feeding on bird eggs, prickly pear fruits, and carrion (a dead goat). In captivity on Dominica they ate mangoes, bananas, lettuce, several local vines (unidentified), raw meat, and eggs, but were never seen to eat papaya or citrus fruits.

Distribution. The range of *Iguana delicatissima* is almost always misstated. Dunn (1934), after carefully noting the records of this species from Martinique (p. 2), sums up its range as being "from Anguilla to Iles des Saintes" (p. 3). Etheridge (1964: 68) gives the range of *I. delicatissima* as the "Leeward Islands and Guadeloupe." Underwood (1962: 66) says, "*Iguana delicatissima* is found only on some of the Leeward Islands." However, he lists the species from the two largest of the "Windward Islands,"—Martinique and Dominica.

On the Martinique Bank this species still occurs in the Bois Montout (I examined the fresh skin of a specimen shot there in August, 1964) and along the north coast from Grande Riviere to Cap St. Martin, where I have seen wild individuals (there was one individual from this area residing in the zoo at Fort Saint Louis, Fort-de-France, until the hurricane of 1962). It is said that iguanas occur on the Ilet Chancel (a coastal cay of Martinique), but I encountered none there. There are said to be iguanas on Fort Saint Louis, and the habitat looks excellent. I suspect these may be zoo escapees and their descendants, but I have never seen one there.

On the Dominica Bank, *Iguana delicatissima* is common along both coasts of Dominica proper. The few, tiny, offshore cays (*e.g.*, Salybia) probably do not support populations. At Picard Estate (leeward coast) and Morne Paix Bouche (windward coast) the species occurs to about 1000 feet.

In Les Iles des Saintes *I. delicatissima* occupies, so far as I have been able to ascertain, only Terre de Bas, where it is abundant, and western Terre de Haut. This area is slightly wetter than the low elevation, dry "crescent" composed of La Coche, Grande Ilet, eastern Terre de Haut, and the Ilet-a-Cabrit, where *Iguana iguana* is abundant.

On the Guadeloupe Bank *I. delicatissima* occurs in the Bois Eusebe, of Grande Terre, and is abundant on La Desirade. Underwood's statement (1962: 144) that this species is "common on the coastal Ilet Gouyave" (= Iles de Pigeon) is unsubstantiated; see *Distribution, Iguana iguana,* and *Discussion,* below.

The Antigua Bank includes the large island of Barbuda, and numerous smaller islands and cays that support large reptile populations (*e.g.*, Long, Great Bird, Guana, Green, Pelican, and York islands). Nevertheless, a thorough search for iguanas all over the Antigua Bank reveals only the colony of *I. delicatissima* in Gaynor's Gut, on the Antigua mainland.

Despite Underwood's (1962: 135) assertion, "Iguanas are known to occur on Redonda," there are no iguanas of any species on that island, and no evidence that there ever were any (see *Discussion,* below).

Iguana delicatissima is locally abundant on St. Eustatius, but I have been unable to find it elsewhere on the St. Kitts Bank. A specimen from Nevis, MCZ 6096, I regard as a reasonable indication that the species was once more widespread on this bank. The species may well still occur on Nevis: I have seen none there, but local reports are conflicting.

On the Anguilla Bank *I. delicatissima* is peculiarly distributed. It is locally abundant on Anguilla (*e.g.*, Katouche Bay) and St. Barts (*e.g.*, Baie de St. Jean). Huge colonies swarm on the Ile Fourchue, Les Iles Fregate, and the Ile Chevreau, or Bonhomme. The species is reported still to occur locally on St. Martin, but to be very rare (I have never seen it there). I have visited most of the other large cays on this bank (Dog Island, Scrub Island, Anguillita, Flat Island or Tintamarre, the Ile Boulanger, the Ile Toc Vers, and the Ile Coco), and have never seen iguanas on any of them.

Comparisons. The two species of *Iguana* are very similar. The only definitive distinction is the presence or size of the subtympanic plate; this large scale is present, separated by not more than 12 small scales from the edge of the tympanum, and has a greatest diameter of at least 80 percent of the greatest diameter of the tympanum in *I. iguana.* In one specimen of *I. delicatissima* there is a scale, one of the sublabial series, separated by ten scales from the edge of the tympanum; the diameter of this scale, however, is *ca.* 75 percent of the diameter of the tympanum. This specimen is clearly *I. delicatissima,* and is not intermediate between the two species, in my opinion; it is MCZ 10969, from Terre de Haut, Les Iles des Saintes.

Some other characters show average differences between the two species. *I. delicatissima* has a higher average number of femoral pores, but the overlap is great (see Table 1). *I. delicatissima* is not usually banded, and *I. iguana* usually is (but see, for example, MCZ 79747 or MCZ 82309, unbanded specimens of *I. iguana*). The dorsal crest scales of juvenile *I. delicatissima* are usually in contact, whereas those of juvenile *I. iguana* are usually separated by undifferentiated dorsals; this difference certainly disappears with age, and its constancy cannot be assumed with only three juveniles of *I. delicatissima* on hand.

The two species are compared with respect to meristic characters in Table 1.

DISCUSSION

Well-entrenched theory in the literature states that West Indian *Iguana iguana* are somehow unnatural interlopers in areas where they have no real right to be. Dunn (1934) thought it possible that some iguanas had been introduced to the Swan Islands, but preferred to believe that the variability in snout squamation there was perfectly natural; I agree with his preference. Schmidt and Inger (1957: 122) state: "The common iguana, *Iguana iguana,* is apparently a recent immigrant to the southern Lesser Antilles and the Virgin Islands from northern South America, and has driven out the native ground iguana (genus *Cyclura* . . .) from these islands." There is no evidence to support any aspect of this contention.

The story of the introduction of *Iguana iguana* into this area reaches its greatest elaboration with Underwood (1962). The groundwork is laid (p. 66) as follows: "It has been suggested that the Caribs may have transported iguanas because they are edible. The Caribs are known to have invaded the Lesser Antilles from South America. They could therefore have carried South American animals northwards into the islands. It could be suggested that *Iguana delicatissima* occupied the Leeward Islands without competition, and that the Caribs brought *Iguana i. iguana* into some of the Leeward Islands where they escaped. If there were no iguanas in an island already, then the newly introduced iguanas colonized without competition; if, as may well have been, *Iguana delicatissima* were in some of these islands the South American form may have supplanted them."

Underwood does not leave us with only these suggestions. In his discussion (p. 117) of *Iguana* in the Virgin Islands, he states: "If they were introduced, as they surely were, one would expect them to be on the principal islands. . . ." Some 12 pages later (p. 129), he tells us that the occurrence of *I. iguana* on Saba "may well be due to human transport. . . ." Montserratian *I. iguana* add a new twist to the burgeoning myth (p. 138): "it seems likely that this iguana has been introduced and, perhaps, supplanted the native species. They were allegedly released about 50 years ago by a Mr. Driver." With respect to *I. iguana* on St. Lucia, Underwood (p. 156) says, ". . . it is perhaps indigenous and possibly the northernmost limit of the natural occurrence of this South American iguana."

As has been pointed out above, the two

species of *Iguana* occur sympatrically in Les Iles des Saintes; while there is evidence of a comparative wet *versus* dry niche segregation between them, the ecological spectrum of these islands is very narrow, and both species are extremely abundant. This is the finest evidence against the suggestion that one species has supplanted, or will supplant, the other; certainly if the two species of *Iguana* can survive together in Les Iles des Saintes, the belief that one of them has driven out *Cyclura* in the larger and more diverse Virgin Islands is hardly tenable.

The finest evidence against the theory of introduction, in any form, is the nature of the variation in *Iguana iguana* itself. The southern Lesser Antillean populations (Grenada to St. Lucia) combine eastern South American laterodorsal banding with what is indistinguishable from Mexican or northern Central American "*rhinolopha*" snout squamation. Some Brasilian individuals could have served as the initial propagule type for these populations; even if this be true, with respect to snout squamation, at least, the southern Lesser Antillean animals have gone far beyond their possible Brasilian ancestors. *Iguana iguana* from the Guadeloupéen Archipelago are quite ordinary, and resemble those from northeastern South America; however, they may be quite patternless, or grey, or both, and these characteristics—especially the latter combination—are rare or nonexistent elsewhere in the species range.

The northern Lesser Antillean *Iguana iguana* (from Montserrat, Saba, St. Croix, and, presumably, the other Virgin Islands) seem to me to display the most convincing evidence against introduction. With respect to their tubercular nape scales and dorsal crest, they fit into the overall geographic variation of their species. Their occasional carpet patterns could be duplicated effectively in Peru or Brasil, and their melanism, which seems to increase as one proceeds northward, reaches extremes that could only be matched, as far as I know, by animals from the Venezuelan coastal cays. If Mr. Driver did, in fact, introduce the iguanas to Montserrat about 50 years ago (Underwood, 1962: 138), he had a wonderful ability to select his stock; the resultant populations have, in 50 years, come to fit perfectly into the group of populations to which they belong geographically in terms of the variation they exhibit.

When I was in Montserrat in 1964 I made a special effort to track down the story of Mr. Driver's introduction. The results were remarkable. He and several other people have been variously credited locally with introducing into Montserrat not only iguanas, but three different species of birds, a large frog of the genus *Leptodactylus*, a toad, the snake *Alsophis* (an endemic form), and the mongoose (*Herpestes*). These introductions were not all successful, of course; some of these animals, like mongooses, do not even reside in Montserrat. Usually each species has proponents for the theory that it alone was the animal introduced, the remaining forms being regarded as native. The best spokesman I could find for the cause of the iguanas assured me that they had come from Dominica, where *I. iguana* is not known to occur, but where *I. delicatissima* is common. The story of Mr. Driver and his iguanas may be dismissed as an occasional variation in the theme of a popular local myth.

Variation, geographic and individual, is discussed in detail under *Description* for *Iguana iguana* in the Lesser Antilles. The facts of this variation convince me, at least, that no human introduction is responsible for the presence of *Iguana iguana* anywhere in the Lesser Antilles.

Underwood (1962: 144) states that *Iguana delicatissima* is "common" on the Iles de Pigeon, or Goyave; I have never seen the species there, but *Iguana iguana* is certainly abundant on these cays. Similarly, Underwood (1962: 149) states that *I. delicatissima* is "common on Terre-de-Haut." The species is recorded from this island, but the common species there, as in the other driest areas of Les Iles des Saintes, is *Iguana iguana.*

Underwood (1962: 135) says that "iguanas are known to occur on Redonda." Mr. Kingsley Howes, of Plymouth, Montserrat, knows more about the animal life of Redonda, first hand, than anyone I know; he reports (personal communication) that he has never seen or heard of an iguana on Redonda. Dr. Richard Howard, Gray Herbarium, Harvard University, has been all over Redonda working on its plant life; he reports the same thing (personal communication). I went to Redonda in the company of three goat hunters who made a good share of their livelihood scrambling over this island; they had never seen or heard of iguanas on Redonda. A search in every conceivable part of this small island revealed no traces of iguanas. Perhaps the source of the Redonda iguana fable is Sloane (1707: 42): "Between *Montserrat* and *Nieves* lies a very small island called *Redondo* or *Rotonda,* discovered by *Colombus* in his Second Voyage, who gave it the Name of *Santa Maria Rotonda,* for its Figure. . . . I was inform'd by those who have been upon it, that . . . it has . . . great store of *Iguanas* of a blackish color." In some parts of the Lesser Antilles where people are unused to seeing *Iguana, Ameiva* are called "iguanas" or "'guanas"; from the color of the animals mentioned by Sloane, I think we may assume that his informant referred to the large, black ground lizard, *Ameiva atrata,* which is endemic.

There are three unconfirmed records of *Iguana iguana* that require discussion here. Boulenger (1885) lists a specimen of this species said to have been taken on Dominica. No reconfirmation of this record is known to me; I do not regard this record as valid.

Duméril and Bibron (1837) mention *I. iguana* (under the name "*tuberculata*") from Martinique. All subfossil material (*e.g.,* Hoffstetter, 1940, 1946, under the name of "*I. i. reverti*") and all the living animals seen (see above) from Martinique are *I. delicatissima.* I suspect that Duméril and Bibron examined specimens from Guadeloupe, or elsewhere, that had been shipped to Paris from Martinique; this was, apparently, all too frequently the source of the locality datum "Martinique." I do not regard this record as valid.

Gray (1845) presented a specimen of *I. iguana* (of the "*rhinolopha*" grade, not "*Iguana iguana iguana*" as stated by Underwood, 1962: 134), said to have come from St. Kitts, to the British Museum. This locality seems most unlikely, in view of the known variation in *I. iguana,* as discussed above. The confusion of the names "St. Kitts" and "St. Lucia" is precedented (see Lazell, 1964), and I think Gray's specimen probably came from the latter island. Apparently no iguanas of either species occur on St. Kitts today; this record should be discounted.

There are three records for *Iguana delicatissima* that are unconfirmed, aside from Underwood's (1962: 144) "Ilet Gouyave" mention from Guadeloupe, discussed above. Cuvier (1829) claims to have seen this species from "Brasil and Guadeloupe" (under the name "*nudicollis*"). I suspect that he saw a specimen either with incorrect locality data or, perhaps more likely, an *Iguana iguana* with a small subtympanic plate and no tubercular nape scales. Similar misidentifications have been made independently (*e.g., I. iguana,* MCZ 24390, Marajo Island, Brasil; see *Description* for this species). *I. delicatissima* does not occur in Brasil.

Cope (1869) records "*nudicollis*" from the Swan Islands; this is certainly an error. I suspect that an individual lacking enlarged, tubercular nape scales (probably a juvenile) is also the basis of the misidentification in this case. Dunn's (1934) suggestion that this animal might have been imported from the Cayman Islands depends on the validity of the last unconfirmed record for this species. An *Iguana delicatissima,* MCZ 10699, bears the data "Cayman Is. W. W. Brown, *leg.*" Lewis (*in* Grant, 1940) notes corresponding with Brown concerning this specimen; Lewis writes further to me: "With regard to the *Iguana delicatissima* . . . (from the Cayman Islands), I did correspond with W. W. Brown the alleged collector . . . He was a meticulous collector who kept excellent notes. He told me quite definitely that he did not collect that specimen . . . (in the Cayman Islands). He assumed, as I had, that somewhere along the line the label must have been switched. There is no reason to doubt that Brown collected it elsewhere. Personally I do not think that any iguanas were ever imported to the Cayman Islands for food." This specimen is largely skinned out; it seems to have been a female, and was probably green. It probably was not over 300 mm, snout–vent length, so it might have come from any part of the range of the species.

All of these unconfirmed records for *Iguana delicatissima* should be discounted.

It is apparent that iguanas once occurred in places where they do not survive today (*e.g.*, Ray, 1964, for *I. iguana* on Barbados); too, in many places iguanas are only locally abundant (*e.g.*, Antigua and St. Croix), and it may be that they were previously more widespread. There is no readily apparent cause for the disappearance of iguanas, and no evidence that man, mongooses, dogs, cats, goats, or pigs—singly or in combination—have affected them is available. Those losses that have occurred may all have happened long before Columbus saw the New World, and there is no certain evidence that appreciable range restrictions on presently occupied land areas have occurred in post-Columbian times. However, it is obvious that small areas of suitable habitat, like Gaynor's Gut, Antigua (*I. delicatissima*), or the pond-dotted East End District of St. Croix (*I. iguana*) can be readily destroyed by man. Steps should be taken to preserve these areas; man is quite sufficiently abundant in the Lesser Antilles already.

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A Systematic Revision and the Evolutionary Biology of the *Ptomaphagus (Adelops)* Beetles of North America (Coleoptera; Leiodidae; Catopinae), with Emphasis on Cave-Inhabiting Species

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A SYSTEMATIC REVISION AND THE EVOLUTIONARY BIOLOGY OF THE *PTOMAPHAGUS (ADELOPS)* BEETLES OF NORTH AMERICA (COLEOPTERA; LEIODIDAE; CATOPINAE), WITH EMPHASIS ON CAVE-INHABITING SPECIES[1]

STEWART BLAINE PECK[2]

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Abstract. The subgenus *Adelops* of the genus *Ptomaphagus* of the New World is revised; figures and descriptions are given for 36 species. Seventeen new species and subspecies of *Adelops* are described: *loedingi julius, loedingi solanum, barri, hazelae, fiskei, walteri, episcopus, cocytus, cavernicola aditus, gypsum, oaxaca, jamesi, altus, newtoni, leo, meximontanus,* and *talamanca.* Twelve new synonymies and new combinations in *Adelops* are recognized.

In the higher categories containing *Ptomaphagus* a conservative classification uses the taxa Leiodidae, Catopinae, Ptomaphagini, and Ptomaphagina. The genus *Echinocoleus* is transferred from the tribe Nemadini to the tribe Ptomaphagini. *Adelops mitchellensis* Hatch is transferred to the genus *Adelopsis* in the Ptomaphagina.

Five ecological categories of habitat specialization hold the species of *Adelops*: forest litter inhabitants, animal burrow and nest inhabitants, soil inhabitants, troglophiles, and troglobites. The biology is discussed, especially that of cave specialization in *Adelops* (progressive and regressive changes), in adults and larvae, and is compared with the Bathysciini.

A phylogeny and zoogeography is proposed for the tribe, and for the species of *Adelops*. These are discussed in detail for the cave species. It is found that many independent cave colonizations occurred in the United States, Mexico, and

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[1] This paper is based on a thesis presented to the Department of Biology, Harvard University, in partial fulfillment of the requirements for the Ph.D. degree.

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Guatemala in the later half of the Pleistocene which produced a total of 19 troglophilic and troglobitic species.

PREFACE

This work began in the spring of 1964 when, as a senior studying under Dr. Thomas C. Barr at the University of Kentucky, I learned of a large unworked collection of several thousand *Ptomaphagus* beetles collected by Dr. Walter B. Jones in caves in Alabama. This collection was assembled by Dr. Jones from the early 1930's to the late 1940's, and was deposited in the Alabama Museum of Natural History. It had been partly studied by Dr. Milton W. Sanderson and Dr. Albert Miller, both then at the University of Arkansas. Because Drs. Sanderson and Miller were forced by other obligations to give up their study of the collection, it lay unworked until it was transferred to Dr. Barr and finally to me.

The Jones collection, combined with my collections and those of Dr. Barr, was the basis of a revision of the systematics of the cavernicolous *Ptomaphagus* of the United States, presented as a Masters Thesis in 1966 to Northwestern University, under the direction of Professor Orlando Park. In that work 3,965 specimens were examined of 14 facultatively and obligately cavernicolous species from 149 localities. Of these, 3,194 specimens from 109 caves in the eastern United States were considered to belong to 11 troglobitic (obligately cavernicolous) species.

Since 1966 work has continued on the systematics and biology of the cave-inhabiting species. The present work recognizes 12 species of troglobites in the eastern United States (of which 5,621 specimens have been examined from 177 cave localities), one species of troglobite from Arizona, two from Mexico, and one from Guatemala. The study has been broadened to encompass the systematics and some aspects of the evolutionary biology of the epigean as well as the hypogean species of the entire subgenus *Adelops*, which ranges from its southern distributional limit in Panama northward to its northern limit in southern Canada. I have supplemented museum and laboratory work with a total of more than five summer seasons of field observations and collecting from 1965 to 1969. One field season was spent in Costa Rica and Panama, and a second in Mexico and Guatemala. Three were spent in the eastern United States, primarily in the Cumberland Plateau region of Alabama and adjacent states. Two weeks each were spent collecting in Puerto Rico and Jamaica.

The work was presented as a Ph.D. thesis to Harvard University in 1970, and was put in final form while I was a Postdoctoral Fellow at Carleton University.

INTRODUCTION

Of all the New World beetles in the family Leiodidae *sensu latu,* I believe that the genus *Ptomaphagus* has the most interesting and complex evolutionary story to tell. The family is generally composed of small, secretive, and drab species, which, with few exceptions, possess the family hallmark of antennae having the eighth segment noticeably smaller than the seventh and ninth. The family occupation is scavenging. Members are generally found in association with decomposing organic material such as humus, carrion, dung, and fungi, and they dwell primarily in moist and forested environments. These habits are consistent around the world. Some species have become specialized scavengers as guests in social insect nests, and others may frequent terrestrial vertebrate nests and burrows.

Frequently, in the work to follow, *Ptomaphagus* and the tribe Ptomaphagini will be compared to, and contrasted with, beetles in the tribe Bathysciini (both in the Catopinae). The Bathysciini are remarkable, and are presently the best generally known group of Leiodidae. They display both great ecological restriction and great phyletic diversification. All but one of the

121 genera and two of the 583 species (Lanyrie, 1967, 1969) are limited to the Palearctic region. The exception is the myrmecophilous and termitophilous *Platycholeus* of California and Washington. All species have lost their flight wings, and all are eyeless except a dozen or so. Their restriction lies in their need for cool moist habitats. A review of the Bathysciini (Lanyrie, 1967) found that in 883 recognized valid species and subspecies, 81 percent are troglobites dwelling in European caves, 10 percent are humus inhabitants in Palearctic forests, and 7 percent are soil inhabitants of the same forests.

In contrast to the Bathysciini, the Ptomaphagini exhibit greater ecological versatility, but less phyletic diversification. The Ptomaphagini are more widely distributed over much of the Old and New Worlds and occupy a greater variety of habitats. But evolutionary diversification has not resulted in as many genera or species. Excluding *Ptomaphagus,* the tribe contains six genera with 50 valid species. Two genera occur in Indo-Malayan forests, two occur only as myrmecophiles (one in north Africa, and one in the southern United States), one genus is an inhabitant of forests and caves in the West Indian Islands and Mexico, and the last is an inhabitant of caves and forest litter in North and South America.

Ptomaphagus is recognized as containing four subgenera. Two are each composed of two species, limited to the Balkans, and to Mexico and Brazil. The subgenus *Ptomaphagus* is Palearctic, containing 22 species found mostly in forested habitats, but also in nests of ants, terrestrial vertebrates, and occasionally in caves. No cave-adapted species are known. The subgenus *Adelops,* the primary subject of this work, is known in the New World from Panama to southern Canada. This paper treats 36 species of *Adelops* as valid, and leaves undescribed a tentative number of seven species from Mexico and Guatemala that are known from inadequate material.

Adelops is ecologically the most versatile group of New World Leiodidae. Most species are fully eyed and winged, with large ranges. These ranges comprise much of the mesic deciduous forests of the eastern United States and Canada. They are inhabitants of the litter on the forest floor, and occasionally the nests and burrows of mice, pocket gophers, and gopher tortoises. The western species often have wide ranges in the more xeric portions of North America, and are more frequently found in association with nests and burrows of *Pogonomyrmex* harvesting ants, prairie dogs, pocket gophers, pack rats, and burrowing owls.

Some described and undescribed Mexican and Central American species are inhabitants of mesic forests at middle and high elevations. They are absent from lowland tropical forests.

In a discussion of phylogeny and zoogeography it is proposed that a Tertiary specialization to forest litter habitats probably resulted in a loss of wings and a reduction of eyes in some species. Under conditions of fluctuating Pleistocene climates some of these specialized species evolved into a suite of 16 cave-specialized (troglobitic) species in the southeastern and southwestern United States and in Mexico and Guatemala. The cavernicolous species display a series of morphological changes in eyes and appendages that reflect various stages of adaptation to cave habitats. In contrast, although other New World Leiodidae do occur in most, or at least many, of the habitats occupied by *Ptomaphagus,* none are known that have invaded and become specialized to caves.

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I was assisted in the field work by many people, all of whom are thanked. Most notable of these are Alan Fiske who helped in the summer of 1967, James Peck in the summers of 1965 and 1969, and Russell Norton in the summer of 1969. Dr. and Mrs. W. B. Jones of Huntsville, Alabama, are warmly thanked for providing a central location for many months of field work in Alabama and adjoining states. I have also been helped with collections from Bill Torode, Dick Graham, Tony Iles, John and Martha Cooper, John Holsinger, Art Dobson, and many others. James Reddell, William Elliott, and other members of the Texas Speleological Survey and the Association for Mexican Cave Studies are especially thanked for providing material from Texas and Mexico.

Drs. Barbara Warburton of Texas Southmost College, Brownsville, Texas, and Thomas C. Barr, University of Kentucky, are thanked respectively for use of the Rancho Del Cielo, Mexico, and Mammoth Cave, Kentucky, field stations under their direction.

The extensive collections of the Museum of Natural History of the University of Alabama were assembled by Dr. W. B. Jones, who was frequently accompanied in the field by J. M. Valentine, A. B. Flannigan, H. P. Loding, A. F. Archer, and L. Hubricht. The extensive cave collections of Thomas C. Barr were contributed to by Leslie Hubricht, H. R. Steeves, Jr., and others. Walter Suter and H. R. Steeves, Jr. provided extensive material, deposited in the FMNH, from their Berlese funnel collections from forest litter. Other collectors and collection curators helping in my study are acknowledged in the list of collections. I regret that space is not available to name every collector individually.

The owners of the caves investigated in this study, as well as the speleologists who gathered helpful cave information, are too numerous to mention, but a debt is owed to each. Special help with cave information was provided by Thomas C. Barr, William W. Varnedoe, Russell Gurnee, and Bill Torode.

Professor F. M. Carpenter of the Biological Laboratories, Harvard University, provided much-needed assistance in administrative matters and details of field-work funding. Professor P. J. Darlington, Jr., Dr. John F. Lawrence, and others from the Museum of Comparative Zoology, Harvard University, offered welcome advice and assistance on many matters of procedure and operation. The completion of the work at Carleton University was made possible under a systematic operating grant to Dr. H. F. Howden from the National Research Council of Canada.

Some of the drawings, and other forms of encouragement and aid, were provided by my wife Jarmila.

METHODS AND MATERIALS

In this study I have examined more than 9,800 specimens of North American *Ptomaphagus*. About 70 percent of this number represents 12 troglobitic species of the eastern United States, and two troglophilic species from the United States and Mexico. The large numbers of cave-collected specimens (contrasted to epigean specimens) represent (1) the greater collecting emphasis that has been placed on caves, (2) the greater ease of collecting a large series from cave populations, (3) the elusive nature or scarceness of the epigean species, and (4) the special collecting techniques needed by, and the beetles' unexciting appearance for, a general epigean beetle collector.

The following list indicates the private and institutional collections and curators from which specimens were borrowed, and the abbreviations (after Arnett and Samuelson, 1969) for these collections used in the paper.

AMNH	Department of Entomology, American Museum of Natural History, New York, New York 10024. L. Herman, Jr.
ANSP	Department of Entomology, Academy of Natural Sciences, Philadelphia, Pennsylvania 19103. M. G. Emsley.
BMNH	British Museum (Natural History), Cromwell Road, London, S.W.7, England. P. M. Hammond.
CAS	Department of Entomology, California Academy of Sciences, San Francisco, California 94118. H. B. Leech.
CCC	Claude Chantal collection, 425 St-Olivier, Quebec 4, Quebec.
CNCI	Canadian National Collection of Insects, Entomology Research Institute, Ottawa, Ontario. H. Howden, J. M. Campbell.
CUIC	Cornell University Insect Collection, Department of Entomology, Cornell University, Ithaca, New York 14850. L. L. Pechuman.
ENCB	Escuela Nacional de Ciencias Biologicas, Instituto Polytecnico Nacional, Mexico 17, D. F., Mexico. C. Bolivar y Pieltain.
FMNH	Field Museum of Natural History, Chicago, Illinois 60605. H. Dybas, R. Wenzel.
FSCA	Florida State Collection of Arthropods, Florida Department of Agriculture, P. O. Box 1269, Gainesville, Florida 32601. R. E. Woodruff.
GHNC	G. H. Nelson, Kansas City College of Osteopathy and Surgery, 2105 Independence Avenue, Kansas City, Missouri 64124.
HAHC	Henry and Anne Howden Collection, Department of Biology, Carleton University, Ottawa, Ontario K1S 5B6, Canada.
INHS	Illinois Natural History Survey, Urbana, Illinois 61803. M. Sanderson.
JHSC	Jorge Hendrichs S., Apdo. Postal 11–774, Mexico 11, D. F., Mexico.
KS	Karl Stephan, 3038 E. Eastland Street, Tucson, Arizona 85716.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138. P. J. Darlington, Jr., J. F. Lawrence.
MNHN	Museum National d'Histoire Naturelle, Laboratoire d'Entomologie, 45 bis, rue de Buffon, Paris V^{e}. M. A. Villiers.
NR	Naturhistoriska Riksmuseet, Entomologiska Avdelningen, 104 05 Stockholm 50, Sweden. T. Nyholm.
NYSM	New York State Museum and Science Service, Albany, New York 12224. J. A. Wilcox.
PISZ	Polish Institute of Systematic Zoology, Slakowska 17, Krakow, Poland. W. Szymczakowski.
PURC	Purdue University Entomology Research Collection, Department of Entomology, Lafayette, Indiana 47907. R. H. Arnett.
SEMC	Snow Entomological Museum, University of Kansas, Lawrence, Kansas 66044. G. Byers.
SBP	Stewart B. Peck, Department of Biology, Carleton University, Ottawa 1, Ontario, Canada.
TCB	Thomas C. Barr, Department of Zoology, University of Kentucky, Lexington, Kentucky 40506.

TAMU	Department of Entomology Collection, Texas A & M University, College Station, Texas 77843. H. R. Burke.
UANH	Museum of Natural History, University of Alabama, Box 5897, University, Alabama 35486. H. Boschung.
UBCZ	Spencer Entomological Museum, Department of Zoology, University of British Columbia, Vancouver 8, British Columbia, Canada. G. G. E. Scudder.
UMMZ	University of Michigan Museum of Zoology, Ann Arbor, Michigan 48104. R. D. Alexander.
USNM	United States National Museum, Smithsonian Institution, Washington, D. C. 20560. P. J. Spangler, J. M. Kingsolver.
VMKC	Vernon M. Kirk Collection, USDA, Northern Grain Insects Research Laboratory, University Station, Brooking, South Dakota 57006.

When sufficient numbers are available paratype and representative specimens of material from my collections are placed in the following collections in the order indicated: SBP, MCZ, TCB and UANH for cave species, USNM, FMNH, AMNH, CAS, CNCI, BMNH, JHSC, ENCB for Mexican and Guatemalan species.

Localities of specimens were determined from labels with the specimens. These localities are given for each species alphabetically, by country, state or province or department, and county in that order. More exact localities are listed after the county, with reference to human settlements and sometimes habitat in parentheses. Distance from settlements and elevations are recorded as on the labels and are not here uniformly changed into the English or the metric system. Variations result from the various maps and instruments available to the different collectors, and whether a distance is taken as road or airline. Localities that cannot be found on maps and atlases available to me and placed in a county are placed at the end of the state list. Material with only state locality is not used. Unlocatable localities are not indicated on the distributional maps. The number of specimens from the locality precedes the parentheses enclosing the abbreviation of the collection in which the particular specimens are located.

Cave locations are generally available only from special publications. I know of the following published surveys concerning areas from which cave-inhabiting *Ptomaphagus* are known to occur: Alabama (Tarkington, Varnedoe, and Veitch, 1965; Jones and Varnedoe, 1968); Guatemala (Gurnee, 1968); Illinois (Bretz and Harris, 1961); Mexico (Russell and Raines, 1967); Missouri (Bretz, 1956); and Tennessee (Barr, 1961a). In Alabama, in a few possibly confusing situations regarding cave names, the name is accompanied by the number of that cave in the Alabama State Cave Survey. I have coined a few names for caves in Tennessee that are not listed by Barr, basing the name on a nearby, named, prominent, topographic feature.

Field Methods

The secretive nature and substrate occupation of *Ptomaphagus* do not lead to easy collecting. Occasional specimens may be found in forest litter, or mammal nests, or in caves. The large series of specimens required for careful population study demands the use of mass collecting techniques. These are baited pitfall traps, and Berlese funnels.

Traps and baiting. The use of baited pitfall traps has been a long-suggested method of collecting terrestrial arthropods. The method has the advantage that it can concentrate a normally dispersed fauna, and then capture and retain the individuals until the investigator has the opportunity to revisit the site. Many techniques of trapping are given in Southwood (1966). A technique of trapping in caves has been described by Barber (1931).

The traps I used in caves from 1965 to 1968 were modified from those of Barber. A plastic cup, without a handle, with a volume of about 3/4 of a pint, was sunk in the floor of the cave in an area suspected to harbor *Ptomaphagus.* Into the cup was poured a 1/2-inch depth of Galt's solution (1 part KNO_3, 1 part chloral hydrate, 5 parts NaCl, dissolved in 100 parts water, all by weight). This salt solution narcotized and drowned the insects, and then retarded decay for over one month. Over the mouth of the trap was placed a square of 1/4-inch mesh hardware cloth, which kept out such large animals as crickets. From the hardware cloth the bait was suspended by a wire so that it hung in the cup above the solution. A large flat rock over the trap was necessary to prevent vertebrate predators and scavengers from stealing the bait. The best bait for trapping cave *Ptomaphagus* was found to be a piece of decayed hog liver or human dung wrapped in a piece of gauze. Similar small traps can be used in animal burrows (gopher tortoise or pocket gopher) or at the entrance to animal dens, all preferably after the vertebrate occupant is removed. These small traps (unbaited) also work on the mounds of *Pogonomyrmex* harvester ants (Melander, 1902).

Larger versions of these traps (using empty number 10 cans) were used extensively in forests in the United States, Mexico and Central America, and the West Indies. Here, the better bait seemed to be human dung. Carrion would attract *Ptomaphagus* only infrequently and unpredictably.

From 1968 to 1970 the fluid used in the traps was water with a small amount of liquid detergent, the salt solution being judged unnecessary. In 1971, in over four months of work in Venezuela, El Salvador, Mexico, and the southeastern United States, I found that an even better trap came into either the carrion or dung. Howfluid is a 50/50 mixture of water and laboratory grade ethylene glycol.

The use of baits, without traps, never gave satisfactory results in forests. It was too difficult to collect any beetles that ever, in caves baiting without traps is a very effective way of attracting the beetles. In several cases, a cave known to be inhabited by *Ptomaphagus* would be searched and none would be found. In such caves, a few pieces of carrion or dung bait placed under rocks in the cave would attract from several to hundreds of beetles within a week. When working on the edge of a species range, baiting is a useful technique to determine if the cave is populated with *Ptomaphagus.* If repeated baiting does not draw the beetles, it is safe to conclude that the cave is not occupied, and is outside the species range.

Berlese funnels. Many specimens of *Ptomaphagus* have been taken by me and others using funnels with the Tulgren modification (see Southwood, 1966: 144). Litter samples were taken from open forest floors, stump holes, root buttresses, and litter accumulations on the uphill sides of logs. The leaves, humus and soil were sifted in the field through a 1/2-inch mesh screen to remove unrotted leaves, stones, and sticks. The sifted debris was carried and stored in large plastic bags (holding 20–30 pounds) until it could be placed in the funnels. The litter was sifted a second time just before being placed in the funnels. When processed, three liters of litter were placed in each funnel (45 cm high, 30 cm across the top, with the screen 10 cm from the top) on a double layer of cheesecloth supported by the screen. A 60-watt bulb was used over the litter. Two thin wood or cardboard strips separated the top of the funnel from the rim of the bottom funnel and provided ventilation and allowed the escape of excess moisture. Samples were changed at 12-hour intervals. During the periods of maximum operation, up to 24 funnels were used, each holding three-liter samples of litter for 12 hours. In this way up to 144 liters of litter could be extracted in each 24-hour period. The magnitude of this collecting is expressed in the following figures. In 1967 I Berlese-extracted the fauna from 3114 pounds (net weight) of sifted litter (2884 liters) from the eastern United States; in 1968, 4401 pounds (4530 liters) from the eastern United States and 192 pounds (199 liters) from Jamaica; in 1969, 1005 pounds (1090 liters) from the eastern United States and 1224 pounds (1312 liters) from Mexico; and in 1970, 152.7 kg (407 liters) from the eastern United States. This is a total of a minimum of 4664 kg (10,422 liters) of litter processed in the term of field work since I began to keep records. The residues of these collections have been deposited in the FMNH.

The arthropods extracted in this way fell into 70 percent alcohol preservative. All other collections were preserved in "Barber's Fluid" (Valentine, 1942). Barber's Fluid does not harden the tissues of the beetles as does alcohol. The soft and flexible tissues allow easy dissection of the male and female internal genitalic structures that are so important in species recognition. With Barber's Fluid preservation, a beetle's appendages can be manipulated into a position for maximum visibility of critical features before mounting on a point.

Laboratory Methods

Cleaning. Freshly collected and preserved specimens as well as old, dry museum specimens are frequently covered with grease, and adhering debris. Specimens were often cleaned in an E/MC Corp. ultrasonic cleaner in 95 percent ethyl alcohol. However, this may result in the breaking off of some of the apical antennal segments. Dry-pinned material was softened for dissection in boiling water.

Dissections. Dissections were made with insect pins. Dissections are easily performed on material preserved in Barber's Fluid because the genital aperture may be easily opened, the genital structures may be easily hooked, and the aedeagus everted or the spermatheca extracted with a pin or minuten needle. This is not the case for material that is pointed and dried. After they have relaxed in boiling water, the last four segments of the abdomen are usually removed from the specimen in 95 percent alcohol. The specimen is repointed and the abdomen dissected for the aedeagus. Dissecting the abdomen in search of the very fragile female spermatheca is risky in previously dried material. The safest procedure is to place the separated end of the abdomen in a hot KOH solution, and to thus dissolve the tissues away from the spermatheca. The KOH treated material was then washed in water acidified with glacial acetic acid.

Mounting. Aedeagi were observed free in alcohol, on temporary glycerine mounts, and early in the study, on permanent slides made with water soluble "Down's Medium" (polyvinyl lacto-phenol clearing medium; Barr, 1961b). Interpretation of permanent slides must be made with caution because distortion can result from the pressure of the cover glass. Female spermathecae were examined in alcohol or as temporary glycerine mounts. All structures removed in dissections were placed in a small polyethylene microvial (obtained from Arthropod Specialties Co., Sacramento, Calif.) with a drop of glycerine and the plastic plug of the vial was fastened to the pin under the specimen.

The specimens not stored in Barber's Fluid were mounted on stiff paper points on insect pins. The adhesive used was an ethyl alcohol soluble plastic compound called "Elvar," made by Dupont. The mounting point, with the tip bent at a 45-degree angle, was touched to the right side of the specimen's mesosternum. Customary labelling procedures followed.

Illustrations. Drawings of antennae, aedeagi, and genital segments were made by tracing projections of glycerine mounts.

Antennae were oriented so that the drawing represents the broadest outline. Parameres and setae are omitted from aedeagal drawings because these do not add to the value of the drawing. Drawings of spermathecae and dorsal views of aedeagal tips were made with an ocular grid and squared paper. Measurements of antennal segments, pronotum, elytra and eyes were made with a calibrated ocular micrometer in a Leitz stereoscopic microscope, with proportions calculated with a slide rule. Other proportions are visual estimates.

Determination procedure. As material became available to me I tentatively identified it by using existing keys and descriptions, and later, I grouped each tentative species into sets representing local populations, using label information. I compared the sets within themselves and between themselves, using the traditionally important characters of antennal segment proportions, shape of the female elytral apex, and the male aedeagus. I did not find these to give unequivocal results. Continued study of structures within populations showed that characters of equal or greater value lay in the mesosternal carina and its notch in the cave species, the genital segment of the male with its sternite (spiculum gastrale) and two lateral pleurites (genital plates), and the shape of the chitinized female spermatheca. At the end of the study I concluded that the generally most valuable single character for species recognition was the female spermatheca. I know of its previous utilization only in three species of *Ptomaphagus* in Great Britain (Kevan, 1963).

I have found *Adelops* species to be delimited by recognizable morphological discontinuities. In all cases but one the "gap" involves the shape of the spermatheca and at least one character on the male aedeagus or genital plate. I have found these characters to be consistent within populations. Populations are considered to be conspecific if they are from the same or different geographical localities and their genitalic morphology is identical, or if they show intergradation of differences in internal or external characteristics (when present) in geographically neighboring areas. Populations are judged to represent different species in the same or different geographical localities if they differ in genitalic morphology and at least one external character, and do not display intergradation. Problems, however, result in the application of these criteria in separating *nevadicus* and its "*piperi* form" and in the spermathecal variation in *hatchi,* and *brevior.*

Subspecies have been used sparingly, and then only with a few cave-limited species. They represent populations that (1) differ in a few characters, mainly minor differences in the spermatheca, and (2) are also judged to be separate evolutionary units owing to isolation of a geologic or physiographic nature from other populations of the species.

Measurements. These have been sparingly used. They are not judged to be of great importance in diagnosis and determination of *Adelops.* The lengths and widths are from individuals that appeared to the unaided eye to represent the limits of the ranges of size variation. The total length is the chord of the arc from the reflexed head to the elytral apex. The ratios of pronotal and elytral lengths to widths are from small samples judged to be representative of the species. The elytral length was measured as the chord of the arc from the tip of the scutellum to the elytral apex.

BIOLOGY

Many of the general aspects of the biology of *Adelops* have been summarized in the introduction to this work. Specific details are found in the systematic revision in the notes on each species. This includes generalizations about habitats and seasonality. The present section will consider the biological and evolutionary modifications of morphology, anatomy, and behavior.

Life cycle data will be presented in a later paper. The emphasis will be upon comparing and contrasting the epigean and the hypogean *Adelops,* and then in comparing and contrasting the *Adelops* with the Bathysciini. More comparative information exists for the biology of the highly specialized bathysciines than for all the rest of the Catopinae combined. Community and population biology will be treated separately in a later paper. Brief data on the life cycle and ecology of some cave species is in Peck, 1967a and 1967b.

For the sake of clarity in the following discussions and comparisons I here introduced my evaluation of the ecological groupings of the species.

Free-living (epigean) species. The species are generally widely distributed and winged, and are usually found in mesic forests. To this category also belong the tentative seven undescribed species from Mexico and Guatemala. The species are: *altus, brevior, championi, consobrinus, jamesi, leo, newtoni, oaxaca ulkei.*

Underground nest and burrow (hypogean) species. These live mostly in the soil in the nests and burrows of small mammals, owls, tortoises, and ants. None are host specific. The eyes and pigment may be reduced. All are fully winged. The species are: *californicus, fisus, nevadicus, schwarzi, texanus.*

Edaphophiles. This category includes species inhabiting deep lowland or montane litter and humus. The species have small, pigmented eyes and are wingless. The species are: *meximontanus, shapardi, talamanca.*

Troglophiles (facultative cavernicoles). These species are abundantly known from caves and reproduce there. Their morphology does not suggest that they are cave limited or adapted. They all have large eyes and large wings. This list excludes species that are known from caves but that are judged to be only occasional cave visitors or inhabitants. The troglophiles are: *cavernicola, clabra, spelaeus.*

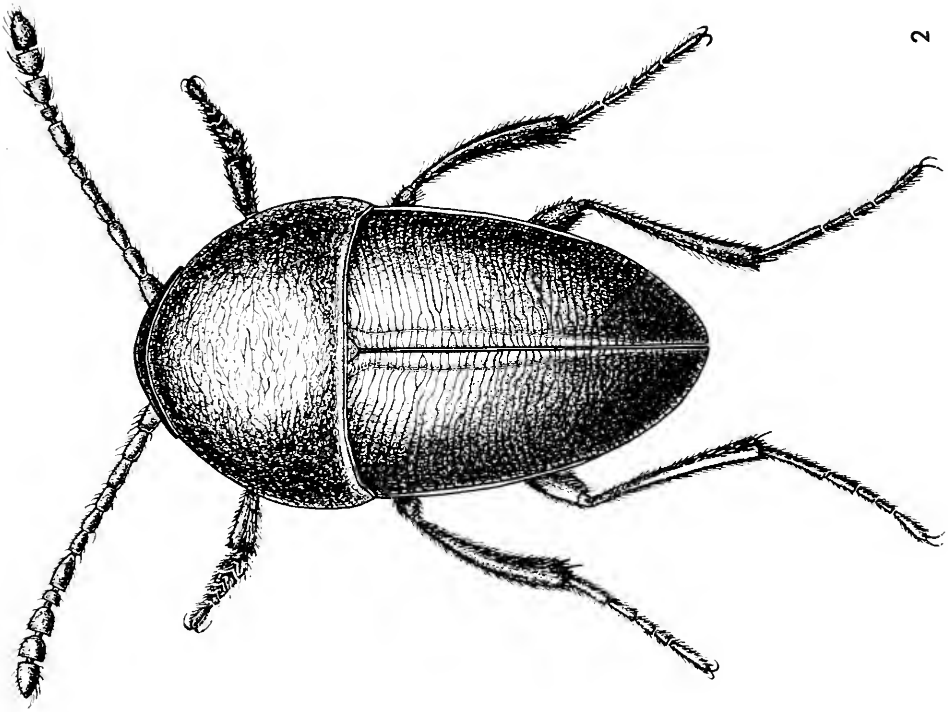
Troglobites (obligate cavernicoles). These species are all known only from caves. They have either small, pigmented eyes, or pale areolae, and all are wingless (or at least with wings reduced to a point judged useless in flight, except in *giaquintoi,* which is fully winged). The species are: *barri, cocytus, episcopus, fiskei, giaquintoi, gypsum, hatchi, hazelae, hirtus, hubrichti, loedingi, nicholasi, troglomexicanus, valentinei, walteri, whiteselli.*

Morphology

Ptomaphagus is mostly holarctic in distribution. Szymczakowski (1964: 60) notes that across this great geographic range the genus presents to the eye a striking monotony. This monotony exists in spite of the considerable number of species. After my following revision of the North American species in the subgenus *Adelops* I find this monotony still to be strikingly present. There has been little development of external morphological differences between the species. This at first forced reliance for species recognition upon the male aedeagus. I now believe the characters of the female spermatheca to be even better for species recognition. However, these species differences are far from being as distinct as the characters of the male and female genitalic structures in many other groups of insects.

Adults. The most striking known changes in the *Adelops* are in the adults (Figs. 1–3). These will be considered first, and the larvae secondly. These differences in morphology are all correlated with what I believe are changes in the occupation of adaptive zones. In other words, as populations began to colonize habitats other than the ancestral habitat of forest litter, the populations experienced new selective pressures, and responded to them. The comparative responses to these pressures, in adult morphology, have been most striking in the troglobitic species.

The morphological expression of adapta-



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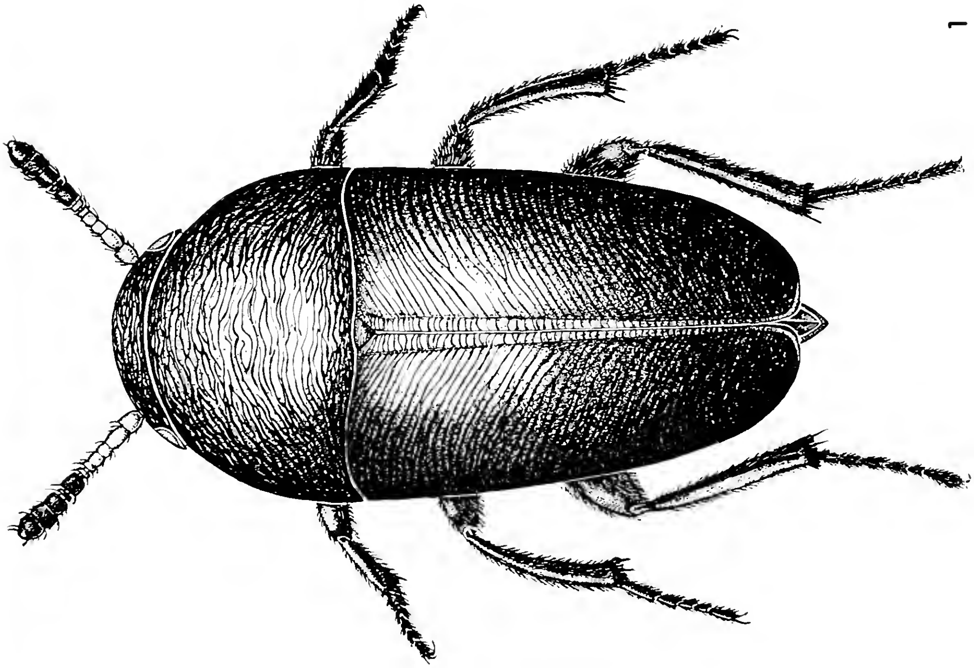

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Figures 1–2. Comparison of general morphology of an epigean and a troglobitic species of *Ptomaphagus*. Fig. 1, *P. consobrinus*. Fig. 2, *P. hirtus*.

tion to subterranean environments is reflected to various degrees in the many species that occupy these habitats. In this category I include not only caves, but cavelike habitats which may offer similar environmental conditions. The *Adelops* of the burrows of animals like pocket gophers display some features very similar to those of species inhabiting caves. Ant nests might also seem to offer cavelike conditions of darkness, a high humidity, and perhaps coolness.

The changes of morphology that have followed the occupation of caves and cavelike habitats can be grouped into two categories. The first category, that of regressive changes, may not be influenced by direct selective pressures for the maintenance of ancestral characters of the population. The character regression may be due to relaxed selection. An alternative explanation is that selection is actively working to remove characters that are no longer advantageous, and may actually be disadvantageous in the cave environment. Under such regressive changes are discussed the reduction of eyes, wings, and pigment. The second category of change, that of progressive changes, seems likely to be a response to active selection. This is most probably the cause of the uniform tendency for elongation of the legs and antennae in the troglobites.

Regressive changes. Numerous explanations have been proposed for the regressive changes in eyes and pigment in cave inhabitants. I will not review these because this has been very well done by Barr (1968). His conclusion is that regressive evolution may be the possible effect of two theories: 1) material compensation (or the economy of developmental energy), or 2) the indirect effect of pleiotropy (combining the effects of pleiotropy, polygeny, mutation pressure, sampling error, limited genetic potential, reduction of variability, and selection). He favors the second alternative.

Eyes. It is possible to construct a sequence of species of *Adelops* exhibiting eye reduction (Figs. 4–6). Such a sequence should be based upon comparing a changing feature of the eyes, such as their horizontal diameter, with a feature that should not be expected to change, such as the lateral width of the head. This has been done in a limited way by Peck (1968) in four species of *Adelops.* Ratios of eye width to head width regress from 0.67 to 0.29 from the largest eyes of *P. brevior* (incorrectly called *consobrinus* in Peck, 1968) to the smallest eyes in *P. loedingi loedingi.*

The ancestral condition of the eye is large, as is seen in Figure 4. This is correlated to forest-litter habitats, and the species generally have wide ranges. In the oldest surviving species group (*hirtus* group), the large-eyed condition no longer exists. An intermediately reduced eye is found in the *hirtus*-group species *shapardi* (Fig. 5), which is a soil and deep-litter inhabitant of the Ozark region. From an ancestor of this sort the remaining *hirtus*-group species (all troglobitic) have probably descended. All these have the eyes reduced to a pale (unpigmented), indistinctly faceted areola (Fig. 6). No *Ptomaphagus* is without at least an eye vestige.

Eye reduction is present but not great in animal-burrow inhabitants of the *consobrinus* group such as *nevadicus, fisus,* and *schwarzi.* In this group, reduction is greatest in the cave-inhabiting *cocytus* and *giaquintoi,* but here the eye width still occupies about half of the head width. In the *cavernicola* group eye reduction is not evident in the cave-inhabitating species *elabra.* All populations of *cavernicola* except that in Cueva de la Boca show little or no eye reduction. Eye reduction in the troglobites *gypsum* and *troglomexicanus* is great, but not as great as in the troglobites of the *hirtus* group. The montane species *altus* (*cavernicola* group), *talamanca* and *meximontanus* (neither assigned to a species group) show marked eye reduction.

In addition to eye size, there is a change

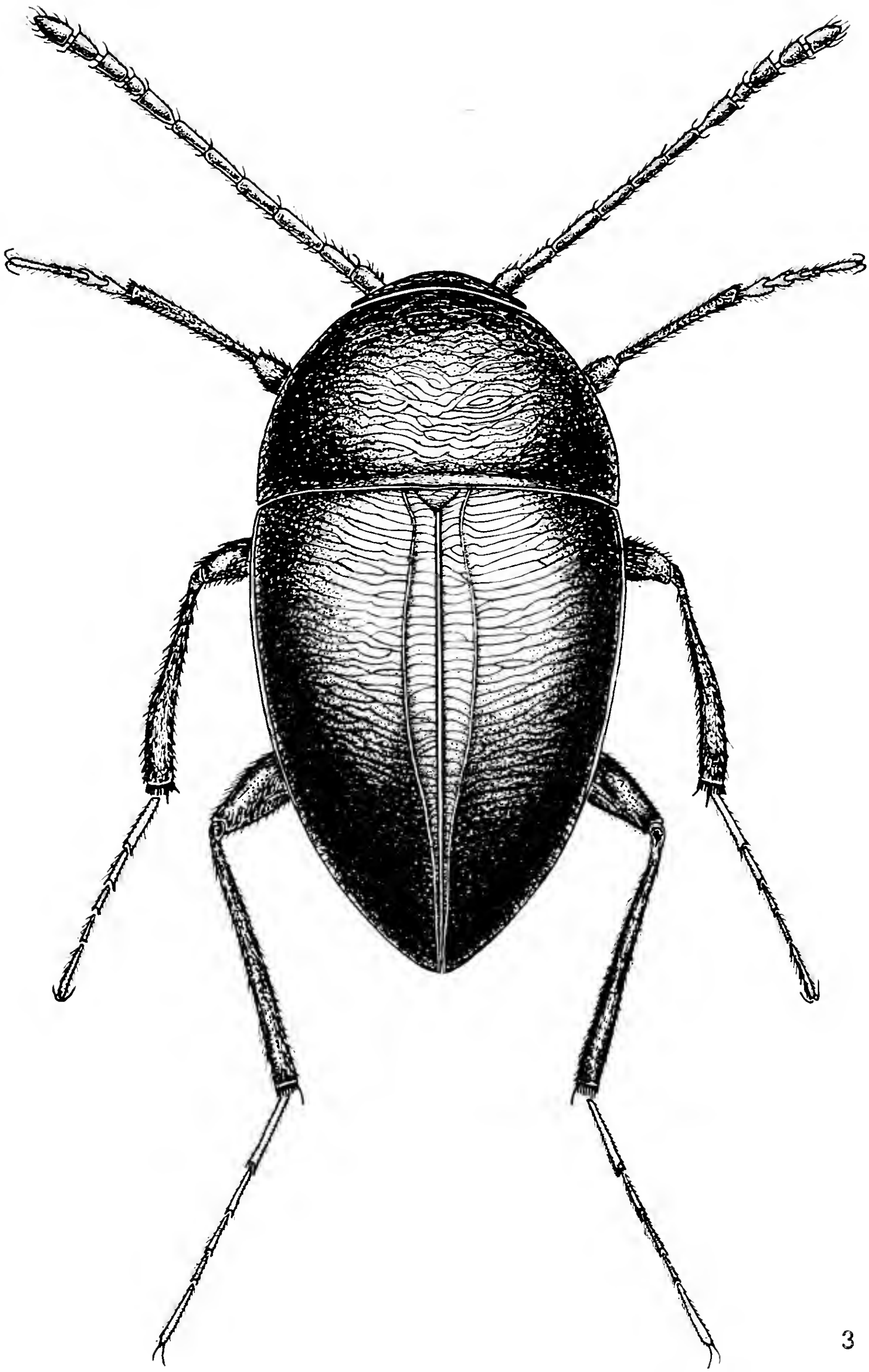
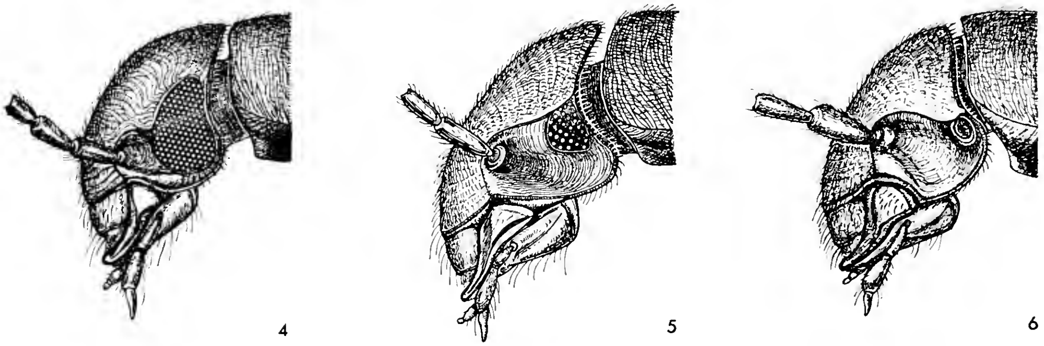


Figure 3. Highly modified troglobitic species, *P. loedingi longicornis*. Compare with Fig. 2, both drawn to same scale.



Figures 4–6. Comparative series demonstrating correlation of eye reduction and habitat restriction. Fig. 4, *P. consobrinus*, wide ranging, epigean. Fig. 5, *P. shapardi*, range in western Ozarks, edaphophilic. Fig. 6, *P. hirtus*, Mammoth Cave region of Kentucky, troglobite. All drawn to same scale.

in the possession of eye pigment. In all cases of eye reduction, only the troglobites of the *hirtus* group, and *gypsum* and *troglomexicanus* have lost the eye pigmentation. The pigmentation is present in the troglobites *cocytus* and *giaquintoi*. Obviously a need exists for the retention of eye pigment in the soil and animal-burrow species so that they can detect light, and avoid it. This need for retention of the optic pigment has obviously decreased for the troglobites.

In the troglobitic *Ptomaphagus* the eyes have not been fully lost. None of them is, strictly speaking, eyeless. However, those that have none of the optic pigment necessary for insect vision can certainly be called blind. Blindness will also result with neural degeneration of the optic tract. The head of the troglobite *P. hirtus* of Mammoth Cave was examined by Packard (1888: 116) and no optic ganglia or optic nerves were found. This lack of neural connection between the brain and the eye rudiment can be assumed for the other troglobitic species of the southeastern United States.

As indicated, all the troglobitic *Adelops* possess eye rudiments. This contrasts strongly with the bathysciines, with the great majority of the 581 Eurasian species being completely anophthalmic. This is a rule in western Europe, but a few eastern European species possess eye vestiges or rudiments. The least reduced of all bathysciine eyes is found in *Adelopsella bosnica*, which is comparable in body size to *P. hirtus*. There are about ten pigmented facets in the eye. The size of these eyes, the least reduced in all the bathysciines, is that of the most reduced *Adelops* eyes.

The American troglobitic trechines also exhibit more eye loss than does *Adelops*. In six trechine genera and about 175 species eye vestiges are completely absent, except in seven species of *Pseudanophthalmus*.

Wings. The loss of wings in beetles is not a phenomenon limited to caves. It occurs in many habitats. Darlington (1936, 1943, 1970) has reviewed and examined some situations selecting for wing reduction in carabid beetles in temperate and tropical, continental and island environments. In many cases in carabids wing dimorphism is present, exhibited as long-winged individuals capable of flight, and short-winged individuals incapable of flight.

In *Adelops*, wing dimorphism within a species is not known. Every individual examined has wings similar to those of the other members of the population and the species. There are three categories of wing condition under which the *Adelops* may be grouped: 1) Fully winged species, which

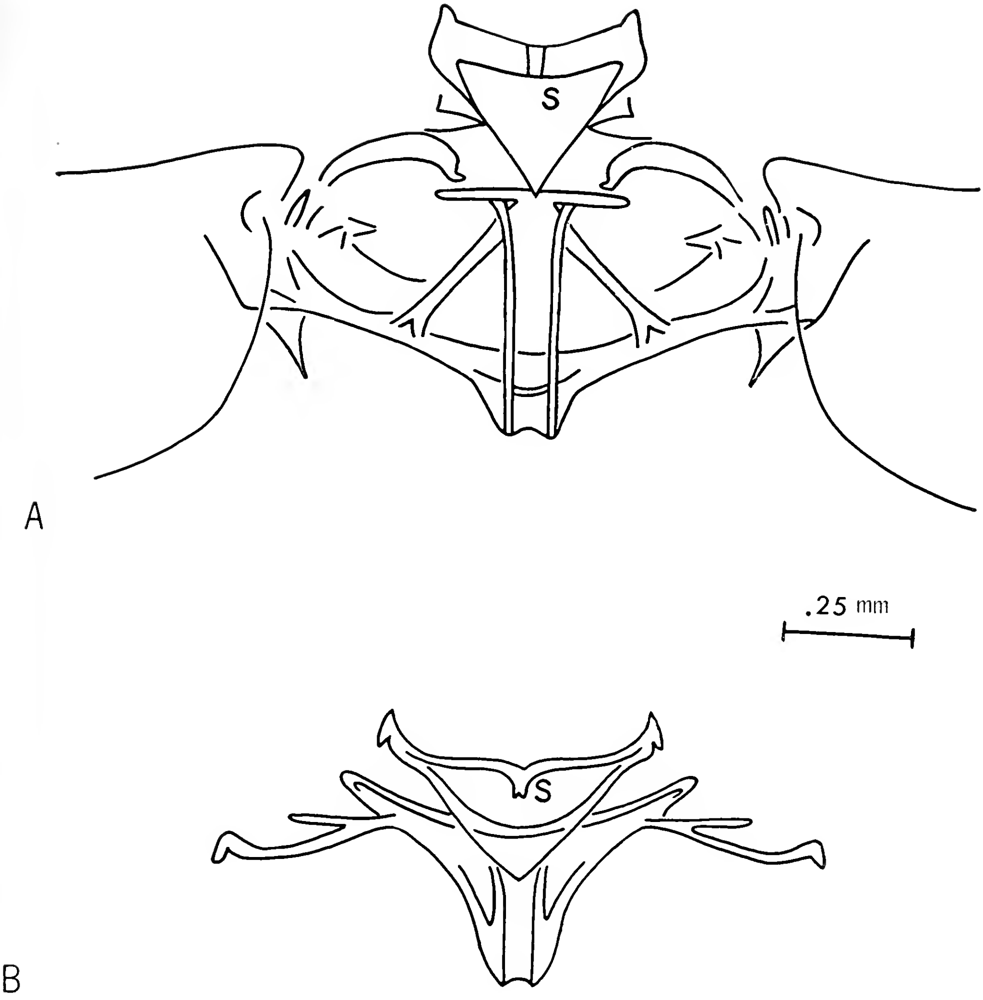


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Figure 7. Meso- and metathoracic tergites in *Ptomaphagus*, showing large condition in winged species (A, *P. consobrinus*) and their reduction in a cave-inhabiting species which has wings reduced to a tiny scale (B, *P. hirtus*).

are "free living" and occupy most epigean habitats, as well as the troglophiles, and the troglobite *giaquintoi*; 2) short-winged species, represented by the troglobites *cocytus* and *gypsum* with wings 3/4 the length of the elytra; and 3) wingless species, possessing only a scalelike wing rudiment, containing the edaphophilic and the remaining troglobitic species.

In addition to loss of wings, meso- and metathoracic changes occur. The changes are due to the loss of flight muscles, and the reduction of sclerotized thoracic surfaces serving as attachment surfaces for these muscles. Figure 7 illustrates the comparative reduction in sclerotized regions of meso- and metathoracic tergites in a winged epigean, and a wingless troglobitic species. Darlington (1970) mentions that metasternum reduction accompanies flightlessness in carabids. This is true also in *Ptomaphagus*, although the generalization was tested only on a small sample of specimens of only two species. In *cavernicola* (winged) the ratio of the metasternal length to width is 1:1.8, and in *troglomexicanus* (a wingless derivative from *cavernicola*) the ratio is 1:2.6. Clearly, in this pair of species, flightlessness is accompanied by a reduction in relative metathoracic length.

Pigmentation. The loss of pigmentation in cave animals is most striking in vertebrates and crustaceans that appear white. Cave beetles never become entirely colorless because of a cuticular darkening that accompanies cuticular sclerotization. However, this darkening is less in the troglobitic beetles, probably because of decreased sclerotization accompanying the reduction or loss of actual pigmentation. The epigean species of *Adelops* are darker than the hypogean species. The burrow inhabitants such as *schwarzi* and *texanus*, and the edaphophile *shapardi* are as light as the *hirtus* group troglobites, and *giaquintoi* and *cocytus*. Pigment reduction is only slight in the troglophiles *cavernicola* and *elabra*.

Progressive changes. Comparatively few groups of animals have been able to adjust successfully to the transition from life above ground to life in caves. The many that have show adjustments in morphology and other qualities that preceded cave occupation. Such changes that are adaptive for certain epigean habitats can also be adaptive for cave habitats, and are referred to as "preadaptive." Successful cave colonizations have occurred in North America only in beetle groups already living in cool, dark, moist habitats, quite often at higher montane elevations. Probably the strongest preadaptations are behavioral and physiological.

The events of preadaptation, colonization, and adaptation are presented by Barr (1968), and will be considered for *Adelops* in the discussion of evolution. Once cave occupation was achieved, different sets of selective pressures operated upon the populations. The most striking progressive adaptation in troglobitic beetles is the tendency for elongation of the appendages (seen clearly in Figs. 1–3). However, their selective advantage is not clear (Barr, 1968). Perhaps elongation of appendages provides more surface area to be covered by sensory hairs. Perhaps leg elongation allows the beetles greater searching ability in food-poor caves. But if there are advantages in having longer appendages, why have they not also appeared in the epigean Trechini, Ptomaphagini, and Pselaphidae? It is probably because the epigean species dwell in habitats constricted by rocks, roots, moss, and debris where the longer appendages would be a hindrance rather than a help. The epigean species must remain in these constricted habitats for the conservation of moisture, and the avoidance of heat, light, and predators. With the ancestral entry into caves, the predation pressures were lessened because the predator species diversity and density in caves was less than in epigean situations. The suitable darkness, coolness, and the moistness of caves allowed an ecological release which opened the possibilities of foraging on the surface of the cave soil substrate rather than under the surface (such as in epigean soil, litter, and moss). In fact, the caves presented very few opportunities for subsurface foraging compared with epigean environments. Hence, one of the requirements for successful cave occupation was the ability of the colonizer to act as a surface forager. From the substrate surface occupation in caves came release from the selective factors that had kept appendages short in epigean subsurface species.

Mesosternal carina. I do not know of any previous works that have considered this structure in relation to cave adaptation. In *Adelops* I have noticed that its degree of development is strongly related to the general degree of cave specialization of the species, and thus it is a progressive structure (Figs. 78–97). In the *hirtus* group it is low in *shapardi,* and of medium-to-high development in the troglobitic species. In the *consobrinus* group the carina is stronger in the troglobite *cocytus* than in *fisus,* the ancestral form. All other species in the group have a low-to-medium carina except for the well-developed carina of *giaquintoi,* a troglobite from Guatemala. In a close-knit cluster of species in the *cavernicola* group, the carina is least developed in the forest-inhabiting *oaxaca,* more developed in *cavernicola,* and most developed in *troglomexicanus,* although in the latter the carina is not as prominent as in the other species-group troglobites.

It is useful to test the idea that the carina is a cave-dependent feature by examining the Bathysciini. The following generalizations are only suggestions because of the limited number of genera (21) and species (38) that I have examined. The carina is low in *Platycholeus* inquilines. In the Bathysciina (Bathysciini of Laneyrie, 1967) the humicoles *Adelopsella* (which has the largest eyes of the subtribe as noted above) and *Sciaphyes* have a low carina. All of the following considered species and genera are troglobites in the list of Lanyrie (1967). For the most simple analysis they will be considered only with regard to their ecology, body shape (defined later), and carina size and not to their phyletic relationship. Of species (within a genus there is variation in carina size) with a bathyscioid body shape, two have a low carina, four have a medium carina, and 18 species (in five genera, 14 species in *Speonomus*) have a high carina. Of those with a pholeuonoid body shape five species (in four genera) have a low carina and two species (in two genera) have a medium carina. Of those with a leptodiroid body shape, one species has no carina, and another has a very low carina. In the Antroherponina (with six genera), which are all troglobites of the leptodiroid (or scaphoid) body form, the carina is present but very low in *Spelaeobates* and absent in *Antroherpon* and *Remyella.*

I interpret the above observations of Bathysciini as suggesting that the carina is a progressive and cave-dependent structure in the early stages of cave specialization and evolution, defined and characterized by the bathyscioid body shape. This is also true in *Adelops,* which also has this body shape. With further evolution and gradual acquisition of the pholeuonoid body shape the carina partly or completely loses what must be a functional significance. The reduction and loss of the carina occurs as the species acquire the very modified leptodiroid body shape in both the subtribes Bathysciina and Antroherponina. Here the carina is very low at most.

Discovery of the functional significance of the carina may come from careful studies of comparative behavior, combined with functional morphology. The answer probably lies in a combination of factors involving digging, walking, burrowing, and hiding.

Appendages. Figure 8 is a series of antennae demonstrating the length-to-width proportions of species of different species groups, ecologies, and levels of adaptation. Figures 15 and 16 demonstrate the comparatively more slender femur of *cocytus,* and its probable ancestor *fisus.* A preliminary documentation with measurements of antennal and leg elongation was presented by Peck (1968). The troglobitic *Adelops,* unlike agonine carabids and some pselaphid beetles do not demonstrate an elongation of maxillary palps.

In comparison to *Adelops* an interesting summary of the morphological trends of the preadaptation and adaptation of the Bathysciini is that of Vandel (1965: 204). He views the process, summarized below, as conclusive "orthogenetic evolution." I do not, because I believe the direction is determined by natural selection, which is excluded in orthogenesis (Mayr, 1963).

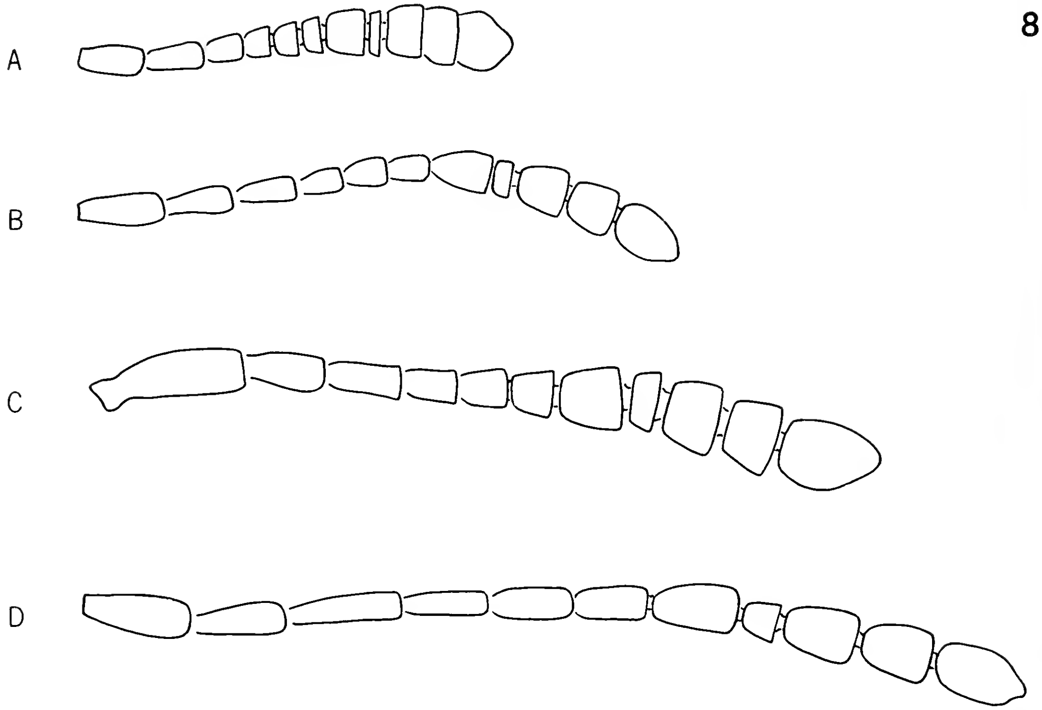


Figure 8. Progressive elongation of antennae in *Ptomaphagus*. The increased length is partially due to an allometric increase in body size, but is more closely related to overall degree of cave adaptation of the species. A, *P. consobrinus*, epigean. B, *P. hirtus*, troglobite. C, *P. cavernicola*, troglophile. D, *P. loedingi longicornis*, troglobite. All to same scale.

The bathysciines were preeminently preadapted for cave life. All of the surviving noncave species possess characters associated with cave life. The early evolution was probably associated with montane forests, during which they became depigmented, wingless, and eyeless (or at least microphthalmic). The early stages of cave colonization were accomplished by preadapted forms similar to the Mediterranean moss-inhabiting genus *Bathysciola*. Cave evolution proceeded independently in two directions in Mediterranean Europe owing to a seaway separating the western Tyrrhenian form the eastern Aegean stocks of Bathysciini. A large number of endogean (edaphobitic) and little-specialized cavernicoles are found today, having an ovoid body and short appendages. Such "bathyscioid" types are *Speonomus* (Pyrenees), *Diaprysus* (Cevennes), *Cytodromus* and *Royerella* (Alps) in western Europe, and *Aphaobius, Bathysciotes,* and *Neobathyscia* in eastern Europe.

In the final stages of evolution, not only the appendages, but also the body became more elongate. Body elongation is not noticeable in *Adelops*. This "pholeuonoid" type of bathysciine also has a thinner pronotum with indistinct or obliterated margins. Such specialized cavernicoles are *Antrocharis* and *Isereus* of western Europe and *Pholeuon* and *Apholeuonus* of eastern Europe. These specialized types sometimes live in extraordinary habitats such as ice caves. For instance *Isereus xambeui* has been found in a French cave with temperatures of 0–1°C, and *Pholeuon glaciale* inhabits an ice hole in Transylvania with summer temperatures rarely exceeding 0.8°C.

Ultra-evolved forms are called the "leptodiroid" type. These are few, and are limited to the Yugoslavian region. The legs and antennae are extremely long, the head and prothorax are narrow and elongate, and the elytra have a tendency to widen. This last results in a spherical abdomen in *Leptodirus*.

A remarkable cave convergence exists between the "leptodiroid" form and a recently described beetle from lava tube caves in Idaho. The Idaho *Glacicavicola bathyscioides* Westcott (Leiodidae; Glacicavicolinae) has a strong external resemblance to the leptodiroid genera *Astagobius* and *Antroherpon*. Its existence in caves in contact with ice recalls the above mentioned pholeuonids, although *Glacicavicola* is seemingly not dependent upon freezing temperatures (Peck, 1969).

Larvae. Except for what will be reported in a later paper on life cycles, I have paid very little attention to *Adelops* larvae. The larvae of only a few epigean species are known to me from only a few specimens. In contrast, through collections and cultures, many larvae are available of several troglobitic species. Although I have not closely compared the larvae of epigean and troglobitic species, in brief examination I have seen that there is only one striking difference between them.

This difference, which may be categorized as regressive, is that in the *hirtus* group troglobites, the larvae have entirely lost the eye spot. No other comparative differences are present.

Larvae of only two species of *Ptomaphagus* have been described and illustrated in the literature: the epigean *P. sericatus* from Spain (Jeannel, 1922: 50) and the troglobitic *P. hirtus* from Kentucky (Jeannel, 1931: 409; Böving and Craighead, 1933: 109). When these larvae from different habitats and different continents are compared no differences are evident except in the eyes.

The larval uniformity of *Ptomaphagus* is, again, in striking contrast to the larval differences of the bathysciines. Deleurance-Glaçon found many regressive changes in larval morphology associated with life-cycle modifications. These modifications are all a response to a decrease in importance of the larval stage in the life cycle.

The classic (nonevolved) larval type, consisting of two or three instars of larvae that feed, was found to be characterized by the following morphological points (Deleurance-Glaçon, 1963a: 71):

1. All large dorsal cranial, thoracic, and abdominal hairs composite.
2. Body normal, not fat with food reserves.
3. Mandibles dissymetrical.
4. Mola with retinaculum and prostheca.
5. Molar teeth numerous, important.
6. Galea with wide thick fringe of setae.
7. Paraglossae visible on dorsal labial face.
8. Cerci long, biarticulated, second article long and ciliated.

The evolved larvae, of only one nonfeeding instar which corresponds to instar I of the classic type, differs in (Deleurance-Glaçon, 1963a: 84):

1. All large dorsal cranial, thoracic, and abdominal hairs single.
2. Body thick, fat with food reserves.
3. Mandibles symmetrical.
4. Mola lacking retinaculum and prostheca.
5. Molar teeth few and small.
6. Galea fringe short and reduced.
7. No paraglossae.
8. Cerci short, uniarticulate.

It can readily be seen that the differences in the evolved larvae are ones involving a decrease or reduction in feeding and sensory structures. The specialized morphology parallels a specialized life cycle.

Anatomy and Histology

The only anatomical and histological work with *Ptomaphagus* is the previously mentioned study of the head of *P. hirtus*

(Packard, 1888: 116), in which it was found that there were no traces of optic nerves or optic ganglia.

The great morphological and life-cycle changes observed in the Bathysciini led Deleurance-Glaçon (1963a) to compare internal characteristics of the beetles. I have not done this with *Adelops* because of the slight prospect of encountering differences. In comparisons of the female reproductive tract, she found that both classic and evolved species have a pair of ovaries, each with five to six ovarioles. There are many active ovarioles in the species that produce small eggs. In the species that produce large eggs, only one ovariole acts at a time in maturing an egg. The ovarioles are acrotrophic (= telotrophic). No major histological differences exist between the ovaries of large and little egg species. The only differences are physiological ones (concerning vitelogenesis), in variation in trophocytes and follicular cells. Oogonia divisions occur in the pupa, beginning in the fourth month of larval life, with no divisions in old pupae or adults of oocytes or trophic tissues.

The ovariole invariability contrasts with findings (Deleurance-Glaçon, 1963b: 234) in a series of troglobitic trechine beetles in which the ovariole number decreases from six per ovary down to one (in five species of *Aphaenops*). This may be connected with the fact that carabid ovarioles are polytrophic.

The bathysciine digestive tract also shows modification between the classic and evolved types. In classic larvae the digestive tract is similar to that of other coleoptera. The mid-gut is large, with a well-developed cavity. The hind-gut is folded upon itself. There are four short and fine Malpighian tubules. In the evolved larvae, the digestive tract is non-functional. The mid-gut is small and closed. The hind-gut is straight, non-functional and very slender. The four Malpighian tubules, entwining the hind-gut, are greatly increased in size and length, with a very narrow lumen. However, the digestive tract of embryos of the evolved species is functional and similar to that of the classic larvae.

Behavior

Most observed insect behavior is associated with reproduction. This is especially true for *Adelops* because, other than in reproduction, they have little or no behavior at all. All the *Adelops* observations reported below were of laboratory cultures of beetles at natural cave temperatures and humidities. The techniques used for culturing the beetles will be discussed in a later paper.

Adults. The beetles are most often observed as motionless. I have not attempted to determine if there is a circadian or other rhythm of activity. Epigean and cave species display a desire to be under soil particles. This is more pronounced in the epigean and troglophilic species. Upon being disturbed the troglobitic species are more inclined to run about than the epigean species.

Nothing differs in feeding behavior between the epigean and troglobitic species except that the epigean species (*brevior*) feed well on human dung but not on wet yeast, which the troglobitic species eat.

There is no courtship behavior. Males will instantly mount females and copulate. I have never seen what appeared to me to be a female rejecting a male. Copulation seldom lasts more than thirty seconds. During copulation the male may antennate the female. I do not know about the other species, but in the troglobites there is no copulatory seasonality or cycle.

During copulation *hirtus* females behave differently than the females of other observed species. Female *hirtus* flex downward at the pronotal-elytral junction, thus elevating the abdominal tip toward the male. The female does not flex in the other species.

All species coat their eggs with small soil particles and debris. This is done by the female at the time that the egg is being extruded from her body. As she extrudes the egg she searches the area around her with her antennae and mouthparts. The soil and debris particles are gathered by the palps and mandibles. As observed in troglobitic species, the female then rears back on her meso- and metathoracic legs, takes the soil particles from the mouthparts with her protarsi and carries them to the egg. The soil is patted onto the egg with both protarsi. This process was observed for up to eight minutes in a female *loedingi longicornis* from Paint Rock Cave.

Data on age at sexual maturity, egg-laying frequency, sperm storage ability and so forth will be given in a later paper. Males and females may remain reproductively competent until their death. This is true for two male *hirtus* at 12.5°C which fathered larvae three years after their capture as adults. There is no obvious egg-laying cycle.

In comparison, Deleurance-Glaçon (1963a) found in the bathysciines that there is no circadian rhythm but that females are more active than the males. In activity, *Speonomus* type (classic) beetles are agile, while *Leptodirus* type (evolved) beetles are slow and clumsy. Activity is a regular variation of rest and activity at temperatures ranging from 0°C–20°C. Lethal points are –5°C and +25°C. There is no feeding cycle in the males, but the females feed according to their egg-laying cycle. There is no pre-copulatory behavior. Copulation is throughout the year, with no refractory period, lasts less than half an hour, and may be accompanied by antennal caressing. Virgins lay infertile eggs irregularly and infrequently. Sperm storage in the females may be as long as 13 months. Sexual maturity is reached three to five months after eclosion. Sexual competency may last through the adult life span of four to five years. Females may lay up to 500 eggs in four years in species with unmodified life cycles (291 actually observed in *Speonomus delarouzeei*) and 60 eggs in four years in species with contracted life cycles (31 actually observed in *Troglodromus bucheti*). There is no seasonal egg-laying cycle. There is a periodicity of egg-laying at about every 25 days in *Isereus serullazi.* The species with the classic (unmodified) life cycle show no periodicity and produce a dozen or more eggs a month. The percent of individuals that are fertile varies from 42 percent to 93 percent and is species dependent.

Larvae. Mature larvae of *cavernicola* show a very strong tendency to climb to the top of the culture box. This may be a reflection of searching for "high ground" for pupation, which may have adaptive significance in lessening the chances of pupal death by flooding. Mature larvae of other species crawled to the top of the culture boxes but never in such large proportions.

Mud cells are made by the larvae only for pupation, never for inter-instar moulting as in the Bathysciinae. A marked difference in cell construction exists between the nontroglobitic and troglobitic species. Both *brevior* and *cavernicola* larvae dig straight down into the clay substrate, pushing the dirt crumbs above them and forming a cell whose top is 2–3 mm under the substrate. Seemingly, predation or other pressures are relaxed in the troglobites because they form a more exposed and vulnerable pupation cell. Their cell is a thin-walled mud igloo rising as a small dome above the substrate. These cells appear not to be strong enough to resist predation of the pupae by cave carabids or crickets. These cells are probably sufficient protection against mites and collembola, which I have seen feed on exposed *Adelops* pupae.

SYSTEMATIC POSITION OF *PTOMAPHAGUS*

Introductory comments are necessary concerning the higher categories containing *Ptomaphagus.* These comments are needed because of the various systems of classification employed in various museums and by various workers in the Old and New Worlds. There is comparative uniformity only on placement of the higher taxa within the superfamily Staphylinoidea. On the family level, the literature of the early 1900's and before placed *Ptomaphagus* in the family Silphidae and usually in the subfamily Catopinae. This is still the case in the *Zoological Record.*

Hatch (1933) reviewed the group for the United States and separated it as a family unit from the Silphidae, a procedure which has been generally followed ever since, and employed the name Leptodiridae. Jeannel (1936) monographed the unit as the family Catopidae, and this usage has strongly influenced continental Europeans ever since.

Within the Staphylinoidea I prefer the conservative, and I believe evolutionarily sound, family classification systems of Hatch (1957) and Crowson (1967). Here the family unit is Leiodidae (=Anisotomidae), containing the subfamilies Catopinae, Leiodinae (=Anisotominae), Catopocerinae, Coloninae, Camiarinae, Scotocryptinae, and Glacicavicolinae. The last was proposed by Westcott (1968).

Family LEIODIDAE

Staphylinoidea with 11-segmented antennae; 5-segmented club; long elytra covering abdomen except for posterior 1 or 2 tergites; front coxal cavities closed behind (except Leiodinae–*Hydnobius*); male almost always with dilated protarsi, hind coxae usually contiguous upon removal of coxae; front coxae transverse or conically projecting. Larvae with mandible with prostheca or retinaculum and mola; maxillae with apex of stipes simple, galea not articulated.

I prefer the family name Leiodidae over Anisotomidae simply because I think it is more widely recognized by coleopterists.

A world study of the subfamily Catopinae was first undertaken by Jeannel (1936). Szymczakowski (1964, 1969a) revised the tribal ranking. I have taken these works and generally lowered the category by a unit to the higher categories that follow because I believe that the taxonomic fragmentation begun by Jeannel is impractical. In the "lumping" system that I follow, the evolutionary relationships are, I believe, better demonstrated. This is a desire on my part to avoid inflating the value of the higher categories. Certainly Jeannel and Szymczakowski contributed many valuable suggestions from their greater breadth of study of the Catopinae and I have tried to pay due consideration to them in the taxonomic arrangement here proposed.

Subfamily CATOPINAE

Characterization. Leiodidae with loose antennal club, segment 8 always smaller than 7 or 9; head with occiput raised posteriorly into a keel which overlies front margin of pronotum (except in Nemadini–Argytodina living only in New Zealand, Australia, and southern South America); front coxal trochantins hidden. Larvae with doubly fringed maxillary galea, urogomphi long, slender, often multi-articulate.

Coordinate taxa. Leiodinae (=Anisotominae), Camiarinae, Scotocryptinae, Coloninae, Catopocerinae, Glacicavicolinae.

The following key, modified from Jeannel (1936), will serve to separate the tribes of Catopinae. Explanatory illustrations may be found in Jeannel. The key is based on male genital characters, which are the least ambiguous characters available, and serve the second function of reflecting relationship and phylogeny.

KEY TO TRIBES OF CATOPINAE

1a. Posterior coxae separated, female with 4 protarsal segments, male with 5 or 4 .... *Bathysciini*

1b. Posterior coxae contiguous, male and female with 5 protarsal segments 2

2a. Male copulatory organ with complete tegmen, parameres not inserted directly on aedeagus 3
2b. Male copulatory organ without tegmen, parameres inserted directly onto aedeagus 5
3a. Genital segment reduced to a chitinous ring around base of aedeagus .... *Catopini*
3b. Genital segment tubular, not reduced 4
4a. Ventral blade of tegmen full and flattened. Epistome indistinct. Next to last maxillary palp segment not swollen. Male mesotarsomeres narrow, or only first segment dilated .... *Nemadini*
4b. Ventral blade of tegmen reduced to narrow transverse chitinous band. Epistome separated at front. Next to last segment of maxillary palp ovoid and swollen, last segment very small. Male with first 2 mesotarsomeres dilated .... *Anemadini*
5a. Aedeagus short, triangular, flat, wide at base; basal blade large and free; last article of maxillary palp long and fusiform .... *Eucatopini*
5b. Aedeagus elongate, oval, narrow at base; basal blade reduced; last article of maxillary palp short and conical .... *Ptomaphagini*

Tribe PTOMAPHAGINI

Ptomaphagus phyletic series, Jeannel, 1922: 41.
Ptomaphagini, Jeannel, 1936: 52.
Ptomaphaginae, Szymczakowski, 1964: 58.

Description of tribe. Form oval, elongate (except in the myrmecophiles *Synaulus* and *Echinocoleus*). Prothorax transversely striate (except in some cave *Ptomaphagus*, and in *Pandania*). Last article of maxillary palps conical, a little longer than preceding segment. Pronotum transverse, widest at base, or up to 1/3 from base. Mesocoxae separated, mesosternum carinate on midline. Mesepimeron and mesepisternum distinct, separated by a suture. Metepisternum wide, triangular or trapezoidal. Metacoxae contiguous. All tarsi pentamerous in both sexes. Summits of all tibiae armed with comb of short equal spines. Genital segment reduced, not tubular, reduced to flattened pleurosternite. Tegmen of male copulatory organ lacking a ventral blade; parameres inserted at base of aedeagus not united by a ventral ring. Aedeagus elongate, sometimes highly modified but never having the form of two triangular valves as in Eucatopini (=Eucatopini *sensu* Jeannel, 1936). Aedeagus basal blade atrophied. Parameres more or less fused to aedeagus. Internal sac of ejaculatory duct armed with long evaginable stylet, but without accessory sclerotized pieces. Aedeagal orifice ventral in primitive species of *Adelopsis, Ptomaphaginus,* and *Proptomaphaginus,* but in most species it has passed to the dorsal surface, cutting the right margin (subtribe Ptomaphaginina) or the left margin (subtribe Ptomaphagina); this displacement produces an asymmetry, sometimes very great (in certain *Adelopsis*).

Coordinate taxa: the subfamilies of Szymczakowski (1964: 59) lowered to tribal status: Eucatopini, Nemadini, Anemadini, Catopini and Bathysciini.

The tribe is distributed throughout much of the New World, and the Palearctic and Oriental Regions. It does not occur in sub-Saharan Africa, or in the Australian Region. It can be easily divided into two major evolutionary lines, here treated as subtribes.

KEY TO SUBTRIBES OF PTOMAPHAGINI

1a. Anterior tibiae with distinct comb of short spines on outer margin, as well as apex (Fig. 11). Mesepisternum transverse, as wide at inner edge as at outer edge (Fig. 9) .... *Ptomaphaginina*
1b. Anterior tibiae with comb of short spines only on apex (Fig. 14). Mesepisternum trapezoidal, wider on outer edge than inner edge (Fig. 10) .... *Ptomaphagina*

Subtribe PTOMAPHAGININA

Ptomaphaginini Szymczakowski, 1964, 1969a.

Characterization. Mesothoracic epimeron small and very transverse (Fig. 9), twice as wide as long, its internal border subequal to external border. Anterior tibiae with comb of short equal spines on apex and outer margin. Migration of aedeagal orifice to dorsal surface by way of right side.

The group contains three genera: *Pro-*

ptomaphaginus, *Ptomaphaginus*, and *Pandania*.

KEY TO GENERA OF PTOMAPHAGININA

1a. Male and female protarsi similar (Figs. 11, 12). West Indies and Mexico .... *Proptomaphaginus*
1b. Male and female protarsi dissimilar, male segments swollen. Oriental Region 2
2a. Pronotum with transverse striae, widest at hind angles of base, mesosternal carina relatively low .... *Ptomaphaginus*
2b. Pronotum without transverse striae, only punctuation; widest before base, mesosternal carina high, leading edge angular .... *Pandania*

Genus *Proptomaphaginus*

Proptomaphaginus Szymczakowski, 1969a: 88. Type species *P. apodemus* Szymczakowski.

Characterization. Sexual dimorphism of protarsi not present, male and female protarsi narrow. This is an exceptional character, because all other nonbathysciine Catopinae have males with widened protarsal segments. Aedeagus symmetrical, with notch in tip. Spermatheca simple crescent-shaped tube.

The genus is reported only from the West Indies, but is known to occur in Mexico. Three species are described: *apodemus* Szymczakowski 1969a from Cuba, *darlingtoni* (Jeannel) 1936 from Cuba, and *puertoricensis* Peck 1970a from Puerto Rico. Szymczakowski (1969a) and Peck (1970a) contain additional discussion of the genus, its ecology, and its zoogeography.

Genus *Ptomaphaginus*

Ptomaphaginus Portevin, 1914: 194. Type species *P. longitarsis* Portevin.

Characterization. Size small, 1.1–3.4 mm. Form oblong, convex. Pubescence short, golden, decumbent. All dorsal surfaces covered with fine transverse striae, oblique on elytra. Winged or wingless, always eyed. Male protarsi wide, female protarsi narrow. Aedeagus broad and short, tip variable in shape, orifice on ventral surface, or cutting right margin of aedeagus in shift to dorsal surface. Spermathecae unknown.

The genus is limited to the Oriental Region. It was revised by Jeannel (1936) and Szymczakowski (1964) with five species later described (Szymczakowski, 1965, 1970; Henrot and Szymczakowski, 1971). Complete literature citations for the older species are in the first two revisions, and are not given in my list of references. The twenty-six recognized species are listed with their localities or ranges as follows:

angusticornis (Portevin) 1921; Java
bryanti Jeannel 1936; Borneo (Sarawak)
cilipes (Portevin) 1907; southern India
clibanarius Szymczakowski 1970; Singapore
flavicornis (Motschoulsky) 1863; Ceylon
gracilis Schweiger 1956; southern China (Foukien)
honestus Szymczakowski 1964; northern Burma
jacobsoni Szymczakowski 1964; Sumatra
latescens Szymczakowski 1964; Sumatra
lacertosus Szymczakowski 1970; Singapore
laticornis Jeannel 1936; Eastern India (Assam)
latipes (Pic) 1929; Philippines (Mindanao)
lewisi Szymczakowski 1964; Ceylon
longitarsis Portevin 1914; Ceylon
murphyi Szymczakowski 1970; Singapore
nitens Jeannel 1936; Ceylon
obtusus Szymczakowski 1959; Sumatra
oribates Szymczakowski 1965; Nepal
parvulus Henrot and Szymczakowski 1971; Ceylon
portevini Szymczakowski 1964; Sumatra
rubidus (Champion) 1927; northern India
rufus Jeannel 1936; Sumatra, Singapore
sauteri Portevin 1914; Taiwan
scaber Szymczakowski 1964; northern Burma
similis Schweiger 1956; southern China (Foukien)
tantillus Szymczakowski 1964; Malaya, Singapore
tarsalis Szymczakowski 1964; Sumatra

Virtually all of these species are known only from the type collections. Little is reported about their habits or habitats (except in Szymczakowski, 1970). They should all be expected as inhabitants of moist forest litter. *P. cilipes* was found marching in a column of ants, and shows some adaptations for myrmecophily. *P. latescens* and *obtusus* were taken in caves in Sumatra but do not look as if they are cave-limited species.

Genus *Pandania*

Pandania Szymczakowski, 1964: 148. Type species *P. oxytropis* Szymczakowski.

Characterization. Length 2.6 mm. Form ovoid, slightly convex. Pronotum widest before base; lacking striae, only sparsely punctate. Mesosternal carina strongly developed, borders projected, forming right angle.

The genus is known only from the female of the type species from Sumatra.

Subtribe PTOMAPHAGINA

Ptomaphagini Szymczakowski, 1964, 1969a.

Characterization. Mesothoracic epimeron large, about as long as wide, its external border wider than the internal (Fig. 10). Anterior tibiae with a comb of small equal spines limited to the apical edge and not occurring on the external margin (Fig. 14). Migration of the aedeagal orifice to the dorsal surface via the left margin of the aedeagus.

This is a large group occurring in the Holarctic and Neotropical regions. Four genera are contained and can be distinguished in the following key:

KEY TO GENERA OF PTOMAPHAGINA

1a. Form oval, with long erect hairs as well as short hairs, myrmecophile (southern United States) .... *Echinocoleus*
1b. Form elongate, with short recumbent hairs only 2
2a. Aedeagus broad and short; apex variable; orifice central, or cutting to dorsal surface by left side (Figs. 9, 10) (southern United States to central South America) .. *Adelopsis*
2b. Aedeagus long and thin; orifice always on dorsal surface, always cutting left side 3
3a. Antennae very short, article 3–10 very transverse, legs and tarsi very short, tibiae flattened and quadrangular, myrmecophile (North Africa) .... *Synaulus*
3b. Antennae and legs not shortened (Holarctic and Neotropical regions) *Ptomaphagus*

Genus *Echinocoleus*

Echinocoleus Horn, 1885: 136. Type species *E. setiger*, holotype seen.

Diagnosis. The pale color, wide oval shape, and long erect golden hairs serve to distinguish this genus. It is known only from ant nests in the southern United States from Alabama to Arizona.

Description of genus. Length 2.5–2.8 mm. Width 1.5–1.8 mm. Color pale yellowish or reddish brown. Form oval, 1.9 times as long as wide; flattened. Head smooth, with fine hairs; eyes large. Antennae short, not reaching the middle of pronotum when laid back; all segments except III transverse; last 8 segments increasingly wider so that XI is widest. Pronotum widest at base, twice as wide as long; sides regularly arcuate; hind angles drawn out but rounded; hind margin straight in middle; striae absent on disc or present as minute striolae; covered with recumbent short, or recumbent short and erect long hairs. Elytra widest at base, as long as wide to 1.2 times as wide as long; external apical angles rounded, hind margins rounded-truncate; sutural angles sharp in male and female; striae transverse to suture; dense vestiture of long erect and short recumbent hairs. Wings absent. Mesosternum with very low carina on midline. Mesepimeron of Ptomaphagina type, trapezoidal. Legs short, flattened; comb of short equal spines on summit of all tibiae; protarsi dilated in both sexes, mesotarsi narrow in both sexes. Aedeagus in side view blunt at base, tapering gradually to narrow tip; style of internal sac long, thin, twisted; in dorsal view narrowing gradually toward tip, tip a blunt point; parameres long, thin, lying close to aedeagus. Genital plates twice as long as broad, median spiculum gastrale elongate, projecting 1/2 length beyond anterior end of genital plates. Spermatheca with narrow posterior, large swollen twisted anterior end.

Species. The genus contains only one named species, *setiger* Horn 1885. Jeannel (1936) transferred *Dissochaetus arizonensis* Hatch 1933 into *Echinocoleus*, without having seen material of either species. I have seen the types of *arizonensis,* and it is a *Dissochaetus,* in the tribe Nemadini. Jeannel (1936) also placed *Echinocoleus* in the Nemadini, which would not have happened if he had seen this very distinctive and highly modified genus of Ptomaphagina.

Ecology and distribution. I have seen material representing three species. Horn reports only two specimens in his series from Arizona. I have seen one taken in March 1919 from Oracle, Arizona, 5000 feet, pinned with *Novomessor albisetosus* ants (F. G. Werner det.), one from Las Vegas, New Mexico, pinned with a *Pogonomyrmex* ant, three taken in April 1970 from a *Pogonomyrmex rugosus* nest in Tucson, Arizona, and one from a *Pogonomyrmex* nest at Selma, Alabama.

One larva was recovered from a *Pogonomyrmex* nest. The larva is modified from the usual elongate shape of Ptomaphagina into a very broad and flat form with abundant large and thick setae.

The genus appears to be an old and highly modified offshoot from a New World *Ptomaphagus* ancestor.

Genus *Adelopsis*

Adelopsis Portevin, 1907: 71. Type species *A. heterocera* Portevin. Jeannel, 1936: 59.

Diagnosis. The genus is very difficult to separate from *Ptomaphagus* by external characters. The species are generally smaller and broader than *Ptomaphagus.* The diagnostic feature lies in the short, thick, blunt aedeagus, often with complicated sculpture at the tip. Sexual dimorphism in the elytral apex is absent in the United States species.

Description. Length 1.7–3.5 mm. Form elongate oval, compact, convex. Color light to dark brown. Pubescent with numerous short recumbent golden hairs. Head finely punctured. Eyes normally large, to absent; in United States species eye width is 1/2 of width of head from antennal base to head margin across eye. Antenna short, compact, not reaching base of pronotum when laid back. Maxillary palp last article as long as preceding, conical, thinner. Pronotum wider than long, sides arcuate, striae distinct and coarse. Elytra gradually tapering to apex in both sexes in United States species; external apical angles rounded; sutural angles rounded; apex truncate; striae distinct, oblique. Wings present or absent, absent in all United States species. Mesosternal carina low, notch distinct. Legs short and compact, comb of spines limited to apex of tibiae, protibial apex oblique in males, rounded in females; tarsi swollen only in males on protarsi. Aedeagus short, stout, blunt, often with complex sculpturing at tip, orifice cutting to dorsal side through left side of aedeagus; internal sac with variable stylet, with short stylet in United States species. Parameres fused to aedeagus. Spiculum gastrale short, thick; less than 1/4 projecting beyond anterior end of genital plates. Spermatheca thin and curved in United States species, undescribed for other species.

Ecology. Members of the genus are either moist forest litter inhabitants or forest soil inhabitants. A few are known to inhabit caves, but do not show modifications for cave life. Those species with no wings and small or functionless eyes are probably scavengers in deeper litter, and in soil. They are rarely collected except by sifting litter. I have taken them in Central America and the United States by Berlese funnels and baited pitfall traps.

Distribution. Except for the species later discussed from Mt. Mitchell, North Carolina, all species previously described were from Mexico and South America. The following list gives recognized species, and locality or range. References are Jeannel (1936) and Szymczakowski (1961, 1963, 1968 and 1969b):

ascutellaris (Murray) 1856; Caracas, Venezuela
asper Jeannel 1936; Brazil (São Paulo; Alto da Serra. Santa Catharina; Blumenau). Paraguay
asperoides Szymczakowski 1963; Brazil (São Paulo)

bellator Szymczakowski 1968; Peru (Dep. Cuzco; Cajon, Bergland. Cosnipata-Ebene)
bernardi Portevin 1923; Brazil (Rio de Janeiro; Teresopolis. São Paulo; Alto da Serra)
bordoni Jeannel 1964; Venezuela (Merinda Prov., Capaya, Cueva Alfredo Jahn)
braziliensis Jeannel 1936; Brazil (Santa Catharina; Blumenau)
bruchi Pic 1926; Argentina (Buenos Aires)
brunneus Jeannel 1936; Colombia
darwini Jeannel 1936; Uruguay (Maldonado)
exiguus (Kirsch) 1870; Brazil. Columbia (near Bogota)
filicornis Jeannel 1936; Colombia
grouvellei Jeannel 1936; Brazil (Bahia, Rio de Janeiro, São Paulo)
heterocerus Portevin 1907; Bolivia (Cochabamba)
insolitus Szymczakowski 1961; Brazil (Santa Catharina; Nova Teutonia)
linaresi Szymczakowski 1969b; Venezuela (Cueva del Guacharo at Caripe)
luculentus Szymczakowski 1963; Brazil (São Paulo)
ovalis Jeannel 1936; Venezuela
ruficollis (Portevin) 1903; Bolivia (Cochabamba)
simoni (Portevin) 1903; Brazil (São Paulo; Alto da Serra). Mexico (Coatepec). Venezuela (Tovar and Rancho Grande)
triangulifer Szymczakowski 1961; Brazil (São Paulo. Santa Catharina; Nova Teutonia)

Though only one Mexican specimen and no Central American material is reported in the literature, the genus occurs in these areas. I have collected it in Mexico, Guatemala, Costa Rica, and Panama. I have also seen many *Adelopsis* taken by H. Dybas in Panama.

The genus has not previously been recognized from the United States. Besides the following species, here transferred to *Adelopsis,* I have seen material of at least six other species from Alabama, Georgia, Tennessee, North Carolina, West Virginia, and New Mexico.

Adelopsis mitchellensis (Hatch)
Figures 17, 18, 98, 139, 198

Adelops mitchellensis Hatch, 1933: 208. Holotype male and allotype female in AMNH, seen. Type locality: North Carolina, Black Mountains.
Ptomaphagus (*Adelops*) *mitchellensis,* Jeannel, 1936: 93; 1949: 99. New Combination.

Diagnosis. This is at present the only described *Adelopsis* in the United States. It is distinguishable from the undescribed species only by the characters of the aedeagus and spermatheca.

Description. Length 2.3–2.6 mm. Width 1.2–1.3 mm. Form oval. Color yellowish to dark reddish brown. Head sparsely punctured. Eyes reduced, pigmented, faceted; head width across eye from antennal base to margin 2.5 times eye width. Antennae (Fig. 98) short, compact; club darker, flattened, reaching middle of pronotum when laid back; segment III shorter than II; segments VI–X wider than long; VIII over twice as wide as long. Pronotum widest 1/3 before base; wider than elytra; 1.45 times as wide as long; hind angles acute; hind margin straight; striae composed of coarse punctures; pubescence moderate in length and amount. Elytra widest at base; 1.15 times as long as wide; external apical angles rounded; apex slightly oblique; striae oblique to suture; pubescentlike pronotum. Wings absent, elytra fused. Mesosternal carina low, notch present. Legs short; protibiae bowed-in; mesotibiae bowed-out; metatibiae straight. Aedeagus (Fig. 17) thick, tip pointed and thin; in dorsal view (Fig. 18) tip blunt; orifice on dorsal surface, right side of tip in dorsal view broad and dorsoventrally flattened, underlying left side. Spiculum gastrale short and thick, less than 1/4 projecting beyond anterior edge of genital plates (Fig. 198). Spermatheca (Fig. 139) simple curved tube, slightly swollen at anterior end, curved with thin crest at posterior end.

Variation. Differences appear in slide mounts of the aedeagus, usually a bending of the flattened plate of the right side of the aedeagus (arrow, Fig. 17) so that some of its dorsal face shows, giving an impression of a broader tip.

Field notes. The only habitat data is from a specimen I collected in a carrion-baited pitfall trap at 6400′ elev. in the balsam forest of the summit of Mt.

Mitchell. Another was taken at 4500′–6000′ elev. (INHS). Other specimens were probably taken by sifting litter and moss. Berlese funnel extraction of litter is probably the best method of recovering this species.

Seasonality. The only available information is that adults have been taken in April, and July through September. Larvae are unknown.

Distribution. Known only from the Black Mountains (and Mt. Mitchell) of Yancey County, North Carolina. I have seen 3 males and 6 females from this area (AMNH, FMNH, INHS, SBP, USNM).

Distributional comments. A second but undescribed species of *Adelopsis* occurs on Mt. Mitchell. This species, upon preliminary study, seems to have a much greater range, extending from Mt. Mitchell southwestward through the Smoky Mountains to northeastern Alabama. The species can be separated only by dissecting out the aedeagus and spermatheca.

Genus *Synaulus*

Synaulus Portevin, 1903: 157. Type species *S. agilis* (Lucas).

Characterization of genus. Length 2.0–2.5 mm. Shape very wide and convex. Color dark brown. Head retractable; eyes large. Antennae short, compact, club wide and flattened. Pubescence short, golden, recumbent. Prothorax and elytra covered with fine transverse striae. Winged. Legs very short, retractable under body, femora wide and flattened. Sexual dimorphism present in elytral apex and slightly in protarsi. Aedeagus like European *Ptomaphagus.*

Species. Two species are named and described, *agilis* (Lucas) 1849 and *pruinosus* (Reitter) 1881.

Ecology and distribution. The genus is known only from northern Algeria and Tunisia. Searching has not produced it in Morocco. It is a myrmecophile in nests of *Aphaenogaster testaceophilis* Lucas. Its role in the ant nest is not known, but the compact body suggests that the beetles have need of protection. They may simply be tolerated, feeding on nest debris.

The genus appears to have evolved from an ancestral European *Ptomaphagus.*

Genus *Ptomaphagus*

Ptomaphagus Illiger, 1798: 84. Type species *P. sericeus* Panzer.

Diagnosis. Aedeagus long and thin, orifice on dorsal surface, cutting left side of aedeagus. Elongate oval body with recumbent hairs, not broad and flattened with flattened legs and antennae and not living with ants.

Distribution. The genus occurs abundantly in the Nearctic and Palearctic regions, and infrequently in the Neotropical Region. One species is known at the edge of the Oriental Region.

Description. Few of the Old World species are available for study in this country. Information on them has been drawn from Jeannel (1936) and Szymczakowski (1964). Length 1.7–6.0 mm. Winged or wingless. Shape generally oblong, or elongate oval, rarely ovoid. Pronotum transversely striate, except in a few North American cave species in which the striae are reduced to random punctures on the disc. Elytra with striae oblique to the suture, except in *schwarzi* and some *nevadicus* in North America in which the striae are transverse to the suture. Pubescence golden, fine, recumbent. Head wide with an occipital carina. Epistome fused with front. Maxillary palps with last segment about as long as preceding. Eyes large, except in some North American species. Antennae with third segment always longer than wide.

Pronotum transverse, usually as wide as elytra, measuring widths at base or near base. Pronotal sides generally little rounded in hind half. Elytral sides narrowing posteriorly, slightly curved, their apical margin often truncate. In some North American species the elytral apex is oblique and the female sutural angle is sharp. Sutural striae entire.

Mesosternum with flattened carina along midline, carina with free edge lightly to strongly rounded. Mesepisternum separated from mesepimeron by strong suture. Mesepimeron large, about as long as wide, its outer edge longer than the inner (Fig. 10). Metepisternum well developed, triangular or trapezoidal.

Anterior tibiae with comb of short equal spines occupying apical border, absent on external border (Fig. 14). Summit of meso- and metatibiae armed with two internal spurs and a comb of short equal spines replacing the outer spurs. Tarsi normal. Male with dilated protarsi (Fig. 14) and hind tibiae sometimes curved and thickened in distal portion. Female protarsi narrow (Fig. 13). First segment of mesotarsi narrow in both sexes.

Aedeagus form very regular, always long and thin, flattened dorsoventrally; apex with simple structure, triangular or ogival, sometimes with a small terminal button (bifid in *P. divaricatus* Jeannel); apical orifice on dorsal surface, cutting left edge; generally 7 setae on ventral surface of each side of tip. Parameres thin but always well developed, a little shorter than the aedeagus, with 3 setae on tips. Genital segment with triangular plates enclosing spiculum gastrale for part of its length.

Spermatheca with central shaft, slender posterior end often with knob, and curve at anterior end. (This has proved to be of great value in determining species in North America. It has been illustrated and described only for three European species by Kevan (1963). I have found Kevan to be correct in predicting that the spermatheca would prove to be of use throughout the tribe in distinguishing the females of species, which are difficult to identify by external characters alone.)

Distribution. The genus is widespread, containing many species that can be grouped into four subgenera. The subgenus *Ptomaphagus* is Palearctic, with its principal center of distribution in Europe. A few species are known to inhabit eastern Asia and Japan. One species occurs at the northern edge of the Oriental Region. A second large subgenus, *Adelops,* inhabits North and Central America. The remaining two subgenera contain two species each. They are *Merodiscus* of Yugoslavia and Rumania, and *Tupania* of Mexico and Brazil. The subgenera may be separated by the following key adapted from Szymczakowski (1961).

KEY TO SUBGENERA OF *PTOMAPHAGUS*

1a. Antennal club long, beginning with segment IV (Fig. 134) or at the summit of III 2
1b. Antennal club normal, beginning with segment VI or VII (Figs. 98–133) 3
2a. Segment II very short, much shorter than III. Pronotum as wide as elytra. Tarsi robust, first metatarsal segment 4–5 times as long as wide. Europe .... *Merodiscus*
2b. Segment II normal, slightly longer than III. Pronotum clearly narrower than elytra. Tarsi thin, first metatarsal segment 7 times as long as wide. Neotropical .... *Tupania*
3a. Legs rather robust, meso- and metatarsi thick, laterally flattened. Male anterior tibiae strongly dilated at summit, anterior tarsi wide. Palearctic .... *Ptomaphagus*
3b. Legs slender, meso- and metatarsi slender and not flattened. Male anterior tibiae long and not dilated, anterior tarsi longer. North and Central America .... *Adelops*

Comments on subgenera. Tupania and *Merodiscus* are well defined. This is not the case for *Adelops* and *Ptomaphagus* s. str. The differences between the two are seemingly mostly subjective impressions of Jeannel. From the material I have seen of European species, Jeannel's impressions seem to be at least mostly correct. Nevertheless, these two subgenera presently have good geographical utility. A critical evaluation of the validity of these two subgenera can be undertaken only with the later study of abundant Palearctic material. Szymczakowski (1961: 147) has noted that the North American species *brevior* and *consobrinus* show a transition from *Adelops* to *Ptomaphagus* s. str. This might be interpreted as a suggestion of the ancestral stock and direction of migration from the Nearctic to the Palearctic Region.

Subgenus *Merodiscus*

Subgenus *Merodiscus* Jeannel, 1934: 162. Type species *Ptomaphagus validus* Kraatz.

Diagnosis. Easily distinguished by the small globose second antennal segment, and the much longer third segment.

Species and distribution. Two species are known. They are *validus* (Kraatz) 1852 from Rumania and Yugoslavia (seen in FMNH), and *biharicus* Jeannel 1924 from Rumania.

Ecology. Known only from under leaves and stones in forests.

Subgenus *Tupania*

Subgenus *Tupania* Szymczakowski, 1961: 146. Type species *Ptomaphagus forticornis* Matthews, 1888.

Diagnosis. Easily distinguished by the antennal club beginning with segment IV (Fig. 134).

Species and distribution. The subgenus contains only two named species, *forticornis* Matthews 1888 from Cordova, Mexico (type in BMNH, seen), and *flabellatus* Szymczakowski 1961 from Bocaina (near São Paulo) (allotype and 10 paratypes seen from PISZ), and Santa Catharina, Brazil. I have seen a broken female of a third species from Tucano, Amazonas State, Brazil, taken at 1500 m by J. & B. Bechyne, 28.iv.1964, in the Universidad Central de Venezuela, Facultad de Agronomia, Instituto de Zoologia Agricola collections at Maracay, Venezuela.

Supplementary descriptive notes on P. flabellatus. The metatibial spurs are proportionately longer than in *Adelops, flabellatus* having the longest spur 0.27 the length of the metatibia and 0.77 the length of the first metatarsomere (which is .44 × .08 mm). The metasternum is generally longer than in *Adelops*, in *flabellatus* its width (same reference axis as for entire beetle) being 1.4 times the length. The aedeagus (lateral view, Fig. 77) is basally bent, and the spermatheca (Fig. 140) is similar to those of the *cavernicola* group of *Adelops*. The male genital segment does not differ in a characteristic way from that generally found in *Adelops*.

Ecology. At least one of a series of 15 from São Paulo was taken under a cadaver (the kind of the cadaver is not mentioned). The Mexican species probably came from mesic forest litter in the region. I was unable to collect any in a week of field work near Cordova and Orizaba in July, 1969.

Subgenus *Ptomaphagus* sensu strictu

Diagnosis. Antennal club beginning with segment VII. Palearctic, with one Oriental species. Difficult to separate from the North American subgenus *Adelops*, except by the characters mentioned in the above key.

Species and distributions. Twenty-two species are recognized from Europe and Asia. The following is a checklist of these species and their general ranges. This list has been mostly compiled from Jeannel (1936) and all earlier references to descriptions can be found in that work. Sokolowski (1957) has been followed concerning synonymies of names used by Jeannel. I thank Dr. Waclaw Szymczakowski of Krakow, Poland, for his kind aid in providing corrections and additions to this list.

amamianus Nakane 1963; Japan
artizensis Jeannel 1934; Sardinia
caucasicus Jeannel 1934; western Caucasus
chendai J. Müller 1921; Italy, Albania, Yugoslavia
circassicus Reitter 1888; western Caucasus, Crimea
clavilis Reitter 1884; Sardinia, Sicily, Majorca
dacicus Jeannel 1934; Rumania
divaricatus Jeannel 1934; Yugoslavia, Albania
kuntzeni Sokolowski 1957; Japan, NE Burma
medius Rey 1889; western, central, and northern Europe
pius Seidlitz 1887; Italy
pyrenaeus Jeannel 1934; France
rhagianicus Sbordoni 1967; Iran

sardus Seidlitz 1887; Sardinia
sericatus Chaudoir 1845; central and southeastern Europe
sibiricus Jeannel 1934; Vladivostock, Japan
subtruncatus Mäklin 1881; Siberia
subvillosus Goez 1777; western and central Europe
tauricus Jeannel 1934; Turkey, Syria
tenuicornis Rosenhauer 1856; Spain, N. Africa
vallombrosae Seidlitz 1887; Italy
variicornis Rosenhauer 1847; Europe

Ecology. Little information is available on the habits and habitats of Palearctic *Ptomaphagus.* Jeannel (1936) provides as much information as can be generally found. The species are usually associated with forested areas. Mountain habitats are indicated for *subvillosus,* and for *kuntzeni* (taken in flight at 2000 m in Burma). Several species have been taken in caves or cave entrances (*chendai, pyrenaeus,* and *sericatus*), though none of these species exhibits cave adaptations. Moss and rotting leaves are indicated for *pius, sericatus, subvillosus, valombrosae,* and *variicornis,* and flood debris has given *tenuicornis.* Small invertebrate bodies (snails, hemipterans, scorpions) have yielded *sericatus* and small mammal cadavers *subvillosus.* Nests of moles, shrews, and hamsters have yielded *sericatus* and *variicornis,* and rabbit nests *subvillosus* and *variicornis.* An anthill yielded the single specimen of *subtruncatus* and *Lasius* anthills have yielded *sericatus* and *tenuicornis.* Malaise traps have taken *kuntzeni* in flight in Burma. In all of the above cases, the beetles show themselves to be lovers of dark moist places, where they are probably feeding as scavengers on decaying plant and animal matter.

Subgenus *Adelops*

Adelops Tellkampf, 1844: 318. Type species *Adelops hirtus* Tellkampf.

Diagnosis. Antennal club beginning with segment VII. North and Central American species. Difficult to separate from the Palearctic subgenus *Ptomaphagus;* see comments above.

Species. A total of 36 species from North and Central America are here recognized and named. Of these species, 44.5 percent are troglobites. Twelve troglobitic species are in the southeastern United States, one in the southwestern United States, two occur in Mexico, and one in Guatemala. An additional 30.5 percent are less specialized hypogean species living in underground environments such as caves, deep humus, and animal burrows from southern Canada to Panama. The remaining 25 percent are epigean in forest litter from southern Canada to Guatemala. An estimated seven species are additionally recognized but are too poorly known to merit description.

Species groups. Jeannel (1949) proposed a system of six species groups for *Adelops.* This was partly followed by Barr (1963). I do not think that Jeannel's groups are sound. Several of the external characters used by him have arisen more than once, and others are convergent adaptations to similar habitats. I prefer a system using internal genital structures, which I believe to be a more sound approach in *Adelops.* I have used as a group name that of the oldest species in the group. The groups are (1) the *hirtus* group, with a reversed "J"-shaped spermatheca, containing the 12 cave-specialized species of the eastern United States, and one edaphophile species from the Ozark region; (2) the *consobrinus* group, with a reversed "S"-shaped spermatheca, with 10 species in the United States, southern Canada, and western Mexico, and one in Guatemala; and (3) the *cavernicola* group, with a reversed "S"-shaped spermatheca with a coil at the posterior end, with 10 Mexican species, and one ranging from northeastern Mexico through much of the eastern and southern United States. Three species, known only from males, are not assigned to a group.

The species groups are not included in the following species key. The groups are characterized above, based on female spermathecae. These groups can be criticized because of seemingly undue emphasis placed on just this one character. However, in justification, I think the chances for convergence through selection to similar forms in the spermathecae of distantly related species are less than for convergences in external structures of an obviously adaptive significance. The spermathecae are less directly affected by selection than other structures. They are useful because they are both conservative enough in overall shape to indicate major groups, and complex enough to indicate specific differences. As a second defense for the groups, I suggest that their included species share broadly common characteristics of distribution and ecology. In this way they are later very useful in discussions of phylogeny, zoogeography, and evolution. Lastly, I could find no other character or even group of characters that I thought had as comparable and potentially reliable an information content.

Species key. The following key will serve to separate the species. The key is an aid to identification, and does not indicate relationship. The species groups are not used here because this would require a dissection of the specimen before the first couplet could be approached. The species are discussed later in the text under the group in which I have placed them. The key does not include *championi* from Guatemala. The key is not easy to work, because there are few distinct, unequivocal external characters in *Adelops*. Quite often the best character is the species distribution, and this has been used in the key. Until a worker gains familiarity with the subgenus, or has a comparative or synoptic collection to work with, positive determinations of the populations sampled by a collector will usually require dissections, preferably of both males and females.

A KEY TO THE NORTH AMERICAN SPECIES OF *PTOMAPHAGUS* (*ADELOPS*)

1a. Eyes unpigmented, greatly reduced; troglobites 2
1b. Eyes pigmented, not reduced or only partly so, may or may not be cavernicoles 19
2a. Troglobites in caves in Mexico 3
2b. Troglobites in caves in the eastern United States 4
3a. In caves in central Nuevo León ..... *gypsum*
3b. In caves in Sierra de Guatemala, Tamaulipas ..... *troglomexicanus*
4a. Aedeagus long, thin, straight (Figs. 35, 37, 38) 5
4b. Aedeagus thicker, curved (Figs. 21–26) 7
5a. In caves in west-central Kentucky ..... *hirtus*
5b. In caves in Illinois or Tennessee 6
6a. In caves in Monroe County, Illinois ..... *nicholasi*
6b. In caves in central Tennessee, on southeastern edge of Nashville Basin ..... *hubrichti*
7a. Aedeagus upturned at tip (Fig. 26) ..... *hazelae*
7b. Aedeagus straight or downturned at tip 8
8a. Mesosternal carina high (Figs. 83–86) 9
8b. Mesosternal carina low (Figs. 79–82, 87–90) 12
9a. Ventral margin of carina sinuous (Fig. 84) ..... *fiskei*
9b. Ventral margin of carina straight 10
10a. Antennal segments II and III subequal (Fig. 108); caves of DeKalb County, Alabama, and Dade County, Georgia ..... *whiteselli*
10b. Antennal segment III clearly longer than II 11
11a. Pronotum widest at base; central Tennessee ..... *barri*
11b. Pronotum widest 1/3 before base; Blount County, Alabama ..... *walteri*
12a. Pronotal sides parallel behind 13
12b. Pronotal sides not parallel behind 17
13a. Spermatheca with thin curved central shaft (Fig. 152) ..... *valentinei*
13b. Spermatheca with stout central shaft (Figs. 142–146) ..... *loedingi*, 14
14a. In caves west of the Flint River, Madison County, Alabama ..... *loedingi loedingi*
14b. In caves east of Flint River 15
15a. In caves in Keel Mountain (in Madison and Jackson counties) between Flint and Paint Rock rivers ..... *loedingi longicornis*
15b. In caves in Jackson County east of Paint Rock River 16
16a. In cave(s) in Tater Knob, immediately N & NW of Scottsboro ..... *loedingi solanum*
16b. In cave(s) in July Mountain, 2–5 miles SW of Scottsboro ..... *loedingi julius*
17a. Spermatheca shaft undulating, without

knob on posterior end (Fig. 157); caves in Bishop Mountain, Marshall County, Alabama .... *episcopus*
17b. Spermatheca shaft straight, or without knob on posterior end (Figs. 153–156) .... *hatchi*, 18
18a. In Caney Hollow Cave at edge of Nashville Basin, in western Franklin County, Tennessee .... *hatchi fecundus*
18b. In caves of escarpment of Cumberland Plateau, in Grundy and eastern Franklin counties, Tennessee, and Jackson and Madison counties, Alabama .... *hatchi hatchi*
19a. Eyes distinctly reduced, their horizontal diameter equal to the space between their anterior margin and the antennal socket 20
19b. Eyes normal or slightly reduced, with diameter greater than width of eye-antennal socket space 23
20a. Antennae short, not extending far into elytra when laid back 22
20b. Antennae long, extending into first 1/4 of elytra when laid back 21
21a. Mesosternal carina very high (Fig. 93); Guatemala; troglobite .... *giaquintoi*
21b. Mesosternal carina low; Panama; high montane forests .... *talamanca*
22a. Ozark region of United States .... *shapardi*
22b. In high montane forests of Querétaro, Mexico .... *meximontanus*
23a. Male metafemur with tooth on hind margin (Figs. 15, 16) 24
23b. Male metafemur smooth on hind margin 25
24a. Fully winged; female elytral apex not drawn out; widespread in western United States .... *fisus*
24b. Wings reduced to 3/4 elytral length; female elytral apex drawn out; cavernicole in Grand Canyon, Arizona .... *cocytus*
25a. Spermatheca simple reversed "S" shape; mostly species inhabiting United States 26
25b. Spermatheca a more complex reversed "S" shape with additional coil at posterior end (Figs. 187–197); species mostly Mexican 32
26a. Mesosternal notch deep, rounded (Figs. 95, 96) 27
26b. Mesosternal notch shallow, right-angled 28
27a. Spermatheca broadly flattened in anterior end (Figs. 180–183) .... *brevior*
27b. Spermatheca narrow in anterior end (Fig. 185) .... *ulkei*
28a. Edge of genital plates bordering genital orifice with concavity (Figs. 203, 206) 29
28b. Edge of genital plates bordering genital orifice straight or convex 30
29a. Spermatheca very broadly flattened at both ends (Figs. 173–174); California .... *californicus*
29b. Spermatheca very thin, not flattened (Figs. 178, 179); southeastern United States .... *consobrinus*
30a. Female elytral apex sinuous; western and Gulf states 31
30b. Female elytral apex obliquely truncate, not sinuous; Gulf Coastal states .... *texanus*
31a. Eyes reduced, 1.15 times width of eye-antennal socket space; spiculum gastrale short (Fig. 201); Florida .... *schwarzi*
31b. Eyes normal to slightly reduced, 1.3–1.9 times as wide as eye-antennal socket space; spiculum gastrale long and thin (Fig. 205); North America west of the Mississippi River .... *nevadicus*
32a. Female elytral tips drawn out, sutural angle sharp (Fig. 135) 33
32b. Female elytral tips not drawn out, sutural angle rounded (Figs. 136–138) 35
33a. Eyes very large, antennal segment II distinctly shorter than III; in forests of Sierra Madre de Oaxaca, Mexico .... *oaxaca*
33b. Eyes somewhat reduced, antennal segments II and III subequal; cavernicole; northeastern Mexico and southern and eastern United States .... *cavernicola*, 34
34a. Eye width 2.0–2.9 times width of eye-antennal socket space; widely distributed .... *cavernicola cavernicola*
34b. Eye width 1.5–1.75 times the width of the eye-antennal socket space; Nuevo León, Mexico .... *cavernicola aditus*
35a. Eyes more coarsely faceted and somewhat reduced, their horizontal diameter 1.9–2.0 times the width of eye-antennal socket space; high forests of Chiapas, Mexico .... *altus*
35b. Not above combination 36
36a. Aedeagus tip blunt in dorsal view (Figs. 63, 71) 37
36b. Aedeagus tip pointed in dorsal view (Fig. 67); forests of Sierra Madre de Oaxaca .... *newtoni*
37a. Aedeagus shorter and thicker (Fig. 62); cavernicole in Sierra de El Abra, Tamaulipas and Nuevo León, Mexico .... *elabra*
37b. Not above combination 38
38a. Aedeagus in lateral view with ventral button at tip (Fig. 72); cavernicole; Guerrero, Mexico .... *spelaeus*
38b. Not above combination 39
39a. Spermatheca longer and thinner at anterior end (Fig. 197); montane forests of Chiapas, Mexico .... *jamesi*

39b. Spermatheca shorter and thicker at anterior end (Fig. 193); middle and low elevation forests of Nuevo León, Mexico .... *leo*

THE *HIRTUS* GROUP

Diagnosis. Spermatheca shaped like a reversed "J," often with the posterior end bent to the left, and the anterior end neither swollen nor broadly flattened (Figs. 141–163).

Description. Shape elongate oval. Color medium brown to light brown or reddish brown. Eyes reduced in all species to small unpigmented areolae with a few facet remnants present (Fig. 6) except in *shapardi* (Fig. 5). Antennae medium or long. Pronotum with hind angles acute. Elytra with external apical angles rounded, apex truncate in females and rounded in males. Wings reduced to tiny elongate scales. Mesosternal carina medium or high. Aedeagus straight and thin, to slightly curved.

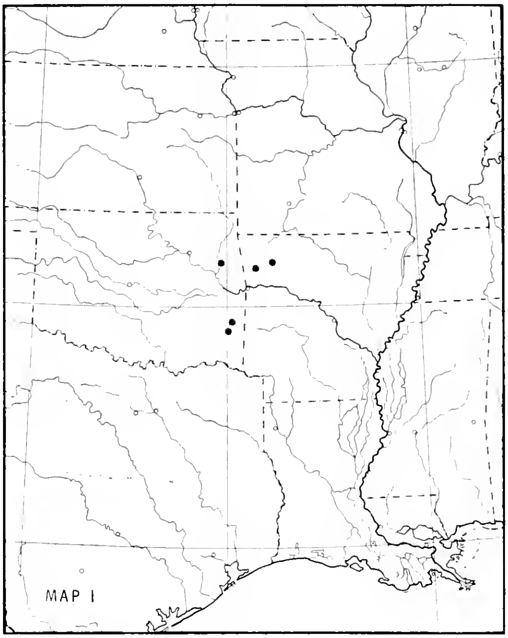
The group contains one edaphophilic species from the Ozark region of the central United States, and twelve troglobitic species (two of which are divided into six subspecies) from the southeastern United States. Reproductive seasonality in the troglobites probably does not exist in individuals living away from the fluctuating environment of cave entrances (winter lowering of temperature and humidity).

Ptomaphagus shapardi Sanderson
Figures 5, 19, 20, 78, 99, 141; Map 1

Ptomaphagus (*Adelops*) *shapardi* Sanderson, 1939b: 121. Holotype male and allotype female in INHS, seen. Type locality: Oklahoma, Cherokee County, Dresser Cave (5 mi. N Ft. Gibson). Jeannel, 1949: 101. Barr, 1963: 53.

Diagnostic combination. This is the only *Ptomaphagus* known from the southwestern Ozark region having eyes reduced to one-half the width of the head from the antennal base to the margin across the eye.

Description. Length 2.4–2.8 mm. Width 1.2–1.4 mm. Color yellowish brown to dark brown. Head finely punctured; eyes reduced, faceted, pigmented (Fig. 5); width of head from antennal base to margin across eyes twice width of eye on same line; ridge present from antennal base to top of eye. Antennae (Fig. 99) medium length, reaching base of pronotum when laid back, club beginning with segment VII; segment I longest; segments II and III subequal; IV, V and VI progressively shorter, wider; VII longer than wide; VIII transverse; IX quadrate; X broader than long; XI longer than broad. Pronotum at base 1.5 times as wide as long; widest 1/3 before base; hind margin straight; striae on disc composed of coarse setigerous punctures. Elytra elongate, sides parallel in anterior half, narrowing in posterior half; as wide as pronotal base; 1.5 times as long as wide. Mesosternal carina (Fig. 78) low, notch right-angled. Aedeagus (Fig. 19) in lateral view slightly curved, gradually narrowing to slender tip; tip in dorsal



Map 1. Distribution of *Ptomaphagus* (*Adelops*) *shapardi*, a wingless, small-eyed, soil and cave inhabitant of western Arkansas and eastern Oklahoma.

view (Fig. 20) with broad point. Spermatheca (Fig. 141) with curved shaft, posterior knob bent to left, opening to right, anterior hook small, no crest.

Variation. None noted.

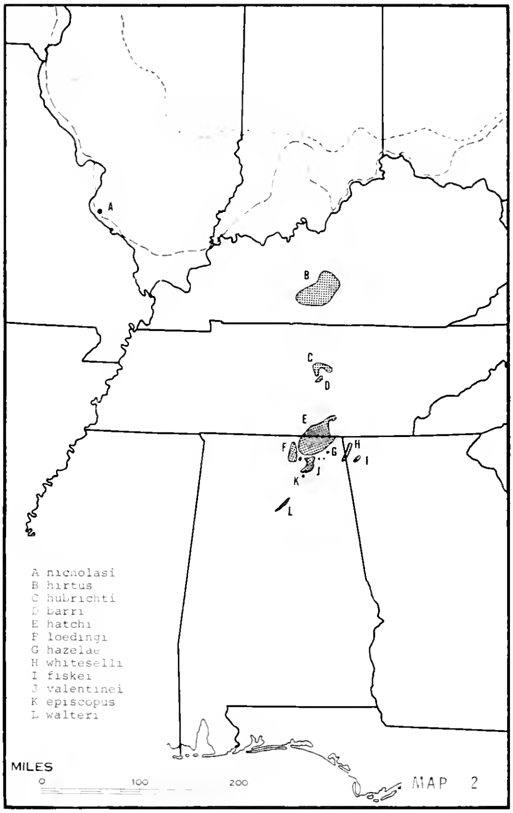
Collecting notes. The type series of 26 specimens came from gravelly debris, in total darkness, about 50 feet from the cave entrance (Sanderson, 1939b). One came to a bait trap in an Arkansas cave, and one to a carrion trap at a pile of rocks in an Oklahoma forest. Berlese collecting has taken them in litter in Oklahoma, and three times in deep litter in Devils Den State Park, Arkansas.

Seasonality. Adults have been taken in January, June, July, and December. Tenerals are known from January and June collections. Larvae are unknown. Reproduction probably can occur throughout the year in protected environments such as caves and deep litter pockets.

Distribution. The species is known from the southwestern Ozark region of Oklahoma and Arkansas, and the Ouachita Mountains of Oklahoma (Map 1). Additional collecting in litter in spring and early summer will undoubtedly widen the range. I have seen 31 specimens from the following five localities: ARKANSAS. *Washington County:* Devils Den State Park, Winslow, 6 (SBP, INHS); Finchers Cave, 10 mi. SE Fayetteville, 1 (INHS). OKLAHOMA. *Cherokee County:* Dresser Cave, 5 mi. N Ft. Gibson, 19 (INHS, MCZ, TCB). *Leflore County:* Cedar Lake Camp, 10 mi. SSW Heavener, 1 (SBP); Winding Stair Mt., 1600′, 12 mi. SSW Heavener, 4 (SBP).

Distributional comments. The Arkansas River is a major potential dispersal barrier crossing the range of this flightless species.

The flightless condition, small eyes, and collecting localities suggest that the species is an inhabitant of forest soil and deep litter. Forests providing such habitats do not extend farther west than the species' western range limits in Oklahoma. Most of Arkansas and Missouri are suitably forested, however. The species may occur in such a larger range, but this is unknown because little or no deep litter and soil collecting has been done in the Ozarks.



Map 2. Distribution of the troglobitic (blind, cave-adapted) *Ptomaphagus* (*Adelops*) in the United States. These species are concentrated in northeastern Alabama and adjoining parts of Georgia and Tennessee. The long-dashed line represents the maximum extent of glaciation of the Illinoian ice sheet. The short-dashed line represents the maximum extent of the Wisconsin ice sheet.

Ptomaphagus loedingi loedingi Hatch

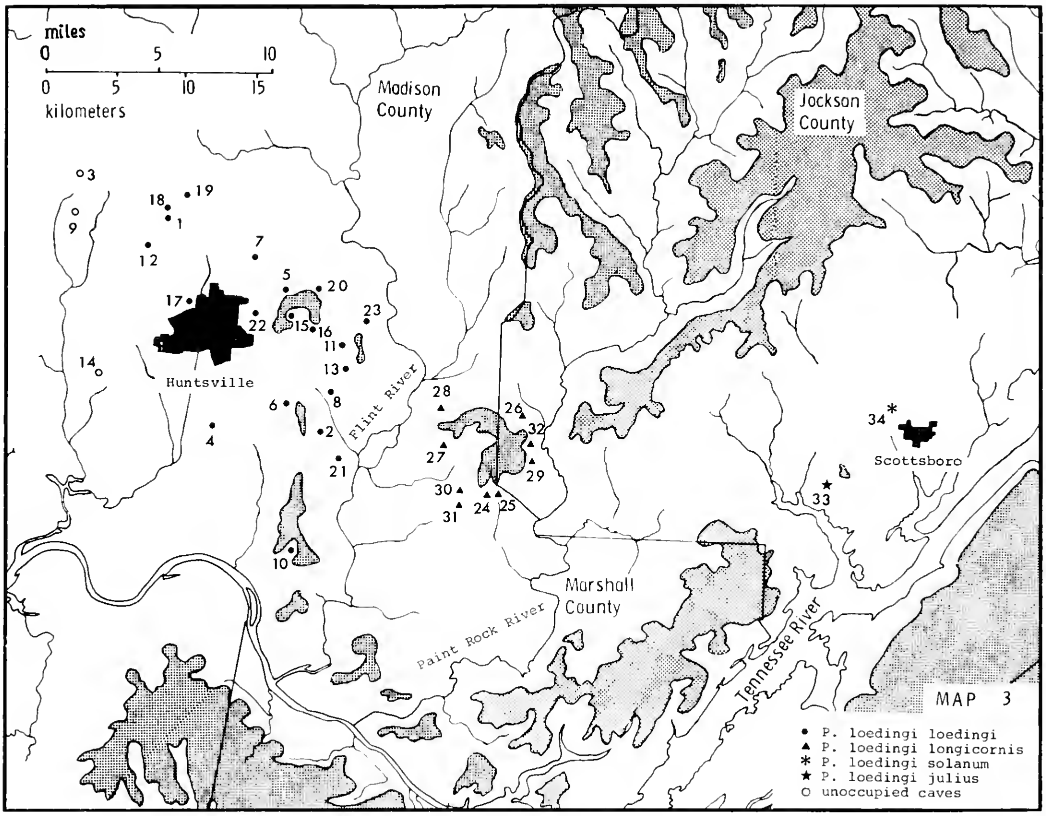
Figures 21, 79, 100, 142, 143; Map 3

Adelops lödingi Hatch, 1933: 209. Holotype male and allotype female in USNM (no. 43763), seen. Type locality: Alabama, Madison County, Shelta Cave.

Ptomaphagus (*Adelops*) *lödingi*, Jeannel, 1936: 93; 1949: 104.

Ptomaphagus (*Adelops*) *loedingi*, Barr, 1963: 57.

Ptomaphagus (*Adelops*) *valentinei jonesi* Jeannel,



Map 3. Distribution of *Ptomaphagus* (*Adelops*) *loedingi*, a troglobitic species of northeastern Alabama. Stippling represents the Pottsville sandstone remnants of the Cumberland Plateau. Caves do not exist under this caprock. Consequently, the plateau remnants, as well as the large rivers and streams, represent barriers to subterranean terrestrial dispersal. Geology from Malmberg and Sanford (1963) and Adams et al. (1926). The localities are as follows: 1 Barclay Cave, 2 Buford Cave, 3 Burwell Cave, 4 Byrd Spring Cave, 5 Cold Spring Cave, 6 Canoe Cave, 7 Cave Spring Cave, 8 Drake Cave, 9 Ellis Cave, 10 Green Grotto, 11 Jett Cave, 12 Kelly Natural Well, 13 Lott Cave and Pitt Sinkhole Cave, 14 Matthews Cave, 15 Natural Well, 16 Sadler Spring Cave, 17 Shelta Cave, 18 Sinks Cave, 19 Spook Cave, 20 The Sinks, 21 Toploe Cave, 22 Toll Gate Natural Well, 23 Twin Caves, 24 Bee Sinkhole Cave and Moon Sinkhole Cave, 25 Butler Sinkhole and Chittimwood Cave, 26 Crossing Cave, 27 Goat Cave, 28 Grayson Spring Cave, 29 Greising Cave, 30 Hering Cave, 31 Labyrinth Cave, 32 Paint Rock Cave.

1949: 103. NEW SYNONYMY. Type in MNHN, Paris, not seen. Type locality: Alabama, Madison County, Pitts Sinkhole Cave.

Ptomaphagus (*Adelops*) *henroti ellipticus* Jeannel, 1949: 102. NEW SYNONYMY. Type male in MNHN, Paris, seen. Type locality: Alabama, Madison County, Shelta Cave. Barr, 1963: 56.

Diagnosis. Ptomaphagus loedingi is a polytypic species, containing four geographically disjunct subspecies, in caves in Madison and Jackson counties, Alabama. The species is characterized by an elongate and thin aedeagus; elongate antennae with segment III clearly longer than II; a low mesosternal carina; and a spermatheca with a curved shaft and a knob at the posterior end.

The nominate subspecies occurs only in caves west of the Flint River in Madison County. It is distinguished from the other subspecies by its spermatheca with a small posterior knob, and trace of a crest on the anterior end.

Description. Length 2.7–3.6 mm. Width 1.2–1.4 mm. Head finely, sparsely punctured. Width of head across eye from antennal base to margin 4 times width of eye. Antennae (Fig. 100) thin and long, reaching into first third of elytra when laid back; segment III longer than II, subequal to I; II subequal to IV; IV, V and VI progressively shorter and wider; VII elongate, conical; VII twice as wide as long; VIII wider than long; X and XI longer than wide. Pronotum at base 1.5 times as wide as long, widest at base, or slightly before; posterior margin parallel or only slightly arcing to hind angles; hind angles slightly acute; hind margin slightly sinuous; striae present but faint. Elytra slightly more narrow than pronotum; at base 1.5 times as long as wide. Mesosternal carina (Fig. 79) medium, notch absent or faint. Aedeagus (Fig. 21) gently arcing and narrow, narrowing gradually to tip. Spermatheca (Figs. 142, 143) with short stout shaft, posterior end slightly swollen into knob, opening to right, or ventral of right; anterior end with small hook, low crest.

Variation. The most conspicuous variation is in the posterior knob and direction of opening of the spermatheca. The proportion of length to thickness of the shaft also varies slightly between populations. These differences are seen in the spermatheca illustrations (Figs. 142–143). Gradation exists from one into the other shape in a clinal fashion.

Distortion that might be interpreted as variation is noticed frequently in this subspecies in permanent slide mounts of the aedeagus. The aedeagal tip appears broad, when twisted down by the cover glass.

The type male of *henroti ellipticus* Jeannel is a small individual of *P. loedingi loedingi,* if there is no doubt that it was collected in Shelta Cave. Its pronotal and elytral lengths and widths and their ratios (PW 1.02 mm at base; PL 0.73 mm; EL 1.43 mm; EW at base 1.05 mm; and EW at widest 1.07 mm) do not separate it from *loedingi.* The key character that Jeannel used to separate *henroti* and *loedingi* was the relative lengths of the third and second antennal segments. In the key of Jeannel (1949) I run the type male to *P. loedingi.*

Field notes. Baiting and trapping has gathered huge numbers of the beetles in a few caves. Walter Jones took 723 in traps in Natural Well in 1937. In an ecology study in 1965 in Barclay Cave I took 534 adults and 357 larvae. Baiting in Cold Spring Cave from 21 August to 14 September in 1968 yielded 1,673 adults, most of which were released. The beetles were originally taken on bat guano in Shelta Cave (Hatch, 1933: 209), but I have never found them on bat guano in any cave.

Seasonality. Laboratory cultures show these beetles to have no reproductive seasonality when maintained under constant cavelike conditions. Adults have been taken in every month except March and April. Larvae have been found throughout the summer. In 1965 larvae were most abundant in Barclay Cave in late August, suggesting a large hatch of eggs laid by a large number of adults two weeks earlier.

Distribution. The subspecies is known only from caves in Madison County, west of the Flint River (Map 3). I have seen 1,915 preserved adults from the following twenty-one localities: ALABAMA. *Madison County:* Barclay Cave, 588 (SBP, TCB, UANH); Buford Cave, 11 (UANH); Byrd Spring Cave, 57 (SBP); Cold Spring Cave, 31 (SBP, UANH); Canoe Cave, 2 (SBP); Cave Spring Cave (No. 60, Chapman Mt.), 37 (SBP, UANH); Drake Cave, 18 (UANH); Green Grotto, 2 (SBP); Jett Cave 1 (UANH); Kelly Natural Well, 31 (UANH); Lott Cave, 22 (UANH); Natural Well, 725 (UANH); Pitt Sinkhole Cave, 93 (UANH); Sadler Spring Cave, 4 (UANH); Shelta Cave, 162 (CAS, TCB, UANH, USNM); Sinks (Simmons) Cave, 3 (TCB); Spook Cave, 6 (UANH); The Sinks, 91 (SBP UANH); Taploe Cave, (UANH); Toll Gate Natural Well, 11 (UANH); Twin Caves, 21 (TCB, UANH).

Distributional comments. The range of the subspecies exists in limestones with no known extrinsic barriers to dispersal and gene flow. The range is roughly in a 17-mile long north-south line, west of the Flint River, from Spook Cave in the north to Green Grotto in the south (Map 3). The Flint River separates this series of populations from those of *P. loedingi longicornis* living in caves in Keel Mountain. The populations of *loedingi julius* and *loedingi solanum* lie even further to the east, beyond the Paint Rock River. These last two subspecies are also separated by intervening populations of *P. valentinei* and *P. hatchi.* I later suggest that the wide distribution of the species was gained by overland dispersal during Wisconsin time, and the subspeciation has occurred since then.

The northwestern limit of the range of *loedingi loedingi* must lie between Drake Mountain and Burwell Mountain where baiting has not taken specimens in Ellis Cave, and Burwell Cave. The western limits of the range do not reach Matthews Cave, as shown by baiting. To the south, the range is limited by the Tennessee River.

Ptomaphagus loedingi longicornis Jeannel
Figures 22, 80, 101, 144; Map 3

Ptomaphagus (*Adelops*) *valentinei longicornis* Jeannel, 1949: 103. New Combination. Holotype male in MNHN, Paris, not seen. Type locality: Alabama, Madison County, Cave Spring Cave (Hering Cave). Barr, 1963: 56.

Diagnosis. Known only from caves in Keel Mountain, an isolated remnant of the Cumberland Plateau, in Madison and Jackson counties, Alabama. The subspecies is clearly defined from other subspecies of *loedingi* only by the shape of the spermatheca, and by the extreme elongation of the third antennal segment as compared with the second.

Description. Like *loedingi loedingi* with the following exceptions: antennae (Fig. 101) with segment III markedly longer than II, II shorter than IV; VII to X more elongate; VIII longer than broad. Mesosternal keel low (Fig. 80). Aedeagus (Fig. 22) slender. Spermatheca (Fig. 144) with knob on posterior end, opening to right on dorsal surface; anterior end with small crest.

Variation. No variation has been noted within the subspecies.

Field notes. I have taken numerous specimens by baiting in Paint Rock Cave and Hering (Cave Spring) Cave, and by trapping in Crossing Cave.

Seasonality. Year-round reproduction is found in laboratory cultures of the beetles, and it undoubtedly occurs also in cave populations. Adults have been collected in February, March, July, August, and September, but this reflects only the activity of collectors, not the beetles. Tenerals were not present in the August 1968 collection of 188 adults. Larvae have been taken in caves only in July, August, and September.

Distribution. Known only from Keel Mountain, an isolated remnant of the Cumberland Plateau, in Madison and Jackson counties, Alabama. The mountain is bounded on the west by the Flint River, on the east by the Paint Rock River, and on the north and south by lowlands containing tributaries to both the Paint Rock and Flint rivers. I have seen 367 preserved specimens from the following 12 localities (Map 3): ALABAMA. *Jackson County:* Crossing (Stewart) Cave, 326 (SBP, TCB); Greising Cave, 2 (SBP); Paint Rock Cave, 12 (SBP). *Madison County:* Bee Sinkhole Cave, 4 (UANH); Butler Sinkhole, 6 (UANH); Chittimwood Cave, 2 (UANH); Goat Cave, 6 (UANH); Grayson Spring Cave, 2 (UANH); Hering (Cave Spring) Cave, 3 (UANH); Labyrinth Cave, 2 (UANH); Moon Sinkhole Cave, 2 (UANH).

Distributional comments. The subspecies is separated from *loedingi loedingi* to the west by the Flint River. To the north, east, and south *P. episcopus, valentinei,* and *hatchi* occupy caves on the east side of the Paint Rock River. To the southwest, baiting in Morring Spring Cave and Clarks Bluff Cave have not taken *Ptomaphagus* in the isolated group of contiguous Meeks, Lemley, Mayo, and McKinney mountains.

Ptomaphagus loedingi julius new subspecies
Figures 23, 81, 102, 145; Map 3

Holotype male and allotype female in MCZ (no. 31902). Type locality: Alabama, Jackson County, House of Happiness Cave (4 mi. SW Scottsboro). Type data: 14.ix.1968, S. Peck. Paratypes: 83 with same data.

Diagnosis. Known only from House of Happiness Cave, in July Mountain. The subspecies is characterized the same as *loedingi loedingi*, but separated from it by the shape of the spermatheca.

Description. Similar in all respects to *loedingi loedingi* with the following exceptions: antenna (Fig. 102) with segments VI, VII, and VIII proportionately longer. Mesosternal carina (Fig. 81) more pronounced, but low, slight notch present. Aedeagus (Fig. 23) less curved. Spermatheca (Fig. 145) with swollen posterior end, no crest on anterior end.

Variation. None noted within the subspecies.

Etymology. Latin, *julius*, July, a noun in apposition, referring to July Mountain to which the subspecies is probably isolated.

Field notes. Six were found on *Neotoma* rat dung. A series of 85 was taken by baiting in the room about 30 meters from the cave entrance.

Seasonality. Seasonality is known only from two collections, made in August 1968. Five teneral adults were taken in the series of 85. Larvae are not known.

Distribution. The subspecies is known only from House of Happiness Cave, in July Mountain, Jackson County, Alabama (Map 3). I have seen 91 specimens.

Distributional comments. July Mountain is a remnant of the Cumberland Plateau. It is bordered on the southwest by the Tennessee River, on the northeast by Roseberry Creek and Roseberry Bottoms, and on the south and southwest by Sauta Creek. The possibility exists for dispersal in limestones to the northwest along Cotton Mountain and for contact with *P. hatchi* in the Plateau escarpment northwest of Larkinsville. This possibility can only be tested by baiting in the few caves known northwest of Larkinsville. No caves are known in Cotton or July mountains except House of Happiness Cave.

This population is 13 miles due east of the nearest population of *P. loedingi longicornis* in Keel Mountain. The intervening distance is occupied by both *P. valentinei* and *P. hatchi*. The distance to the northeast to Sheldons Cave, inhabited by *P. loedingi solanum*, is only 4.5 air miles. However, dispersal between these caves through limestone would involve a distance of at least 14 miles, around the head of Boxes Cove. Only one other population is known along this route, and it is of *P. hatchi*, in Indian Rocks Cave, in the head of Boxes Cove.

Ptomaphagus loedingi solanum new species
Figures 24, 82, 103, 146; Map 3

Holotype male and allotype female in MCZ (no. 31903). Type locality: Alabama, Jackson County, Sheldons Cave. Holotype data: 6.viii.1967, S. Peck, A. Fiske leg. Allotype data; 12.vii.67, S. Peck, A. Fiske leg. Paratypes: 16 from above locality; 4–8.iv.67, S. Peck, 2; 8.iv.67, S. Peck, 6; 6.viii.67, S. Peck, A. Fiske, 3; 14.ix.68, S. Peck, 1; 27.i.67, S. Peck, 1; 12.vii.67, S. Peck, A. Fiske, 3.

Diagnosis. The subspecies is known only from Sheldons Cave, 1 mile northwest of Scottsboro. It is characterized the same as *loedingi loedingi*, but separated from it by the shape of the spermatheca.

Description. Similar in all respects to *loedingi loedingi* with the following exceptions: Head. Eye remnant smallest of troglobitic *Ptomaphagus*, width of head from antennal base to margin across eye 6–8 times width of eye. Antennae (Fig. 103) more elongate; segments VII, IX, and X proportionately more slender; VIII longer than wide in side view only. Pronotum widest 1/3 before base. Mesosternal carina (Fig. 82) higher, notch faint. Aedeagus (Fig. 24) wider through middle. Spermatheca (Fig. 146) with fairly straight central shaft; posterior end bent to left into offset knob, opening to right; anterior end with no crest.

Variation. None has been noted in this subspecies.

Etymology. Latin, *solanum*, potato, a noun in apposition referring to Tater Knob, in which the subspecies lives.

Field notes. Taken by baiting along the stream, and on the flow-stone in the first 20 meters of the cave.

Seasonality. Adults have been collected in January, April, July, August, and September. Tenerals are not known, and only one larva has been collected.

Distribution. Known only from the type locality (Map 3), a cave in Gasper Limestone, in Tater Knob one mile northwest of Scottsboro. I have seen 18 specimens from the type locality collected by myself in six visits to the cave in 1967 and 1968.

Distributional comments. Tater Knob is connected by limestones to the Cumberland Plateau escarpment near Skyline with no obvious barriers to subterranean dispersal. In a straight line distance, eight miles of limestone lie between Sheldons Cave, and the *P. hatchi* population in Indian Rocks Cave. Roseberry Bottoms and Roseberry Creek to the southwest of Sheldons Cave separate it from July Mountain and House of Happiness Cave, inhabited by *P. loedingi julius.*

Ptomaphagus barri new species
Figures 25, 83, 104, 147; Map 4

Holotype male and allotype female, in MCZ (no. 31887). Type locality: Tennessee, Cannon County, Henpeck Mill Cave, 22.viii.1967, S. Peck and A. Fiske. Paratypes: 55 with same data.

Diagnosis. Ptomaphagus barri is one of two blind *Ptomaphagus* living in caves in central Tennessee. It may be told from the other (*hubrichti*) by the second antennal segment being clearly shorter than the third, and the emargination in the basal third of the pronotum. Neither are found in *hubrichti.*

Description. Length 2.8–3.2 mm. Width 1.3–1.5 mm. Head smooth; width of head from antennal base to margin across eye 4.7 times width of eye. Antennae (Fig. 104) elongate, reaching into first third of elytra when laid back; segments I and III subequal, longer than II; VIII conical, longer than wide; IX and X 3/4 as wide as long. Pronotum at base 1.5 times as wide as long, widest at base, emarginate in basal third when viewed from above; hind margin sinuate; striae pronounced on disc. Elytra at base wider than pronotal base, widest 1/3 from base; 1.6 times as long as wide at base. Mesosternal carina (Fig. 83) strong, notch absent. Aedeagus (Fig. 25) slightly curved, widest at middle, slender at tip. Spermatheca (Fig. 147) with long slender central shaft, small knob on posterior end, irregular slender hook on anterior end with distinct crest.

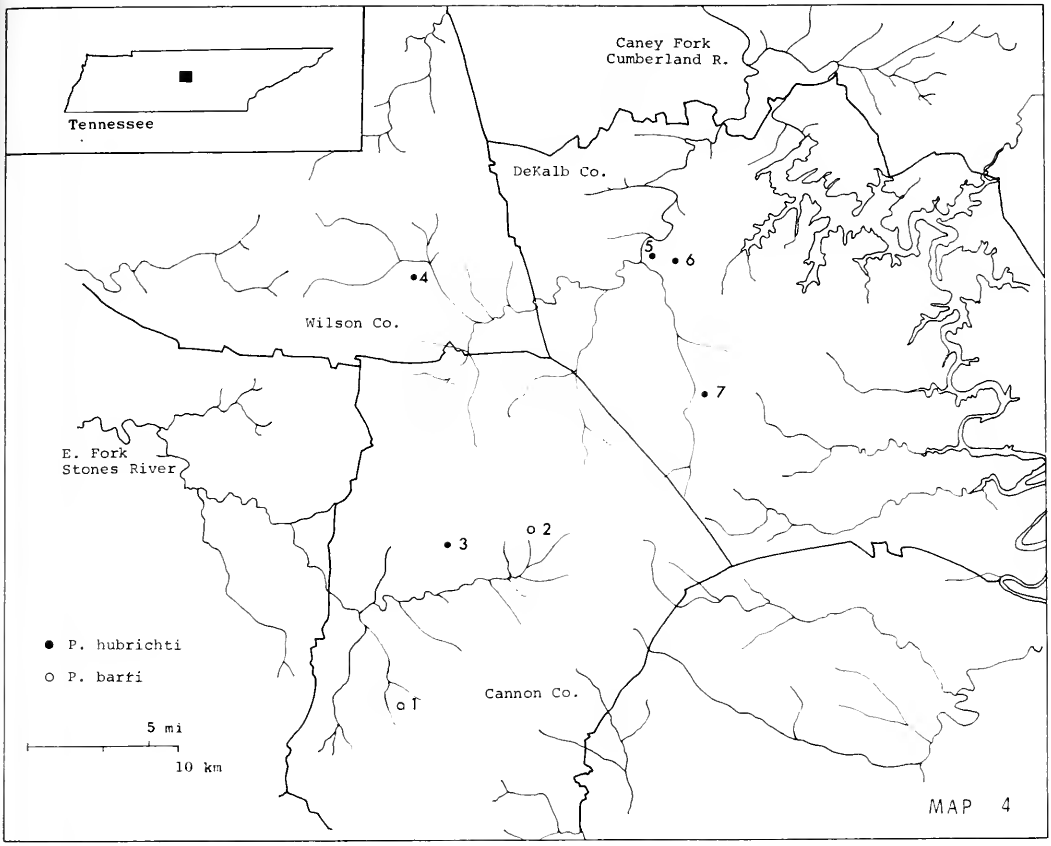
Variation. No variation noted.

Etymology. Named for Dr. Thomas C. Barr, in recognition of his aid to my studies of cave fauna and beetles.

Field notes. In the two caves in which the species has been taken, it has been found in wet gravels along cave streams, by baiting.

Seasonality. Collections have been made in March, July, and August. Teneral adults were found in August. Larvae are not known.

Distribution. Known only from two caves in Ordovician Bigby-Cannon Limestone, in Cannon County, Tennessee, on two tributary branches of the east fork of Stones River (Map 4). I have seen 63 specimens from the following localities:



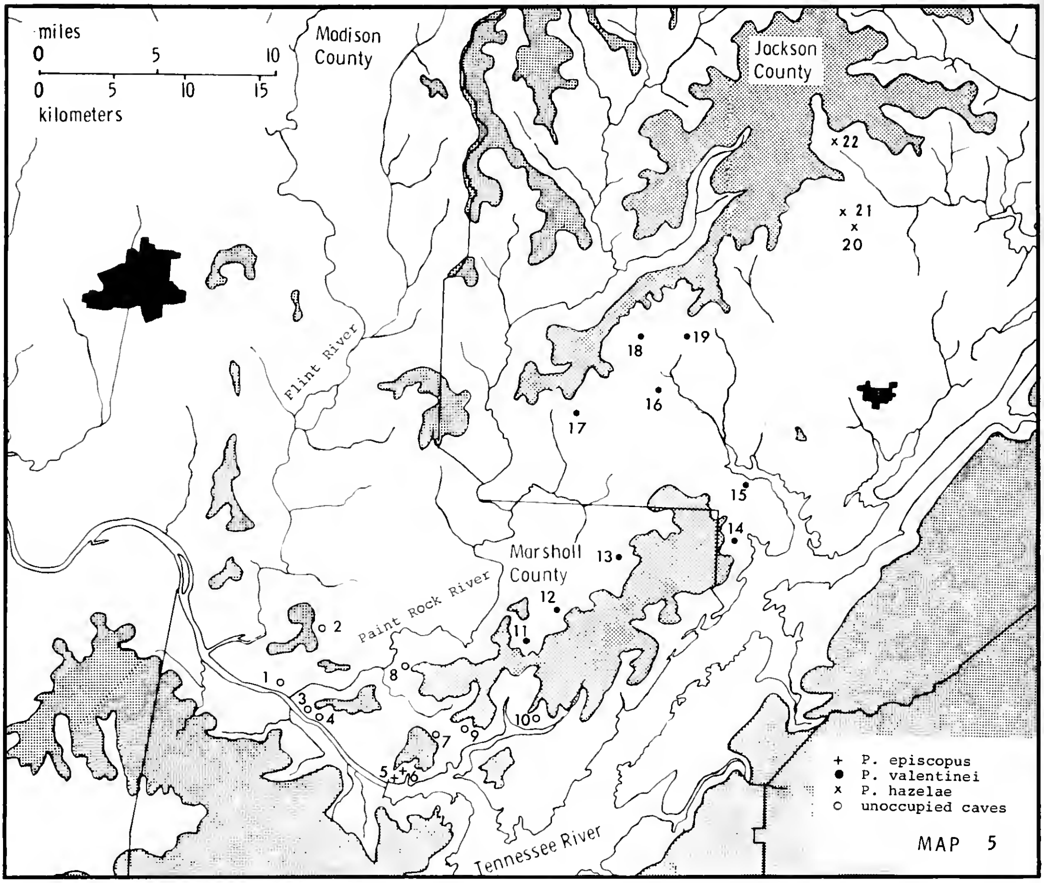
Map 4. Distribution of *Ptomaphagus* (*Adelops*) *hubrichti* (dark circles) and *Ptomaphagus* (*Adelops*) *barri* (open circles), troglobites of caves in central Tennessee. The localities are as follows: 1 Espey Cave, 2 Henpeck Mill Cave, 3 Tenpenney Cave, 4 Hays Cave, 5 Gin Bluff Cave, 6 Avant Cave, 7 Cripps Mill Cave.

TENNESSEE. *Cannon County:* Espey Cave, 6 (SBP, TCB); Henpeck Mill Cave, 57 (SBP).

Distributional comments. The species may be expected in other caves lying between the two known populations, 8 air miles from each other along the eastern flank of Nashville Basin. Several of these other caves (see Barr, 1961a for locations) have been visited but not baited. John Hollins Cave, north of Henpeck Mill Cave, was heavily baited with no success. The nearness of Henpeck Mill Cave, a *barri* locality, to Tenpenny Cave, a *hubrichti* locality, is interesting. They are separated by only two and one-half air miles, with only two minor streams between them as possible dispersal barriers (Map 4). These two species may be found sympatrically in caves to the north. Baiting in Reed Cave, two miles south of Espey Cave, has not produced the beetle. It also has not been found by hand collecting in Davenport Cave. Baiting of this and other Cannon County caves is needed.

Ptomaphagus hazelae new species
Figures 26, 105, 148; Map 5

Holotype male and allotype female in MCZ (no. 31889). Type locality: Alabama, Jackson County, Tumbling Rock Cave. Type data: 3.vii.1969, S. & J. Peck leg. Paratypes: 10 with same data.



Map 5. Distribution of *Ptomaphagus* (*Adelops*) *episcopus*, *valentinei* and *hazelae*, troglobitic species of northeastern Alabama. Stippling as in Map 3. Geology from Malmberg and Sanford (1963) and Adams et al. (1926). The localities are as follows: 1 Clark Bluff Cave, 2 Marring Spring Cave, 3 Merrill Cave, 4 Painted Bluff Cave, 5 Honeycomb Cave, 6 McHardin Cave, 7 Bishop Cave, 8 Keller Cave, 9 Ledbetter Cave, 10 Dunham Cave, 11 Kirkland Cave, 12 Guffey Cave, 13 Cathedral Cave, 14 Mink Cave, 15 Souta Cave, 16 Larkin Cave, 17 Pig Pen Cave, 18 Schiffman Cove Cave, 19 Limrock Blowing Cave, 20 Ivey Bottom Cave, 21 Driftwood Cave, 22 Tumbling Rock Cave.

Diagnosis. Limited to caves in the headwaters of Mud Creek, Jackson County, Alabama. Similar to *valentinei* but the combination of the elongate thin spermatheca without a crest and the strongly curved aedeagus with an upturned tip serves to distinguish this species from *P. valentinei.*

Description. Length 2.6–3.0 mm. Width 1.2–1.5 mm. Shape oval. Head width, from antennal base to margin across eye, 5.8 times width of eye. Antennae (Fig. 105) flattened, thin and long, reaching into first third of elytra when laid back; segment III clearly longer than II; in profile IV, V, and VI gradually widening and shortening; VII elongate conical; VIII longer than wide. Pronotum sides parallel in hind half; 1.4 times as wide as long; striae on disc present but faint. Elytra 1.5 times as long as wide at base. Mesosternal carina medium height, notch absent or vaguely present. Aedeagus (Fig. 26) strongly bent in lateral view, broad at base, narrowing gradually to apex, tip upturned. Spermatheca (Fig. 148) shaft of medium thickness, posterior end curved under and opening to left, anterior end without crest.

Variation. No variation noted.

Etymology. The species is named for Mrs. Hazel Jones, in recognition of her help and hospitality during more than two seasons of field work in northern Alabama.

Field notes. Forty-one of the specimens have come from Tumbling Rock Cave where they were baited in moist sections of the cave, or from garbage dumps left by people camping in the cave. Two specimens from Driftwood Cave were on a dead mouse.

Seasonality. Adults have been taken in seven months of the winter and summer seasons. Teneral adults have been taken in January, and larvae in December.

Distribution. Known only from three caves on the edge of the Cumberland Plateau in the headwaters of Mud Creek, Jackson County, Alabama (Map 5). I have seen 47 specimens from the following caves: ALABAMA. *Jackson County:* Driftwood Cave, 4 (SBP); Ivey Bottom Cave, 2 (TCB); Tumbling Rock Cave, 41 (SBP, TCB).

Distributional comments. The species is bounded in a few miles both to the north and southwest along the escarpment by populations of *P. hatchi.* Other caves exist in the region but have not been visited or have not been baited. Consequently, the two species may actually exist in closer proximity than is now known.

Barr (1963) surmised the species to be an allopatric population of *P. loedingi* and suggested that it might have subspecific status.

Ptomaphagus fiskei new species
Figures 27, 84, 106, 149; Map 6

Holotype male and allotype female in MCZ (no. 31890). Type locality: Georgia, Walker County, Mountain Cove Farm Cave. Type data: 20.vi.1967, S. Peck and A. Fiske leg. Paratypes: 91 with same data.

Diagnosis. This is the only troglobitic *Ptomaphagus* known from east of Lookout Mountain in Georgia. It is characterized by the third antennal segment being longer than the second, the sinuous ventral surface of the prominent mesosternal carina, and a spermatheca with a small crest on the anterior end and a knob on the posterior end with a dorsal opening.

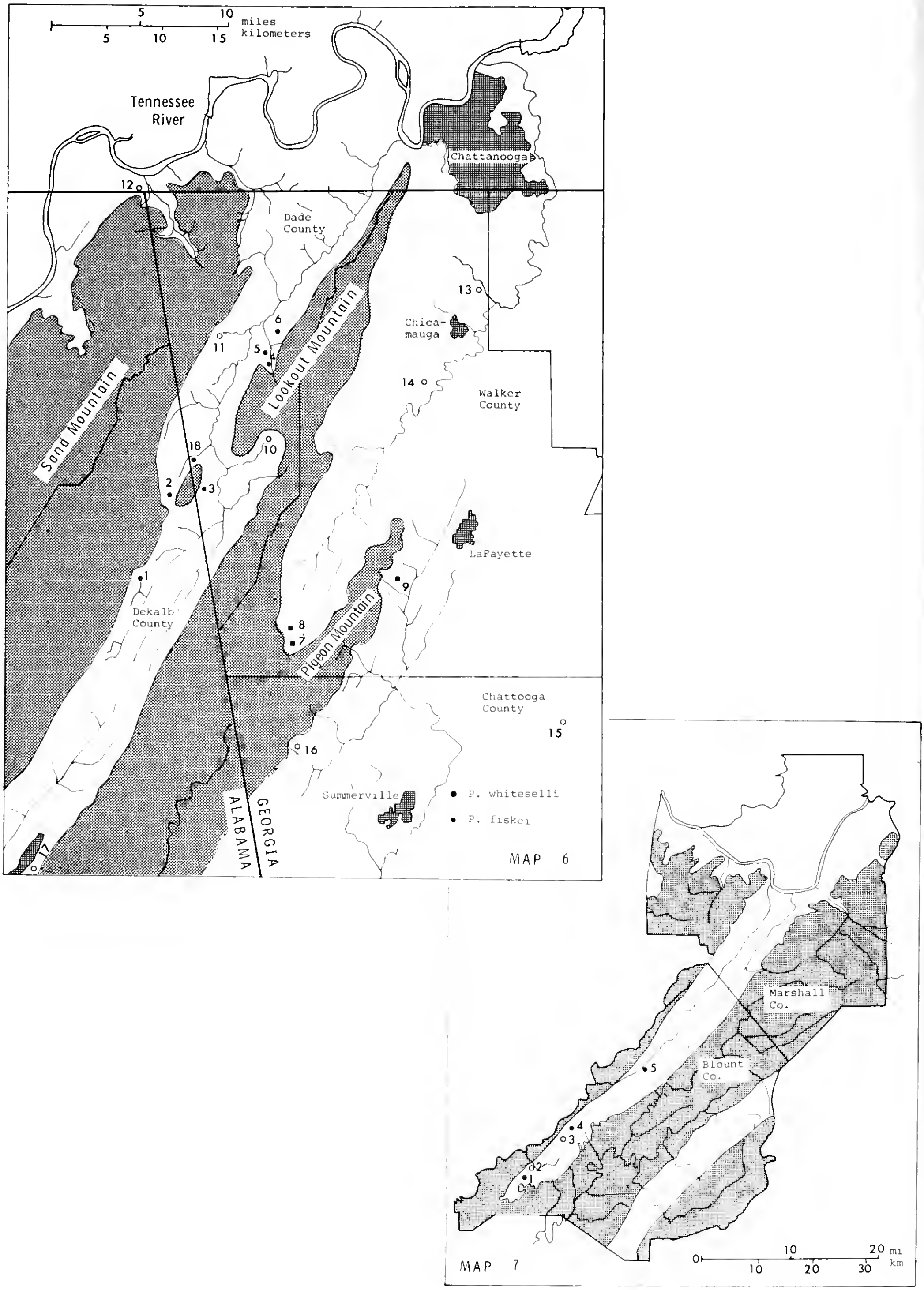
Description. Length 2.8–3.1 mm. Width 1.3–1.5 mm. Shape oval. Head punctured. Width of head across eye from antennal insertion to margin 3.2 times width of eye. Antennae (Fig. 106) elongate, slender, reaching into first 1/4 of elytra when laid back; segment III longer than II; IV, V, and VI sequentially shorter and wider; VII conical; VIII longer than wide; IX and X longer than wide. Pronotum at base 1.4 times as wide as long; widest 1/3 before base; hind margins sinuous; striae absent on disc, faint at margins. Elytra 1.5 times as long as wide at base, slightly wider 1/3 from base. Mesosternal carina (Fig. 84) prominent, ventral margin sinuous; notch absent or only faintly present. Aedeagus (Fig. 27) thin, slightly curved, tapering to tip, tip downcurved. Spermatheca (Fig. 149) with straight shaft; posterior end with knob, opening dorsally; anterior end with hook, bearing small crest.

Variation. No variation noted.

Etymology. Named for Alan Fiske in recognition of his great aid in field work in 1967 and 1968.

Field notes. Taken in all three known localities by baiting. Abundant on damp *Neotoma* rat dung in Mountain Cove Farm Cave. Found in Pettijohn Cave only in the entrance room. Extensive trapping and baiting in Bible Spring Cave took only two specimens in a pile of rocks at the top of a small dome pit, and none along the streams.

Seasonality. Specimens have been collected only in June and July. Larvae were taken in all three localities and tenerals only in Mountain Cove Farm Cave (of the 93 in the type series collected in late June, 13 are teneral).


5 10 miles
5 10 15 kilometers
Tennessee River
Chattanooga
Dade County
Sand Mountain
Lookout Mountain
Chicamauga
Walker County
LaFayette
Pigeon Mountain
Dekalb County
Chattooga County
Summerville
ALABAMA
GEORGIA
● P. whiteselli
• P. fiskei
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
MAP 6
Marshall Co.
Blount Co.
1
2
3
4
5
0 10 20 mi
10 20 30 km
MAP 7

Distribution. Known only from caves on the east and west flanks of Pigeon Mountain, a spur of Lookout Mountain (Map 6). I have seen 154 specimens from the following 3 localities: GEORGIA. *Walker County*: Bible Spring Cave, 2 (SBP); Mountain Cove Farm Cave, 115 (SBP); Pettijohn Cave, 37 (SBP).

Distributional comments. This species demonstrates how closely the distribution of the troglobitic *Ptomaphagus* is tied to the flat-bedded rocks of the escarpment of the Cumberland Plateau. Baiting in three nearby caves to the east in rocks of the folded and faulted Appalachian Valley yielded no *Ptomaphagus.* Subterranean dispersal into the limestones of these more easterly caves may be limited by the discontinuous nature of the limestones resulting from the folding and faulting in the Appalachian Valley. A prominent fault flanks the eastern scarp of Lookout-Pigeon Mountain, bringing to the surface less cavernous Cambrian Knox dolomites (Butts, 1946).

Extensive baiting in Blowing Spring Cave, about 10 miles to the southwest along the Plateau escarpment, did not yield beetles. Between these points may exist the true southwestern range limit of the species.

Biological survey work has been conducted in other caves in the folded and faulted rocks of the Valley and Ridge Province of northwestern Georgia and eastern Alabama, but has not yielded *Ptomaphagus* (Holsinger and Peck, 1971; Peck, unpublished data). This seems to confirm the observation of the restriction of troglobitic *Ptomaphagus* to the flat-bedded limestones of the Interior and Cumberland plateaus.

Ptomaphagus walteri new species

Figures 28, 85, 107, 150; Map 7

Holotype male and allotype female in MCZ (no. 31891). Type locality: Alabama, Blount County, Bryant Cave. Type data: 19.iii.1966, S. Peck leg. Paratypes: 14 with same data.

Diagnosis. This is the only troglobitic *Ptomaphagus* known from Blount County, Alabama. It is characterized by the prominent mesosternal keel, without a notch; the thin, slightly curved aedeagus; and the spermatheca with both a posterior knob with an opening to the right, and an anterior end with no crest.

Description. Length 2.8–3.0 mm. Width 1.3–1.5 mm. Head punctured; width of head from antennal base to margin across eye 4.1 times as wide as eye. Antennae (Fig. 107) medium length, thin, reaching into first 1/4 of elytra when laid back; segment III longer than II, both shorter than I; IV, V, and VI shorter than II, each sequentially wider; VIII 1 1/2 times as long as wide; VIII twice as wide as long; IX and X subequal, quadrate. Pronotum at base 1.5 times as wide as long; widest 1/3 before

←

Map 6. Distribution of *Ptomaphagus* (*Adelops*) *whiteselli* (dark circles) and *Ptomaphagus* (*Adelops*) *fiskei* (dark squares), troglobitic species of caves in northeastern Alabama and northwestern Georgia. The open circles are caves in which baiting has attracted no *Ptomaphagus.* Stippling as in Map 3. Geology after Butts (1946). The localities are as follows: 1 Sequoyah Cave, 2 Deerhead Cove Cave, 3 Byers Cave, 4 Case Caverns, 5 Sittons Cave, 6 Morrison Cave, 7 Mt. Cove Farm Cave, 8 Bible Spring Cave, 9 Pettijohn Cave, 10 Johnson Crook Cave, 11 Howards Waterfall Cave, 12 Nickajack Cave, 13 Cave Spring Cave, 14 Horseshoe Cave, 15 Parker Cave, 16 Blowing Spring Cave, 17 Manitou (Ft. Payne) Cave, 18 Twin Snakes Cave.

Map 7. Distribution of *Ptomaphagus* (*Adelops*) *walteri,* a troglobite of caves in Blount County, in northcentral Alabama, in the southern end of the Sequatchie Valley. Closed circles indicate known localities, open circles are localities in which baiting has yielded no specimens. Dark stippling (south of Tennessee River only) as in Map 3. Caves occur in the valley in the Bangor Limestone. Limestone is also exposed in Murphree Valley in southeastern Blount County. Topography and geology from Adams et al. (1926). Numbers refer to the following localities: 1 Bryant Cave, 2 Randolf Cave, 3 Catfish Cave, 4 Bangor Cave, 5 Wildcat Cave.

base; hind margin entire; striae on disc absent, faint on margins. Elytra 1.4 times as long as wide at base; slightly wider 1/3 from base. Mesosternal carina (Fig. 85) strong, prominent; ventral surface straight; notch absent. Aedeagus (Fig. 28) almost straight in middle, arcing to ends, narrowing to sharp tip, tip downcurved; setation reduced to two or three on each side of tip; parameres with only two (rarely three) apical setae. Spermatheca (Fig. 150) with slightly curved shaft; knob on posterior end with opening to right; anterior end with hook, no crest on knob.

Variation. No variation noted.

Etymology. Named for Dr. Walter B. Jones, in recognition of his hospitality and encouragement to myself and other students of the cave fauna of Alabama.

Field notes. The type series was taken on human dung on dryish soil a few hundred feet from the entrance of Bryant Cave. The one specimen from Wildcat Cave was found under a rock. The Bangor Cave collections were made by Walter B. Jones in June 1937 and September 1940. I have repeatedly tried to bait specimens from Bangor Cave. The failure may reflect extinction of the Bangor Cave population. The extinction may have resulted from two events. (1) A gaming house and beer hall were at one time operated in the cave. These structures burned in the 1940's, and the fire may have consumed the oxygen in the cave, killing the fauna. (2) The cave environment may have been unfavorably altered with the opening of a back entrance to the cave in the 1950's. The opening, made in a mushroom farming venture, may have altered air flow and soil moisture conditions. However, other cave fauna is now present in the cave; *i.e.*, the troglobitic millipede *Scoterpes,* the troglobitic collembolan *Pseudosinella hirsuta,* and the troglophilic pselaphid beetle *Batriasymmodes spelaeus.*

Seasonality. Adults have been collected only in March, May, and June. Tenerals and larvae are not known.

Distribution. Known from three caves, lying in a straight line along the southern end of the Sequatchie Valley in the Bangor Limestone, in the drainage of the Black Warrior River (Map 7). I have seen 24 specimens from the following three localities: ALABAMA. *Blount County:* Bangor Cave, 7 (UANH), Bryant Cave, 18 (SBP), Wildcat Cave, in southwest Blountsville, 1 (FMNH).

Distributional comments. The straight line range from Wildcat Cave to Bryant Cave is 21 miles. Bryant Cave lies 9 miles to the southwest of Bangor Cave. I have frequently and heavily baited two caves (Randolf and Catfish) between Bryant and Bangor with no success. All these caves, and others not yet collected, are in the Bangor Limestone, which is exposed in an unbroken line on both sides of this southern end of the Sequatchie Valley from a few miles southwest of Blount Springs to the northeast of Guntersville.

The species may exist in other caves to the northeast of Blountsville (Wildcat Cave). The limestones sink below the Pennsylvanian rocks a few miles to the southwest of Bryant Cave (near Rickwood Caverns), so this will mark the limits of the range in this direction.

Ptomaphagus whiteselli Barr
Figures 29, 86, 108, 151; Map 6

Ptomaphagus (*Adelops*) *whiteselli* Barr, 1963: 55. Holotype male, in AMNH, seen. Type locality: Georgia, Dade County, Sittons Cave.

Diagnosis. This is the only troglobitic species known from the caves in Lookout Valley between Sand and Lookout mountains in DeKalb County, Alabama, and Dade County, Georgia. The combination of a very slender and curved aedeagus and a spermatheca with only a slight knob at the posterior end of the straight shaft serves to distinguish this species from others.

Description. Length 2.2–2.6 mm. Width 1.3–1.4 mm. Head punctured; width across head from antennal base across eye to margin 3.6 times width of eye. Antennae (Fig. 108) medium length, extending to base of pronotum when laid back; segment II and III subequal, shorter than I; IV, V, VI progressively shorter and thicker, VII conical, VIII 3/4 as long as wide; IX longer than X. Pronotum 1.5 times as wide at base as long; widest 1/3 before base; sides behind curving into hind angles; hind margin sinuous; striae on disc fainter than on sides. Elytra 1.4 times as long as wide at base. Mesosternal carina (Fig. 86) high, notch absent. Aedeagus (Fig. 29) slender, slightly curved, gradually tapering to point at tip, tip slightly bent downward. Spermatheca (Fig. 151) shaft straight, posterior end with slight knob, opening to right, anterior end with small hook, crest absent.

Variation. No variation noted.

Field notes. Most of the specimens of the species have been taken by baiting. In Sequoyah Cave the beetles live both in gravels along the stream and in sections appearing to be only slightly moist sand and soil with no obvious food source.

Seasonality. No reproductive seasonality exists in a laboratory culture from Morrison Cave, and none probably exists deep in caves. Adults have been collected only in June, July, August, November, and December. Tenerals are known only from one November collection, and larvae only from one June collection.

Distribution. The species has a straight line range of 15 miles (Map 6) in Lookout Valley between Sand Mountain and Lookout Mountain. I have seen 209 specimens from the following seven localities: ALABAMA. *DeKalb County:* "Cave in Deer Head Cove," 1 (SBP); Sequoyah (Ellis) Cave, 56 (SBP). GEORGIA. *Dade County:* Byers Cave, 105 (SBP); Case Caverns, 3 (SBP); Morrison Cave, 20 (SBP); Sittons Cave, 27 (SBP, TCB); Twin Snakes Cave, 1 (SBP).

Distributional comments. The species occurs in caves on both sides of Lookout Creek, flowing into the Tennessee River, and is apparently restricted to this drainage. The valley and its limestone escarpment sides continue unbroken southward over the low drainage divide into the drainage of Wills Creek which flows into the Coosa River. Though *P. whiteselli* has not dispersed out of the drainage of Lookout Creek, other troglobitic beetles have. The carabid *Pseudanophthalmus alabamae* occurs in both drainages from Sequoyah Cave southwestward 35 miles to caves at Collinsville (personal data).

A lack of similarity in ranges of two other *Pseudanophthalmus* exists when compared to *Pt. whiteselli* (Map 6). *Ps. fulleri* ranges from Byers Cave and Johnson Crook Cave, northward along Lookout Creek, through Howards Waterfall, Sittons, and Morrison caves, to Tennessee Caverns in Hamilton County just over the state border into Tennessee (personal data). It also occurs east of Lookout Mountain in Horseshoe Cave. In contrast, *Pt. whiteselli* is not known as far north as Tennessee Caverns, nor has it been found by baiting in Johnson Crook Cave, or in Horseshoe Cave. *Ps. digitus* also ranges from Tennessee Caverns southwestward to Byers and Johnson Crook caves, but is not known inbetween (personal data, and data in Holsinger and Peck, 1971).

Ptomaphagus valentinei Jeannel
Figures 30, 87, 109, 152; Map 5

Ptomaphagus (*Adelops*) *valentinei* Jeannel, 1933: 252. Type in MNHN, not seen. Type locality: Alabama, Jackson County, Sauta (Old Salter) Cave. Jeannel, 1936: 93.

Ptomaphagus (*Adelops*) *valentinei valentinei* Jeannel, 1949: 103; Barr, 1963: 56.

Diagnosis. This species is distinguished from others in the caves of northeastern Alabama by its parallel hind pronotal margins, vague mesosternal notch, elongate antenna with segment III markedly longer than II, and spermatheca with thin curved central shaft with distinct crest on anterior end and posterior end curving and opening to left.

Description. Length 2.5–3.2 mm. Width

1.3–1.7 mm. Head punctured; width of head from antennal base to margin across eye 5.5 times width of eye. Antennae (Fig. 109) slender, elongate, reaching into anterior third of elytra when laid back; segment III markedly longer than II; IV, V, and VI sequentially decreasing in length and increasing in width; VII conical, VIII longer than wide. Pronotum at base 1.5 times as wide as long, widest at base; sides parallel at base; hind margin slightly sinuous; striae on disc feeble. Elytra at base wider than pronotum at base; 1.5 times as long as wide at base. Mesosternal carina (Fig. 87) medium, notch present but vague. Aedeagus (Fig. 30) thin, only moderately tapered, tip thin and downturned or broad. Spermatheca (Fig. 152) with thin curved central shaft, posterior end with curve, anterior hooked end small with prominent crest.

Variation. The aedeagus is more heavily hooded at the tip in Sauta Cave, and thinner and downcurved at the tip in Limrock Blowing Cave. The shape of the hind femora varies between populations, being more slender in Limrock Blowing Cave. The spermathecal posterior tip opens to the right in a few specimens.

Field notes. Most of the specimens of this species have been collected by baiting. It is abundant on cricket guano in a crawl way at the back of Schiffman Cove Cave. Twenty-seven were taken on a damp, rotting *Neotoma* rat nest in a side passage near the entrance of Limrock Blowing Cave, and on *Neotoma* droppings in Pig Pen Cave.

Seasonality. No seasonality exists for reproduction in this species. A laboratory culture has been maintained of material from Schiffman Cove Cave, and reproduction continues with no seasonal fluctuation. Adults have been taken in seven caves in January, February, March, July, and August. Larvae have been found in five caves in June, July, August, and December.

Distribution. The species is distributed in caves in Mississippian limestone at the edge of the Cumberland Plateau in southern Jackson and northern Marshall counties, Alabama, between the Tennessee and Paint Rock rivers. I have seen 239 specimens from the following nine caves (Map 5): ALABAMA. *Jackson County:* Larkin Cave, 2 (SBP); Limrock Blowing Cave, 34 (SBP, UANH); Mink Cave, 22 (SBP); Pig Pen Cave, 24 (SBP); Sauta (Salter) Cave, 95 (SBP, TCB, UANH); Schiffman Cove Cave, 22 (SBP). *Marshall County:* Cathedral Caverns (Bat Cave), 32 (SBP, TCB, UANH); Guffey Cave, 8 (TCB); Kirkland Cave, 16 (SBP).

Distributional comments. The species may be expected to occur in other caves on the southeastern flanks of Gunter Mountain, and between presently known localities. I did not take *Ptomaphagus* by baiting in Kellers Cave in the western end of Gunter (Grassy) Mountains. Baiting by Dick Graham, and later, myself, did not yield beetles on the southern flank of Gunter Mountain in Dunham Cave. Baiting failure was also met by Graham in Ledbetter Cave, Bishop Cave, Natural Bridge Cave, Walnut Cave, and Freyder Cave.

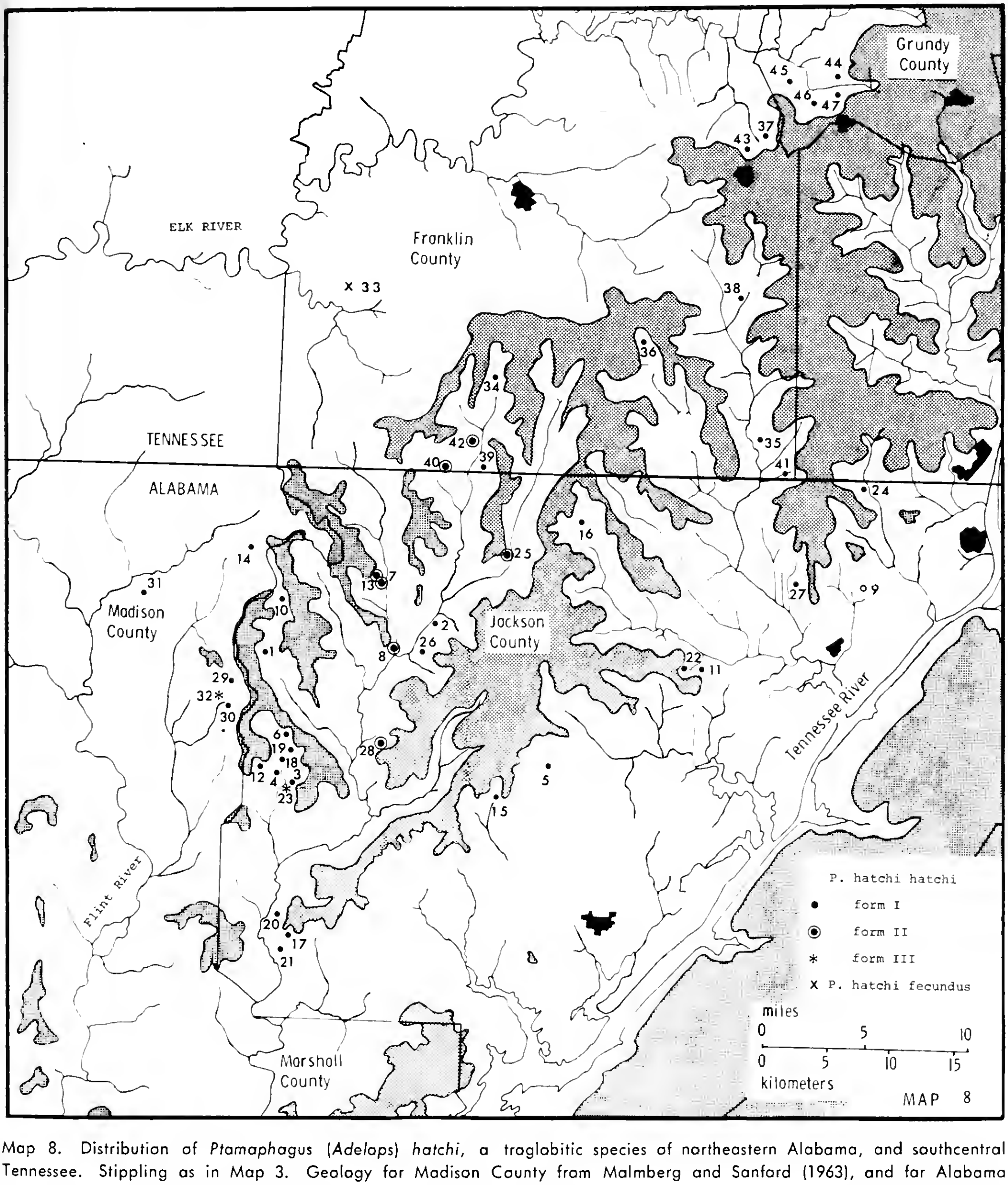
The potential dispersal barrier of the low limestones of Stephen's Gap has been crossed, connecting the Gunter Mountain populations and those three in the southeastern flank of the unnamed mountain running from Woodville to Larkinville. These latter three populations are bounded by populations of *P. hatchi* (form I) to the west and northeast.

Ptomaphagus hatchi hatchi Jeannel Figures 31, 32, 88, 110, 111, 153–155; Map 8

Ptomaphagus (*Adelops*) *hatchi* Jeannel, 1933: 252. Type, in MNHN, Paris, not seen. Type locality: Tennessee, Grundy County, Wonder Cave. Jeannel, 1936: 93; 1949: 101; Barr, 1963: 54.

Ptomaphagus (*Adelops*) *henroti* Jeannel, 1949: 102. NEW SYNONYM. Co-type in MNHN, Paris, not seen. Type locality: Alabama, Madison County, Aladdin Cave. Barr, 1963: 56.

Ptomaphagus (*Adelops*) *laticornis* Jeannel, 1949:



Map 8. Distribution of *Ptomaphagus* (*Adelops*) *hatchi*, a troglobitic species of northeastern Alabama, and southcentral Tennessee. Stippling as in Map 3. Geology for Madison County from Malmberg and Sanford (1963), and for Alabama from Adams et al. (1926). The localities are as follows: 1 Borderline Cave, 2 Bouldin Cave, 3 Cave Stand Cave, 4 Clemmons Cave, 5 Cornellison #2 Cave, 6 Devils Stairstep Cave and Keels Cave, 7 Doodlebug Pit-Blowing Cave, 8 Doug Green Cave, 9 Edgefield Cave, 10 Hambrick Cave, 11 Happy Hollow Cave, 12 Honey Hollow Saltpeter Cave, 13 Horseshoe Cave, 14 Hurricane Cave, 15 Indian Rocks Cave, 16 Jess Elliott Cave and Tate Cave, 17 Kennamer Cave, 18 McFarland Cave, 19 McFarland Hollow Blowing Cave and McFarland Spring Cave, 20 Margue Cave, 21 Nat Cave, 22 Rainbow Cave, 23 Rousseau Cave, 24 Russell Cave, 25 "Section 20" Cave, 26 Swaim Cave, 27 Talley Ditch Cave, 28 Williams Saltpeter Cave, 29 Aladdin Cave, 30 Hutton Cave, 31 Jacks Cave, 32 Scott Cave, 33 Caney Hollow Cave, 34 Caroline Cave Cave, 35 Crownover Saltpeter Cave, 36 Custard Hollow Cave, 37 Dry Cave, 38 Lost Cave Cave, 39 Mill Hollow Head Cave, 40 Putnam Spring Cave, 41 Ronnie Willis Cave, 42 Round Mountain Cave, 43 Wet Cave, 44 Crystal Wonder Cave, 45 Partin Spring Cave, 46 Trussell Cave, 47 Wildman Cave.

102. NEW SYNONYM. Type male in MNHN, Paris, seen. Type locality: Alabama, Madison County, Scott Cave. Barr, 1963: 55.

Diagnosis. This is the most variable species of the troglobitic *Ptomaphagus.* It ranges through Grundy and Franklin counties, Tennessee, and Madison and Jackson counties, Alabama. It is distinguished by its smaller size, short antennae which reach into the first quarter of the elytra, the low mesosternal keel with a distinct notch, and the curved hind sides of the pronotum. It is distinguished from *hatchi fecundus* by the characters of the spermatheca.

Description. Length 2.3–2.7 mm. Width 1.2–1.5 mm. Head finely punctured; width of head from antennal base to margin across eye 3.0–4.1 times width of eye. Antennae (Figs. 110, 111) medium, reaching into first quarter of elytra when laid back; segments II and III subequal, to III definitely longer, both shorter than I; IV, V, and VI subequal in length and width, to progressively shortening; VII elongate conical; VIII 3/4 to 1/2 as long as wide; IX longer than X; X quadrate. Pronotum at base 1.4 times as wide as long, sides gradually arcuately narrowing in front; widest 1/3 before base, slightly narrowing behind to base; surface with distinct striae on disc. Elytra at base slightly narrower than prothorax base, widest 1/3 from base; 1.4 times as long as wide. Mesosternal carina medium, notch conspicuous (Fig. 88). Aedeagus (Figs. 31, 32) in profile gradually curved; tip thin to expanded. Spermatheca (Figs. 153–155) of three forms: with fairly straight shaft; anterior end with or without crest; posterior end with or without knob, opening to right, or dorsally.

Variation. There is considerable variation when populations are compared from the extremes of the range (Map 8) of the species. The southwestern populations were formerly recognized as *P. henroti.* But no sharp break in character variation is encountered when a geographic sequence of populations is examined. Previous workers did not have the intermediate populations to work with that I have. Generally, the antennae are less slender, the eyes are smaller, and the hind lateral margins of the pronotum are more curved in the northeastern populations. Larger eye remnants, more slender antennae, and a tendency for parallel hind lateral pronotal margins are found in the southwest around Scott Cave. In the southwest the aedeagus is broader in the base in side view, and the tip is broader in side view in populations in Jacks Cave, Scott Cave, Aladdin Cave, the Morgue Cave, and Hurricane Cave.

The species *laticornis* Jeannel was separated from *henroti,* which inhabits the same cave, solely on the basis of different proportions in the antennal segments. It is synonymized because I believe the type is only a variant individual with slightly shorter and thicker antennal segments.

The spermatheca is clearly polymorphic, with three forms, each having a general geographic distribution. Form I (Fig. 153), without a knob at the distal end, is the most widespread. Form II (Fig. 154) is a very elongate thin spermatheca with a distal twist and large basal crest. This form is found in the following seven caves in the upper Paint Rock River drainage: Round Mountain Cave, Putman Spring Cave, "Section 20" Cave, Horseshoe Cave, Doodlebug Pit-Blowing Cave, Doug Green Cave, and Williams Saltpeter Cave. Form II is allopatrically distributed on both sides of the river, and populations are separated from each other on each side by populations of form I. Form III (Fig. 155), without a basal crest and having a large dorsally opening distal knob, has been found only in Scott and Rousseau Caves in the southwestern end of the species range.

Rather than informally treat the variation in the spermatheca, as I have, another procedure would be to recognize each form as a subspecies or species. I do not believe this is warranted at this time. Each form is without a continuous range. Additional characters that correlate with the distribution of the spermathecal forms have not been found. Intermediates, indicating hybridization, are not known. The natural test of the species, reproductive isolation in sympatric populations, has not occurred because all populations are allopatric for each form. Only future laboratory breeding studies will determine if intrinsic reproductive barriers have been established. The spermathecal forms may be characters indicating allopatrically distributed sibling species. If greater weight is later given to this character for indicating relationship, form II would be placed as a subspecies of *Pt. valentinei,* or as a species close to *valentinei.*

Field notes. Most of the specimens of this species have been taken by baiting. Large collections were taken on damp *Neotoma* rat dung in Rainbow, Nat, and Mill Hollow Head caves, and in entrance debris and rocks in Jacks Cave. Sixty-two adults were collected from a decaying box turtle where it had fallen in the entrance twilight zone of Horseshoe Cave.

Seasonality. The species probably has no seasonality for populations living deep in caves. I have seen adults taken in every month except October and November. I have seen teneral adults in 12 collections taken in the months of January, February, July, August, September, November, and December. Out of 55 adults taken in August in Talley Ditch Cave, 20 were teneral. Larvae have been taken in six caves in the months of June, July, and August. The beetles may be closer to entrances in the moist spring months, as indicated in Swaim Cave, which yielded beetles to bait in March 1966 but not in July 1967 when the soil was noticeably drier.

Distribution. The species is widely spread in caves in Mississippian limestones at the edge of the Cumberland Plateau, northwest of the Tennessee River and east of the Flint River in Franklin and Grundy counties, Tennessee, and Madison and Jackson counties, Alabama. I have seen 1,487 specimens from the following 45 cave localities (Map 8):

ALABAMA. *Jackson County:* Borderline Cave (no. 830), 3 (SBP); Bouldin Cave (no. 652), 2 (SBP); Cave Stand Cave, 23 (UANH); Clemmons Cave, 4 (UANH); Cornellison Cave no. 2, 45 (SBP); Devils Stairstep Cave, 4 (UANH); Doodlebug Pit-Blowing Cave, 5 (SBP); Doug Green Cave, 44 (SBP); Hambrick Cave, 2 (UANH); Happy Hollow Cave, 44 (SBP); Honey Hollow Saltpeter Cave (no. 74), 38 (UANH); Horseshoe Cave, 62 (SBP); Hurricane Cave, 62 (SBP); Indian Rocks Cave, 89 (SBP); Jess Elliott Cave, 4 (SBP, TCB); Keel Cave, 12 (UANH); Kennamer Cave, 1 (SBP); McFarland Cave, 7 (UANH); McFarland Hollow Blowing Cave (no. 66), 45 (UANH); McFarland Spring Cave, 52 (UANH); Morgue Cave, 8 (SBP); Nat Cave, 11 (SBP); Upper Rainbow Cave, 44 (SBP); Rousseau Cave, 6 (SBP, UANH); Russell Cave (Montague, or Pig entrance), 6 (SBP); "Section 20" Cave, 10 (SBP); Swaim Cave, 22 (SBP); Talley Ditch Cave, 60 (SBP, TCB); Tate Cave, 1 (SBP). *Madison County:* Aladdin Cave, 89 (SBP, TCB, UANH); Hutton Cave, 83 (UANH); Jacks Cave, 51 (SBP, UANH); Scott Cave, 229 (SBP, TCB, UANH). TENNESSEE. *Franklin County:* Caroline Cove Cave, 9 (SBP); Crownover Saltpeter Cave, 19 (TCB); Dry Cave, 22 (TCB); Mill Hollow Head Cave, 37 (SBP); Putman Spring Cave, 45 (SBP); Rannie Willis Cave, 40 (SBP, TCB); Round Mountain Cave, 24 (SBP); Wet Cave, 1 (TCB). *Grundy County:* Crystal Cave, 10 (TCB); Trussell Cave, 2 (TCB); Wildman Cave, 2 (SBP, TCB).

Distributional comments. I have not seen material from Wonder Cave, the type locality, but nearby Crystal Cave is part of the same system and would be inhabited by the same population. Barr (1963) reports the following localities from which I have not seen material: Grundy County, Partin Spring Cave; Franklin County, Custard Hollow Cave. Jeannel (1949) reports material from Lost Cove Cave, Franklin County, but I have seen none and I found none in August 1968.

Within its range, the beetle may be expected in every cave. When not found by hand collecting, it has been taken by bait in every cave but Edgefield Cave. Other caves in the range have been visited but hand collected only. No extrinsic barriers to dispersal exist to break the subspecies distribution. Continuous limestone suitable for interconnecting subterranean dispersal corridors connects all known populations. However, one notably distinct cluster of populations exists (Map 8), bounded by populations of other species. The Indian Rocks Cave and Cornellison Cave populations are bounded on the east in the same escarpment by *P. hazelae,* and on the southwest by *P. valentinei.* I later suggest that at least part of the complex distributional pattern of spermathecal variation in this subspecies is a result of overland dispersal of already spermathecally differentiated ancestors in Wisconsin time.

The disjunction of the populations of spermathecal forms has been discussed under variation. I have made only a simple analysis of this variation. It is certainly more complex and will reward additional collecting and study.

Ptomaphagus hatchi fecundus Barr
Figures 33, 89, 112, 156; Map 8

Ptomaphagus (*Adelops*) *fecundus* Barr, 1963: 57. New Combination.

Holotype male and allotype female in AMNH, seen. Type locality: Tennessee, Franklin County, Caney Hollow Cave.

Diagnosis. Known only from the type locality cave, in the edge of the Central Basin of Tennessee. The subspecies is characterized the same way as *hatchi hatchi,* but separated from it by the shape of the spermatheca.

Description. Similar in all respects to *hatchi hatchi* with the following exceptions: Head width from antennal base to margin across eye 3.5–4.5 times width of eye. Antennae (Fig. 112) with segment III distinctly longer than II; IV, V, and VI progressively shortening; VII elongate conical; VIII twice as wide as long; IX and X slightly longer than wide. Pronotal striae on disc faint or absent, distinct on margins. Mesosternal carina (Fig. 89) lower. Aedeagus (Fig. 33) thinner, tip expanded in side view. Spermatheca (Fig. 156) with sinuous shaft; posterior end bent to left, opening dorsal; anterior end with small hook, distinct crest.

Variation. No variation noted.

Field notes. Barr (1963) reported the beetles to be "so numerous that it was difficult to traverse the cave without stepping on them." They were feeding on bat guano. I visited the cave, but did not bait it, in July and August 1965 and found no beetles. The marked decline in the apparent population density may be connected with the disappearance since 1963 of the bat colony that formerly occupied the cave.

Seasonality. Known only from the single collection of Barr in May 1959.

Distribution. Known only from the type locality (Map 8). I have seen the 94 paratypes.

Distributional comments. The type cave lies in the limestones of the Catheys formation exposed in the margin of the Central Basin and Highland Rim of Tennessee. It is only four air miles from Caney Hollow Cave to the limestones of the escarpment of the Cumberland Plateau, inhabited by *hatchi hatchi.* However, these two limestones are separated by the noncavernous Chattanooga Shale. This geologic horizon must act as a barrier to subterranean dispersal and gene flow between the beetle populations.

There are no known nearby caves in the Catheys Formation. The subspecies may well be limited to Caney Hollow Cave.

Ptomaphagus episcopus new species
Figures 34, 90, 113, 157; Map 5

Holotype male and allotype female in MCZ (no. 31892). Type locality: Alabama, Marshall County, McHardin Cave. Type data: 14.viii.1967, S. Peck and A. Fiske leg. Paratypes: two with same data, and two from same locality, 3.xii.1967, R. Graham leg; 35 from Honeycomb Cave, Marshall Co., 24.i.1939, W. B. Jones.

Diagnosis. The species is known only from caves in Bishop Mountain, Marshall County, Alabama. It is most similar to *P. hatchi.* The combination of the low mesosternal carina with a notch, the stout aedeagus, and the posterior end of the spermatheca without a knob serve to characterize the species.

Description. Length 2.5–2.9 mm. Width 1.3–1.6 mm. Head punctured; width of head from antennal base to margin across eye 4.7 times width of eye. Antennae (Fig. 113) medium length, reaching first 1/4 of elytra when laid back; segments II and III subequal, to III distinctly longer than II, both shorter than I; IV, V, and VI subequal; VII elongate conical; VIII 3/4 as long as wide; IX and X slightly longer than wide. Pronotum at base 1.4 times as wide as long; widest 1/3 before base; hind margin slightly sinuous; striae faintly present on disc. Elytra 1.5 times as long as wide at base. Mesosternal carina (Fig. 90) low, notch distinct to faint. Aedeagus (Fig. 34) stout, gently arcing; distinct crest on tip. Spermatheca (Fig. 157) with curved shaft, posterior end undulating to dorsally facing opening, tiny crest on anterior end.

Variation. Some variation exists in the posterior end of the spermatheca, and the shape of the hind femora. The McHardin Cave specimens are larger than those from Honeycomb Cave, and have antennal segment III distinctly longer than II.

Etymology. Latin, *episcopus,* bishop, a noun in apposition, referring to Bishop Mountain in which the species is probably limited.

Field notes. The six type specimens were taken with liver bait, under a large rock at the back of McHardin Cave, about 20 meters from the entrance. The Honeycomb Cave specimens were collected in January 1939 by Walter B. Jones, who collected 120 specimens, and reports (personal communication) they were so abundant that several hundred more could have been collected. Honeycomb Cave is now mostly flooded by the impoundment of the Tennessee River, behind Guntersville Dam. An upper entrance still exists to the cave, which I visited in 1968. From the Tennessee River there is free circulation of warm river water into the cave, which raises the cave air temperature. Normal cave temperature in Jackson County, Alabama is 15°C. In late August, Honeycomb Cave was 25°C near the ceiling, with a water temperature of 27°C. Soil in the side chamber was 22°C. Baiting did not yield *Ptomaphagus*, but other beetles (the carabids *Agonum caudatum* and *Tachys*) were unusually abundant for an Alabama cave. The warm conditions may have exterminated most of the cave-adapted fauna. One specimen of the troglobitic millipede *Tetracion* was collected, so all the cave-adapted fauna is not yet gone.

Seasonality. The species has been collected in January, August, and December. Tenerals and larvae are not known.

Distribution. The species is known only from two caves in Bishop Mountain (Map 5). I have seen 41 specimens from the following two localities: ALABAMA. *Marshall County:* Honeycomb Cave, 35 (UANH); McHardin Cave, 6 (SBP).

Distributional comments. Baiting did not take the species in Bishop Cave, on the north slopes of Bishop Mountain. Nearby Hambrick Cave in Honey Bluff is now the home of a large *Myotis sodalis* bat colony. It may now be as unsuitable as Honeycomb Cave as a beetle habitat because it too is warmed by circulating waters of the Tennessee River.

The species may have crossed from

Bishop Mountain through limestones under low Ricketts Gap into the Grassy Mountain to the northeast. Caves exist there, and some have been collected, but have not been baited. Dispersal may be also possible to the west of Bishop Mountain, under the low valley to Russell Ridge and Merrill Mountain. Merrill and Painted Bluff Caves in Merrill Mountain have been unsuccessfully baited.

Across the Paint Rock River to the northwest of Merrill Mountain are the contiguous Mayo, Lemley, McKinney, and Meeks mountains in Madison County. *Ptomaphagus* are not known here. The Paint Rock River may have prevented dispersal to them from the east, and the Flint River may have prevented dispersal from the west. Baiting in these mountains in Morring Spring Cave and Clark Bluff Cave took no *Ptomaphagus* but did take *Tetracion*, showing that this large troglobitic millipede was able to disperse into the caves here, but from which direction is not known.

Ptomaphagus hirtus Tellkampf
Figures 2, 6, 35, 36, 91, 114, 158–161; Map 9

Adelops hirtus Tellkampf, 1844: 313, fig. 106. Type: location unknown. Type locality: Kentucky, Edmonson County, Mammoth Cave. Packard, 1871: 745 (record); 1874: 563 (larva); 1876: 283 (ecology and larva); 1888: 78 (biology and pupa). Jeannel, 1922: 90; 1931: 408 (systematics and larva). Hatch, 1933: 210 (systematics, records). Hubbard, 1880: 80 (ecology).

Ptomaphagus (*Adelops*) *hirtus* Jeannel, 1936: 93, figs. 154–155 (systematics); 1949: 99. Barr, 1962: 282 (biology); 1963: 53; 1967c (ecology and distribution).

Diagnosis. This is the only blind cave *Ptomaphagus* in the Mammoth Cave area of Kentucky.

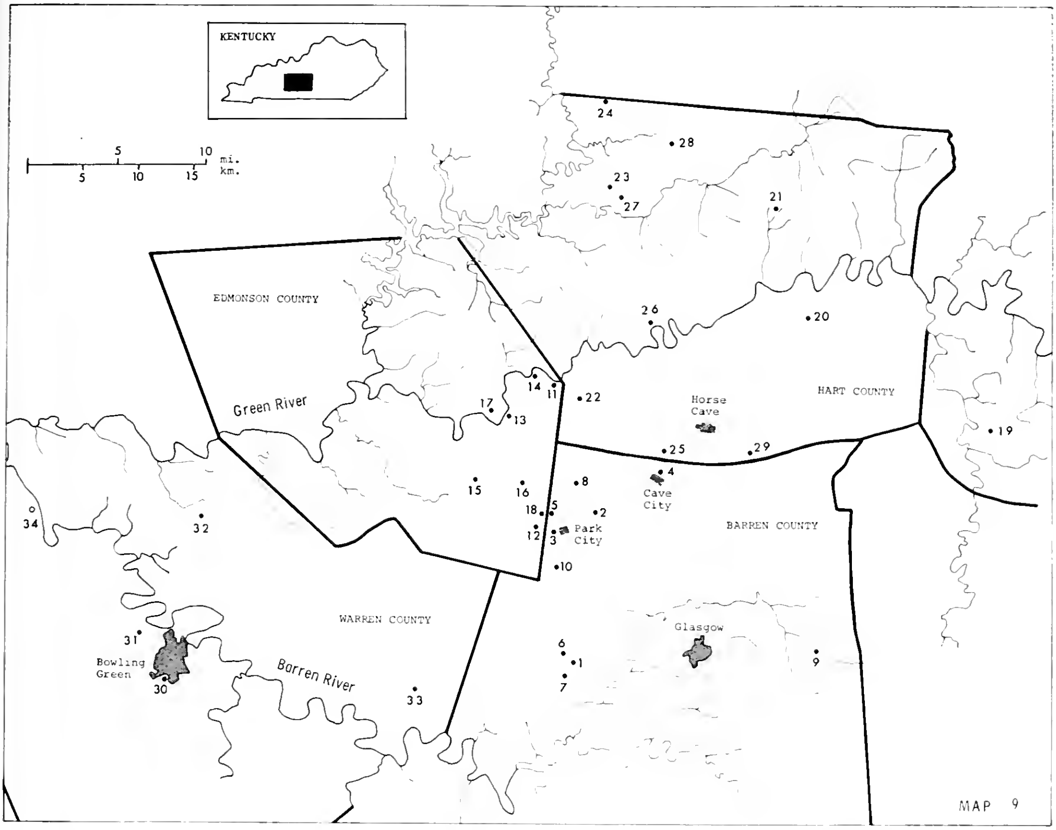
Description. Length 2.0–2.8 mm. Width 1.2–1.4 mm. Head smooth; width of head from antennal base to margin across eye 3.8 times width of eye. Antennae (Fig. 114) medium length, reaching beyond margin of pronotum when laid back; segments II and III, and IV–VI subequal, width uniform; VII elongate, cylindrical; VIII transverse, IX longer than wide, X quadrate, XI longer than wide. Pronotum at base 1.4 times as wide as long; sides arcuately narrowing in front, front angles rounded, widest 1/3 from base, arcuately narrowing behind to hind angles; surface smooth, only traces of striae at margins. Elytra at base slightly narrower than prothorax base, gradually narrowing apically. Mesosternal carina (Fig. 91) strong and prominent. Aedeagus (Fig. 35) in profile straight and thin, fairly uniform width, tip downcurved, narrowing gradually to tip in dorsal view (Fig. 36). Spermatheca (Figs. 158–161) with a slightly curved central shaft, a knob on posterior end with an apical depression and a hooked, curved knob on anterior end.

Variation. The only variation within the species that has been noticed is that of the female spermatheca. Figures 158–161 demonstrate the spermatheca from the center of the range and three extreme populations. The western population (Bypass Cave) has a more stout central shaft. The anterior end is of different proportions in all populations.

Field notes. The ease of collecting the species by baiting with decaying organic material has led to the abundant representation of it in collections at many museums. Barr (1962) reports that guano of the cave cricket *Hadenoecus subterraneus* may be the normal food of the beetle. I have seen them on cricket guano in the Frozen Niagara section of Mammoth Cave, and in Proctor, Whites, and Great Onyx caves. Barr (1962) gives various localities for the beetle in Mammoth Cave.

Seasonality. I have seen specimens collected in every month but January. In the laboratory, reproduction takes place throughout the year.

Distribution. The species is limited to Hart, Edmonson, Barren, and Warren counties, Kentucky. It is known from 41



Map 9. Distribution of *Ptomaphagus* (*Adelops*) *hirtus*, a troglobitic species of central Kentucky. The closed dots represent known localities, and are as follows: 1 Beckton Cave, 2 Brushy Knob Cave, 3 Burnett Cave, 4 Cave City Cave, 5 Diamond Caverns, 6 Duval Saltpeter Cave, 7 Edmunds Cave, 8 Indian Cave, 9 Slick Rock Cave, 10 Walnut Hill Cave, 11 Buzzard Cave, Cathedral Cave and Collins Crystal Cave, 12 Coach Cave and James Cave, 13 Dixon Cave, Mammoth Cave and Whites Cave, 14 Great Onyx Cave, 15 Martins Cave, 16 Proctor Cave, 17 Running Branch Cave, 18 Short Cave, 19 Wisdom Cave, 20 Bald Knob Cave, 21 Barnes Smith Cave, 22 "Cave," 23 Chattlin Cave and Coach Webb Cave, 24 Copelin Cave, 25 Hogan Cave and Ronalds Cave, 26 Logsdon Valley Cave, 27 Puckett Cave, 28 Saltpeter Cave, 29 Bear Wallow Cave, 30 Bypass Cave, 31 Horseshoe Cave, 32 Pruett Saltpeter Cave, 33 Gorman Cave, 34 Thomas Cave.

caves in Mississippian limestones in the western Pennyroyal Plateau, and the Dripping Springs Escarpment, both north and south of the Green and Barren rivers (Map 9). I have seen 861 specimens from the following 41 locations:

KENTUCKY. *Barren County:* Beckton (Tarbarrel) Cave, 3 (TCB); Brushy Knob Cave, 2 (TCB); Burnett Cave, 3 (TCB); Cave City Cave (Railroad Cave), 7 (CAS, TCB, FMNH); Diamond Caverns, 1 (SBP); Duval Saltpeter Cave, 4 (TCB); Edmunds Cave, 47 (SBP, TCB); Indian Cave, 5 (SBP); Lyon Cave (Cave City), 49 (USNM); Slick Rock Cave, 22 (TCB); Walnut Hill Cave, 2 (TCB). *Edmonson County:* Buzzard Cave, 23 (TCB); Cathedral Cave, 1 (SBP); Coach Cave (=Hundred Domes Cave), 5 (TCB, SBP); Collins Crystal Cave, 52 (TCB); Dixon Cave, 20 (CAS, MCZ, TCB, UANH); Great Onyx Cave, 10 (SBP, TCB); James Cave, 20 (TCB); Mammoth Cave, 294 (CAS, AMNH, MCZ, FMNH, TCB, USNM;) Martins Cave, 1 (TCB); Proctor Cave, 5 (SBP, TCB); Running Branch Cave, 20 (SBP, TCB); Short Cave, 2 (TCB); Whites Cave, 29 (MCZ, SBP, TCB, USNM, UANH). *Green County:* Wisdom Cave, 86 (SBP, TCB). *Hart County:* Bald Knob Cave, 7 (TCB); Barnes Smith Cave, 15 (SBP); "Cave" 2 miles SW Northtown, 14 (TCB); Chattlin Cave, 2 (TCB); Cooch Webb Cave, 5 (TCB); Copelin Cave, 15 (TCB); Hogan Cave, 10 (TCB); Logsdon Valley Cave, 2 (TCB); Puckett Cave, 3 (TCB); Ronalds Cave, 9 (TCB, USNM); Saltpeter Cave, 1 (TCB); Webb Cave, 4 (TCB). *Warren County:* Bypass Cave, 7 (TCB, SBP); Horseshoe Cave, 1 (TCB); Pruett Saltpeter Cave, 57 (SBP); Garman Cave, 1 (SBP).

Distributional comments. It is interesting to note that the Barren and Green rivers have not acted as barriers to dispersal of this species. The maximum extent of the known range is a 55-mile long line from Bypass Cave to Wisdom Cave. Insufficient information exists to answer the question of whether the species has migrated across the rivers, or around the headwaters to inhabit caves on opposite sides of the drainages. I later suggest that the rivers were crossed by individuals dispersing overland in Wisconsin time. A careful study of variation may help answer this question.

The limits of the species range may be partly due to geological conditions. The species does not penetrate deeply the region of the Salem and Warsaw limestones to the east. The northern boundary is considerably beyond the Pennsylvanian river channel crossing northern Hart County, just north of Munfordville. The southwestern limit, lying on the Pennyroyal Plateau of continuous limestones, offers no explanations. Other species of the "Mammoth Cave faunal province" extend farther in this direction than does *P. hirtus.* See Barr (1967c) for a more complete discussion of this zoogeographic province.

Various collections contain specimens from localities that are not now identifiable. These localities, such as the "Lyon Cave" of Packard (1888), are not listed. They are all undoubtedly in the vicinity of Mammoth Cave, and not of importance in gaining a full picture of the range of the species.

Jeannel (1931) reports on a collection from Hidden River Cave, in the town of Horse Cave. I have twice visited the cave but have not found *Ptomaphagus.* Serious pollution of the cave stream resulted in a noticeable deficiency of oxygen in the cave when visited in September 1967. This may have altered the terrestrial cave community.

Extensive baiting did not yield the species in Thomas Cave, Warren County.

Ptomaphagus nicholasi Barr
Figures 37, 115, 162; Map 2

Ptomaphagus (*Adelops*) *nicholasi* Barr, 1963: 53. Holotype male and allotype female in AMNH. Type locality and data: Illinois, Monroe County. Fogelpole Cave, 22.x.1961, Bro. G. Nicholas leg. Three paratypes, same data (TCB). I have seen all specimens.

Diagnosis. This is the only blind cave *Ptomaphagus* known from Illinois. Virtually identical in morphology to *P. hirtus.* The key characters of Barr (1963) do not clearly separate the species from *P. hirtus* when the range of *hirtus* variation is seen.

Description. Length 2.3–2.7 mm. Similar to *P. hirtus* in all features except the following: antennae (Fig. 115) with segments slightly more elongate than in *P. hirtus;* segment VIII about 1/2 as long as wide. Aedeagus (Fig. 37) like that of *P. hirtus,* more slender, tip slightly less deflexed than in *hirtus.* Spermatheca (Fig. 162) like that of *hirtus,* most similar to populations in center of *hirtus* range.

Field notes. The type series was found under a rock at edge of stream in type locality cave (personal communication with Rev. P. Wightman of Bellville, Illinois, who was present at time of collection of the type series).

Seasonality. Known only from the October 1961 collection. Two specimens are teneral.

Distribution. Known only from the type locality (Map 2).

Distributional comments. If this species still is extant, it is exceptionally secretive, or rare. I have extensively baited and trapped in the type locality cave, and in over 15 other caves in Monroe County, Illinois, in summer and winter seasons, for several years, with no success. Cave locations are in Bretz and Harris, 1961.

Ptomaphagus hubrichti **Barr**
Figures 38, 116, 163; Map 4

Ptomaphagus (*Adelops*) *hubrichti* Barr, 1958: 170. Holotype male and allotype female, in AMNH, seen. Type locality: Tennessee, DeKalb County. Cripps Mill Cave. Barr, 1963: 56.

Diagnosis. It is distinguished from other members of the *hirtus* group by the pronotum being widest at its base. It is one of two blind species inhabiting caves in central Tennessee. The straight aedeagus of the male and more curved spermatheca serve to distinguish it from *P. barri,* the other central Tennessee cave species.

Description. Length 2.6–3.3 mm. Width 1.3–1.4. Head finely punctate. Antennae (Fig. 116) slender, reaching first 1/3 of elytra when laid back; segments II and III, and IV–VI subequal, width uniform; VII large, conical, half as wide as long; VIII wider than long. Pronotum at base 1.6 times as wide as long; widest 1/4 before base, tapering only slightly to hind angles; sides arcuately narrowing to rounded front angles; surface faintly striate at margins. Elytra at base subequal to pronotum, gradually narrowing apically; 1.3 times as long as wide at base. Mesosternal carina strong and prominent. Aedeagus (Fig. 38) very slightly curved in profile, widest in basal third, tip slender and downcurved. Spermatheca (Fig. 163) central shaft curved; posterior end with knob; anterior end with hooked bulge.

Variation. The hind angles of the pronotum are less rectangular in the Tenpenny Cave population. No other variation has been noticed.

Field notes. P. hubrichti is found in very damp situations in the caves. Barr (1958) reports it in wet places, under rocks, on raccoon dung, and on a dead bat. The type locality is not now available for collecting because the waters of the cave feed a fish farm whose owners have closed the cave. The closing is to prevent possible pollution of the cave stream by visitors to the cave. I took 20 specimens in a small hole in silt in Hayes Cave, under a *Ceuthophilus* roost.

Seasonality. Adults have been collected in winter and summer, with tenerals in August. Larvae have been taken in two caves in August.

Distribution. The species is limited to caves in the eastern edge of the Nashville Basin in Ordovician limestones in Cannon, DeKalb, and Wilson counties, Tennessee (Map 4). I have seen 77 specimens from the following localities: TENNESSEE. *Cannon County:* Tenpenny Cave, 7 (SBP). *DeKalb County:* Avant Cave (Lindsay Williams Cave), 3 (TCB, FMNH, UANH); Cripps Mill Cave, 29 (TCB); Gin Bluff Cave, 9 (TCB). *Wilson County:* Hayes Cave, 29 (TCB, SBP).

Distributional comments. The species may be expected in other caves. Baiting has not yielded it in two caves near caves known to contain populations (Reed Cave and John Hollis Cave). Baiting is needed in other Cannon, DeKalb, and Wilson County caves.

The *Consobrinus* Group

Diagnosis. Spermatheca shaped like reversed "S," the anterior and posterior ends either narrow or wide and flattened (Figs. 164–186).

Description. Shape elongate oval. Color light to dark (piceous) brown. Eyes large or partially reduced, pigmented (Fig. 4). Antennae medium or short, long in *giaquintoi.* Pronotum with hind angles faintly acute, discal striae distinct, normally about 10 striae per 0.25 mm, finer and more closely spaced in *schwarzi* and some populations of *nevadicus* with about 13 per 0.25 mm. Elytra with striae normally about 7 per 0.25 mm and oblique to suture, finer with about 10 per 0.25 mm and transverse to suture in *schwarzi* and some *nevadicus*. Wings fully developed in all species except *cocytus*. Mesosternal carina low except in *giaquintoi*. Legs normal. Aedeagus long, thin, and curved, to short and fairly straight, tip blunt or sharp.

The group contains a total of ten species, collectively distributed from southern Canada and throughout the United States southward to a few populations of species ranging into western Mexico, and with one species limited to eastern Guatemala. One species each from Arizona and Guatemala are troglobites. The others are free living or nest and burrow inhabitants.

Ptomaphagus fisus Horn

Figures 15, 41, 42, 118, 165–170, 200; Maps 10, 13

Ptomaphagus fisus Horn, 1885: 137. Lectotype here designated as male in ANSP (no. 2996), seen. Type locality: Arizona. Hatch, 1933: 204.

Ptomaphagus (*Adelops*) *fisus*, Jeannel, 1936: 91; 1949: 97.

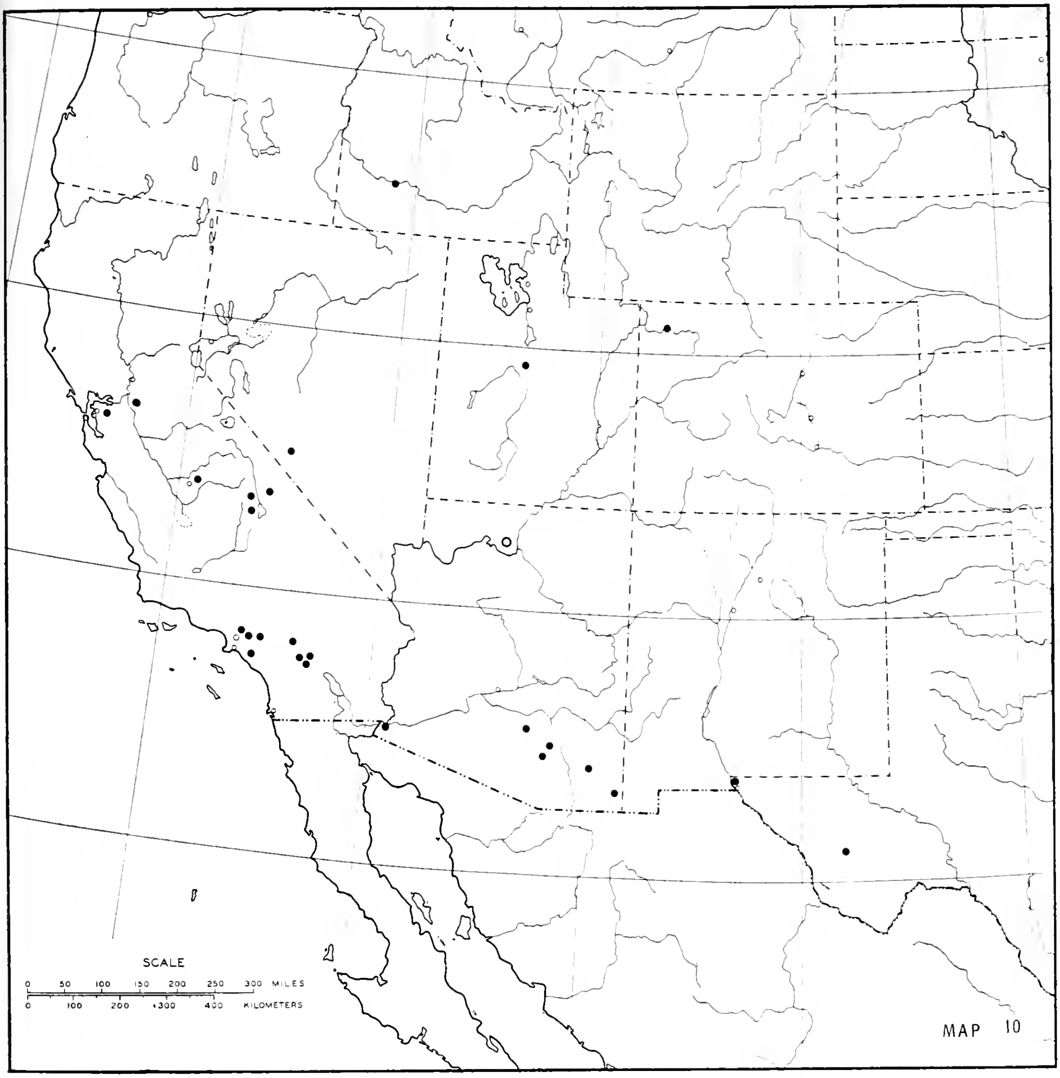
Ptomaphagus (*Adelops*) *inermis* Jeannel, 1933: 251. NEW SYNONYMY. Holotype male in British Museum (Nat. Hist.), Fry Colln., seen. Type locality: "Mexico." Jeannel, 1936: 92.

Diagnosis. The species is widely distributed in the xeric United States from the Rocky Mountain states westward, and south into Mexico. It is distinguished from all others by the female spermatheca, and by the male aedeagus and genital segment. Most males also possess a tooth on the metafemur, a character otherwise found only in *cocytus*.

Description. Length 2.4–2.7 mm. Width 1.1–1.4 mm. Color light to medium reddish brown, head darker, appendages lighter. Head finely punctured. Eyes large, normal; their horizontal diameter 2.7 times width of space between anterior margin and antennal socket. Antennae (Fig. 118) short, not reaching edge of pronotum when laid back; segments II–V longer than wide, VI–X wider than long. Pronotum widest at base, 1.4 times as wide as long; sides gradually widening. Elytra 1.6 times as long as wide at base; male apex rounded transversely truncate; female apex truncate; weakly oblique to suture. Mesosternal notch low, as in *consobrinus* (Fig. 94). Legs with male metafemur with low, broad tooth near middle of posterior margin (Fig. 15) in most populations. Aedeagus (Fig. 41) thin, curved, narrowing gradually to sharp tip; tip in dorsal view (Fig. 42) bluntly to sharply pointed. Genital plates not anteriorly projected, enclosing over 3/4 of medium spiculum gastrale (Fig. 200). Spermatheca (Figs. 165–170) shaft curved; posterior end not broad or flattened, with small crest; anterior end widened, slightly flattened.

Variation. Variation is noted most in the male metafemur and the spermatheca. The metafemoral tooth is present but indistinct in the Colorado specimens, and absent in the male serving as the type of *P. inermis* Jeannel. The spermatheca varies in size and proportion throughout the range, but maintains its distinctive features (Figs. 165–170). The antennal and elytral differences cited by Jeannel for *inermis* do not separate the Mexican material from *fisus* populations. The type of *inermis* has an aedeagal tip sharper than that in Figure 42. The doubtful record from Chihuahua is missing both antennae and spermatheca. Its elytral apex is more drawn out, with a sharper sutural angle than in other observed females.

Field notes. The species was reported by Hubbard (1901) as an inhabitant of ground squirrel and kangaroo rat nests at Palm Springs, California. They were most abundant in nests made of grass near the surface, and not in nests deep in the burrows (at depths up to 8 feet). They have since been taken in kangaroo rat



Map 10. Distribution of *Ptomaphagus (Adelops) cocytus* (open circle in northcentral Arizona), a troglobite from Grand Canyon, Arizona, and *Ptomaphagus (Adelops) fisus* (dark dots).

(*Dipodomys*) burrows at Cathedral City, California; in ground squirrel burrows (*Citellus*) in Orange County, California; and in prairie dog burrows in Colorado. A series of 24 was taken under a stone at Palm Springs, and one under a stone and one in a grass pile at Claremont, California.

Seasonality. The species has most commonly been taken in the winter and spring months from October to May. Only two specimens come from outside this period (from Tucson in August). That they have not been taken in the hot summer months from June to September may reflect inactivity of collectors. Larvae are unknown.

Distribution. The species ranges through the xeric regions of the western and southwestern United States from southern California eastward to west Texas, north to southern Idaho (Map 10) and south into Mexico. I have seen 127 specimens from the following localities:

MEXICO. Locality unknown; Truqui leg., 1 male, 1 female (BMNH, Fry Colln.). The male, the type of *P. inermis*, and the female arrived back at the BMNH in fragments, broken in shipment, according to Mr. P. M. Hammond. Doubtful record: Chihuahua, Majalca Road, 5500′ elev., 30 mi. NW Chihuahua, 14–17.iv.1961, Howden & Martin, 1 damaged female (CNCI). **UNITED STATES.** ARIZONA. *Cochise County:* Apache, 1 (FMNH); Dragoon, 1 (CAS). *Pima County:* Santa Catalina Mts., 2 (CAS); Tucson, 8 (USNM, CAS). *Pinal County:* Picacho, 1 (CAS). *Yuma County:* Yuma, 2 (USNM, INHS). *Unknown state localities:* Catal Springs, 1 (USNM); Galiuro Mt., 1 (USNM); Pinal Mts., 1 (USNM). CALIFORNIA. *Contra Costa County:* Russellman Park (Mt. Diablo), 2 (CAS). *Fresno County:* Lanes Bridge, 1 (CNCI). *Inyo County:* Owens Lake, 5 (CNCI, MCZ); Saline Valley (freshwater spring 1500′ above valley floor on SW slope), 5 (CAS); Goodale Creek (N of Lone Pine), 1 (CAS); No locality, 1 (CNCI). *Los Angeles County:* Azusa, 14 (CAS, MCZ, USNM); Claremont, 2 (INHS); Pasadena, 1 (MCZ). *Orange County:* Santa Ana Canyon, 2 (USNM). *Riverside County:* Cathedral City, 1 (CAS); Palm Springs, 53 (CAS, USNM); Thousand Palms, 1 (CNCI); Pine Springs Ranch (5 mi. E Idyllwild), 1 from malt trap (GHNC). *San Bernardino County:* Kelso Dunes, 1 (CAS); San Bernardino Valley, 1 (MCZ). *San Joaquin County:* Stockton, 4 (CAS). COLORADO. *Moffat County:* Maybelle (prairie dog burrow), 5 (CNCI). IDAHO. *Elmore County:* Glenns Ferry, 1 (USNM). NEVADA. *Esmeralda County:* No locality, 1 (CNCI). TEXAS. *El Paso County:* El Paso, 2 (MCZ). *Jeff Davis County:* Ft. Davis, 1 (MCZ). UTAH. *Juab County:* Levan, 1 (CAS).

Distributional comments. Jeannel (1933) gave the type locality of *P. inermis* Jeannel as Iruqui, Mexico. This was a misinterpretation of the label bearing the collectors name, Truqui, who may have taken the specimens in the vicinity of Guadalajara or Morelia. An exact location probably cannot be determined.

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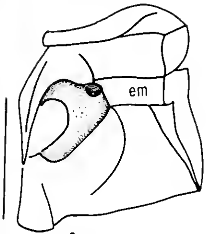
Figures 9–24. Figs. 9–10, left lateral view of thorax; Figs. 11–16, legs; Figs. 17–24, aedeagi. Scale line in lower right 0.5 mm for lateral view of *Ptomaphagus aedeagi*, 0.3 mm for *Ptomaphagus aedeagus* tip. Fig. 9, *Proptomaphaginus puertoricensis*, meso- and metathorax, scale 0.5 mm. Fig. 10, *Ptomaphagus consobrinus*, Torreya Park, Florida, meso- and metathorax, em = mesepimeron, scale 9.5 mm. Fig. 11, *Proptomaphaginus puertoricensis*, male protibia and protarsus, scale 0.2 mm. Fig. 12, *Proptomaphaginus puertoricensis*, female protarsus, scale as in 11. Fig. 13, *Ptomaphagus consobrinus*, Torreya Park, Florida, female protarsus, scale line 0.2 mm. Fig. 14, *P. consobrinus*, Torreya Park, Florida, male protibia and protarsus, scale as in 13. Fig. 15, *P. fisus*, "Ariz., paratype 2996," male metafemur. Fig. 16, *P. cocytus*, paratype, Grand Canyon National Park, Arizona, male metafemur. Fig. 17, *Adelopsis mitchellensis*, Mt. Mitchell, N. Carolina, lateral view aedeagus. Fig. 18, same as 17, dorsal view aedeagus tip, same scale as 17. Fig. 19, *Ptomaphagus shapardi*, Dresser Cave, Oklahoma. Fig. 20, same as 19. Fig. 21, *P. loedingi loedingi*, Pitts Cove, Alabama. Fig. 22. *P. loedingi longicornis*, Crossing Cave, Alabama. Fig. 23, *P. loedingi julius*, House of Happiness Cove, Alabama. Fig. 24, *P. loedingi solanum*, Sheldons Cove, Alabama.



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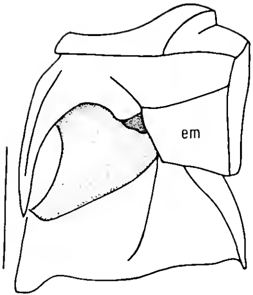

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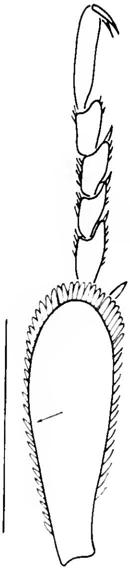

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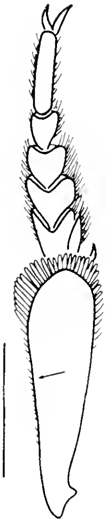

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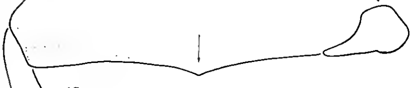

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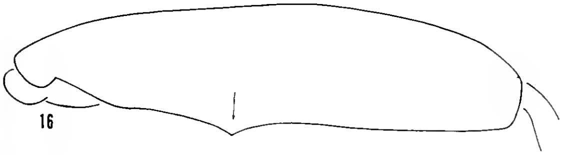

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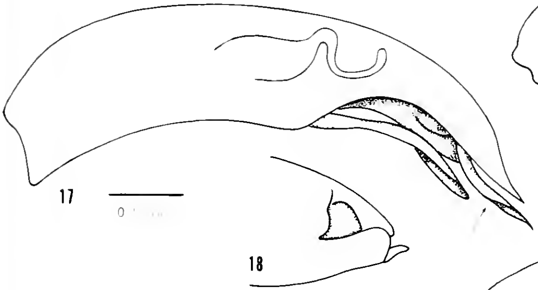

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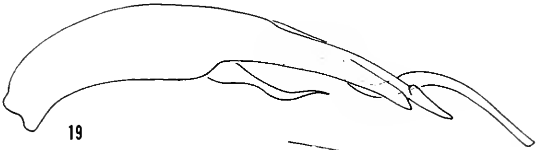

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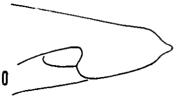

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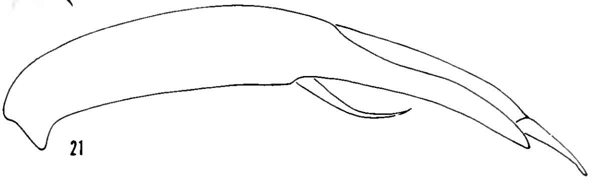

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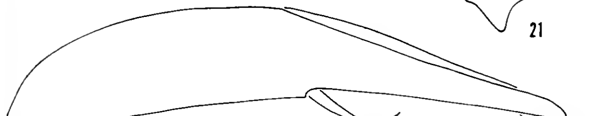

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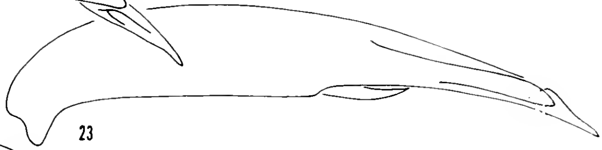

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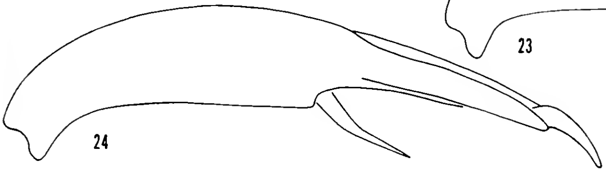

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Figures 25–38, aedeagi of *Ptomaphagus*. Scale line in lower right 0.5 mm for aedeagi lateral views, 0.3 mm for dorsal view of tip. Fig. 25, *P. barri*, Henpeck Mill Cave, Tennessee. Fig. 26, *P. hazelae*, Tumbling Rock Cave, Alabama. Fig. 27, *P. liskei*, Mt. Cove Farm Cave, Georgia. Fig. 28, *P. walteri*, Bryant Cave, Alabama. Fig. 29, *P. whiteselli*, Sittons Cave, Georgia. Fig. 30, *P. valentinei*, Sauta Cave, Alabama. Fig. 31, *P. hatchi hatchi*, Rousseau Cave, Alabama. Fig. 32, *P. hatchi hatchi*, Dry Cave, Tennessee. Fig. 33, *P. hatchi fecundus*, Caney Hollow Cave, Tennessee. Fig. 34, *P. episcopus*, McHardin Cave, Alabama. Fig. 35, *P. hirtus*, Mammoth Cave, Kentucky. Fig. 36, same as 35. Fig. 37, *P. nicholasi*, Fogelpole Cave, Illinois. Fig. 38, *P. hubrichti*, Cripps Mill Cave, Tennessee.


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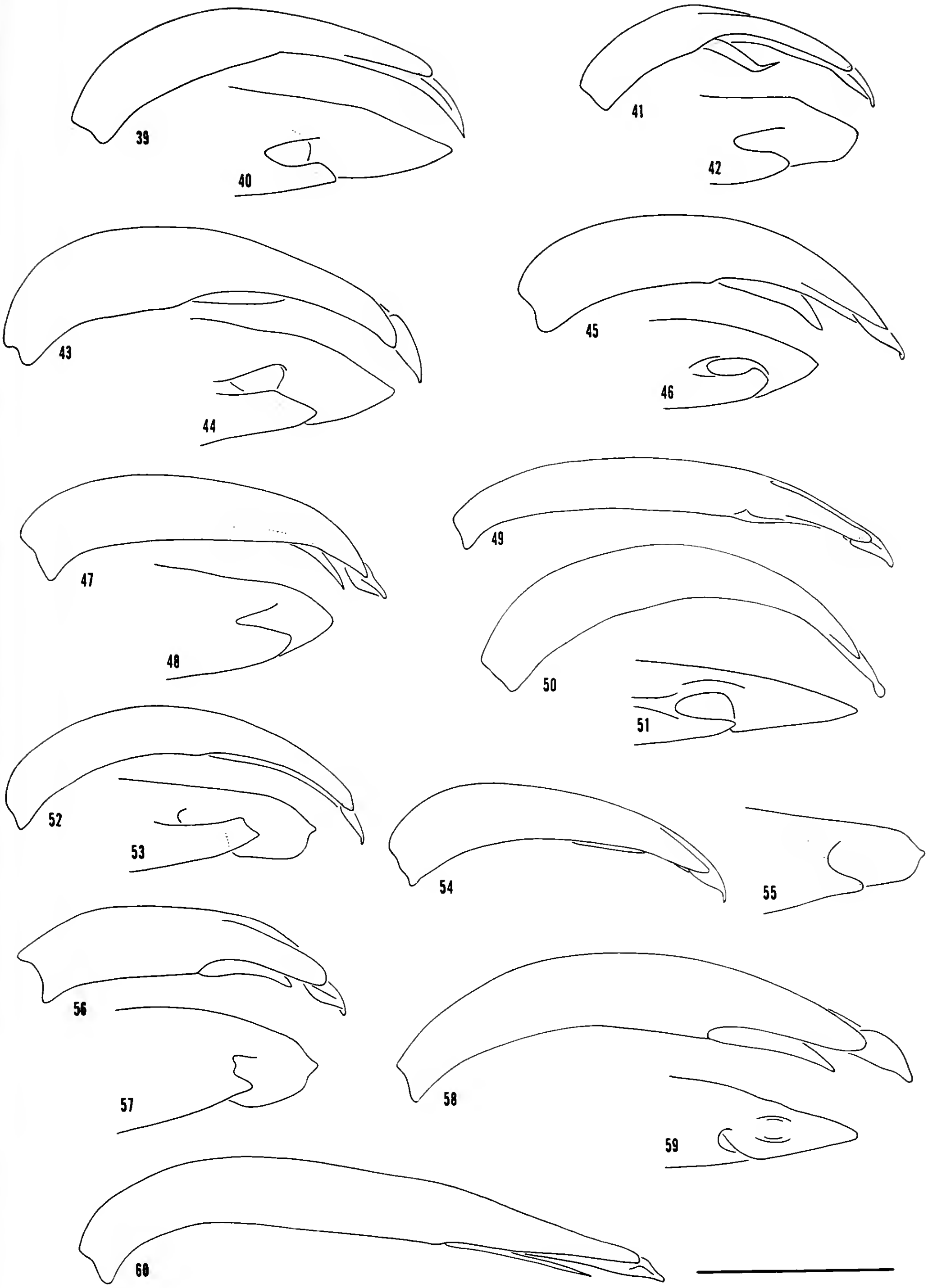
Figures 39–60, aedeagi of *Ptomaphagus*. Scale line in lower right 0.5 mm for aedeagi lateral views, 0.3 mm for aedeagal tips. Fig. 39, *P. cacytus*, Roaring Spring Cave, Arizona. Fig. 40, same as 39, dorsal view aedeagal tip. Fig. 41, *P. fisus*, Arizona, paratype 2996–5. Fig. 42, same as 41, dorsal view aedeagus tip. Fig. 43, *P. schwarzi*, holotype, Crescent City, Florida. Fig. 44, same as 43, dorsal view aedeagus tip. Fig. 45, *P. texanus*, Alachua Co., Florida. Fig. 46, same as 45, dorsal view aedeagus tip. Fig. 47, *P. californicus*, Danville, California. Fig. 48, same as 47, dorsal view aedeagus tip. Fig. 49, *P. giaquintai*, Seamay Cave, Guatemala. Fig. 50, *P. nevadicus*, Danville, California. Fig. 51, same as 50, dorsal view aedeagus tip. Fig. 52, *P. consobrinus*, Alexandria, Louisiana. Fig. 53, same as 52, dorsal view aedeagus tip. Fig. 54, *P. brevior*, holotype, Putnam Co., Indiana. Fig. 55, same as 54, dorsal view aedeagus tip. Fig. 56, *P. ulkei*, Plummers Island, Maryland. Fig. 57, same as 56, dorsal view aedeagus tip. Fig. 58, *P. cavernicola*, Marvel Cave, Missouri. Fig. 59, same as 58, dorsal view aedeagus tip. Fig. 60, *P. troglomexicanus*, Cueva Capilla de la Perra, Mexico.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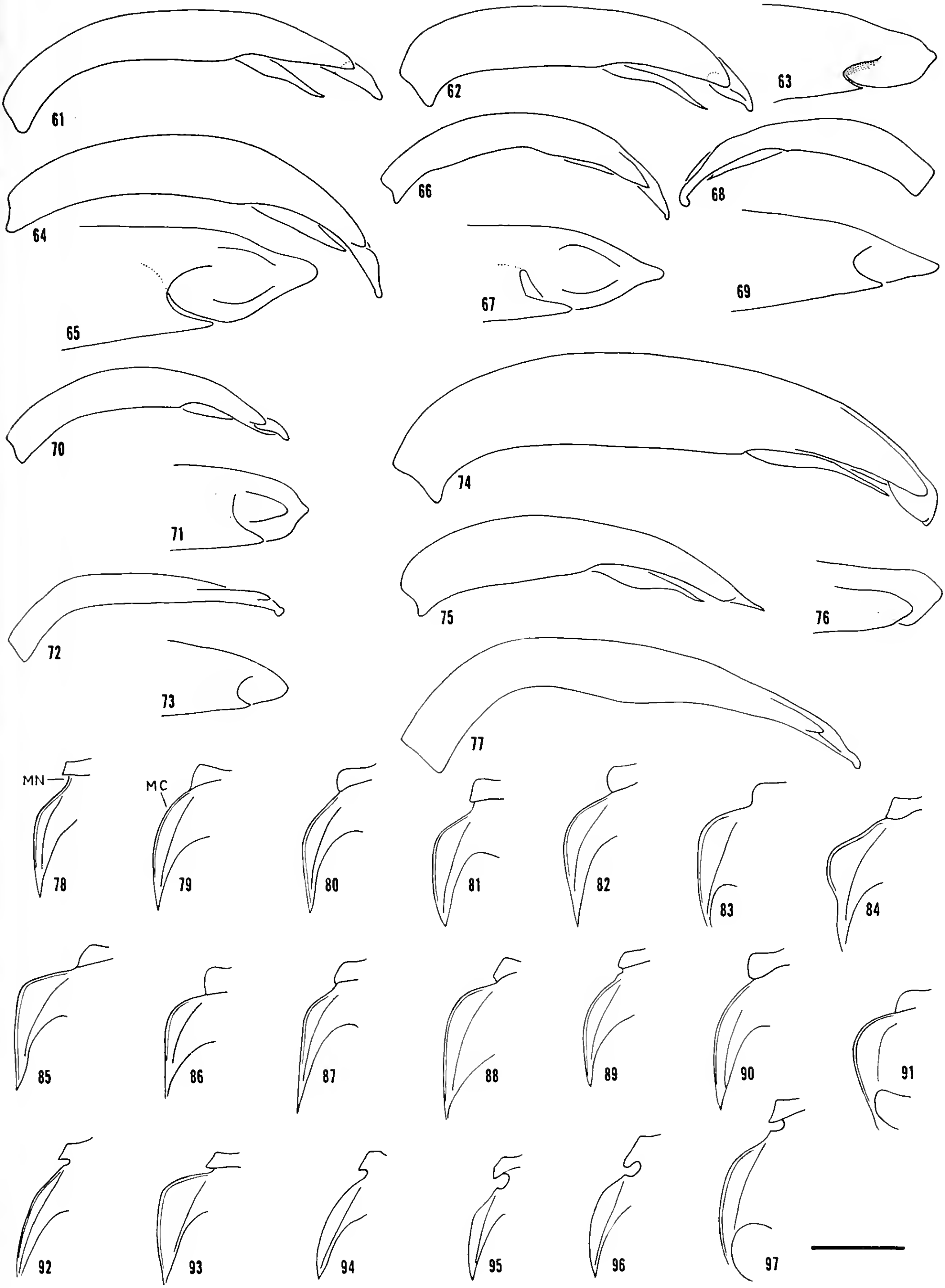
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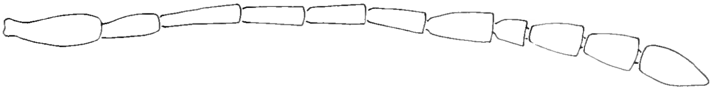

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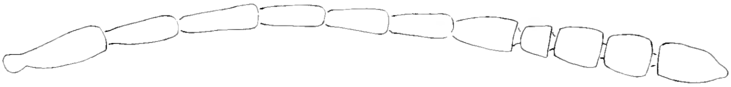

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Figures 114–134, *Ptomaphagus* antennae. Scale line 1.0 mm for Figs. 114–132. Fig. 114, *P. hirtus*, Mammoth Cave, Kentucky. Fig. 115, *P. nicholasi*, Fogelpole Cave, Illinois. Fig. 116, *P. hubrichti*, Cripps Mill Cave, Tennessee. Fig. 117, *P. cocytus*, Roaring Springs Cave, Arizona. Fig. 118, *P. fisus*, Palm Springs, California. Fig. 119, *P. schwarzi*, Alachua Co., Florida. Fig. 120, *P. texanus*, Alachua Co., Florida. Fig. 121, *P. californicus*, Danville, California. Fig. 122, *P. brevior*, Jefferson Co., Missouri. Fig. 123, *P. giaquintoi*, Cueva Seamay, Guatemala. Fig. 124, *P. nevadicus*, Danville, California. Fig. 125, *P. consobrinus*, Alexandria, Louisiana. Fig. 126, *P. cavernicola*, Benton Co., Missouri. Fig. 127, *P. ulkei*, Madison Co., Kentucky. Fig. 128, *P. elabra*, Cueva El Pachón, Mexico. Fig. 129, *P. altus*, San Cristóbal, Mexico. Fig. 130, *P. leo*, Chipinque Mesa, Mexico. Fig. 131, *P. troglomexicanus*, Cueva Capillo, Mexico. Fig. 132, *P. talamanca*, Chiriquí, Panama. Fig. 133, *P. championi*, Santa Cruz del Quiché, Guatemala. Fig. 134, *P. flabellatus*, São Paulo, Brasil.

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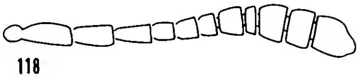

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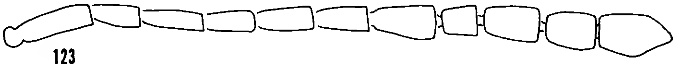

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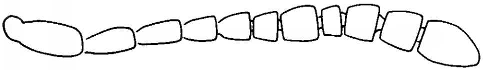

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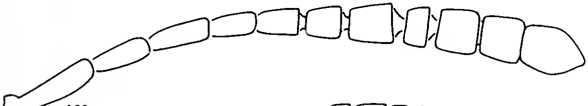

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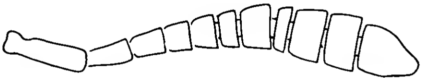

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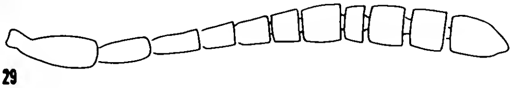

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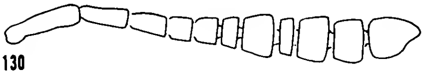

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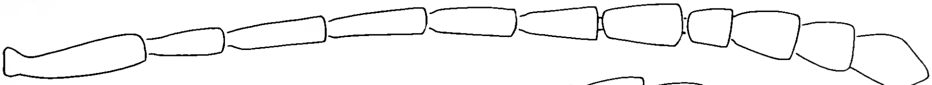

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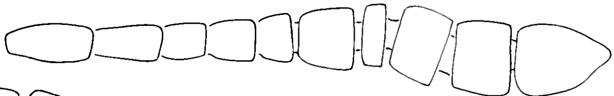

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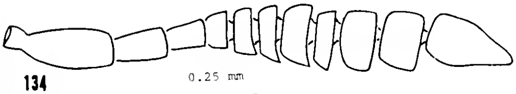

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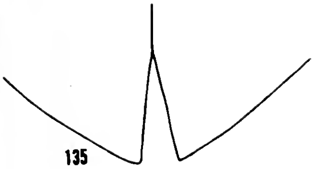
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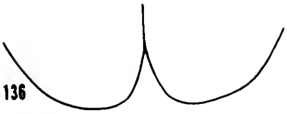
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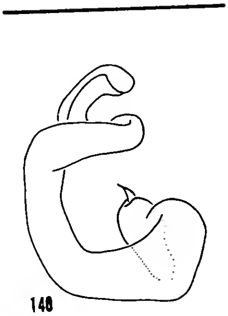
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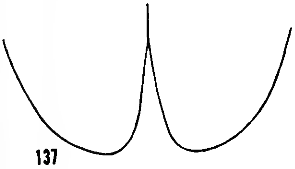
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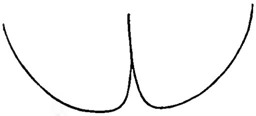
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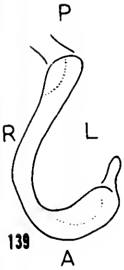

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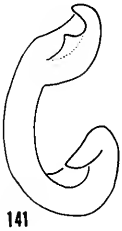
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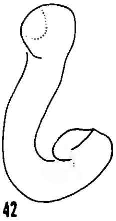
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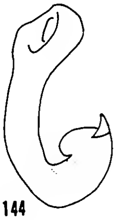
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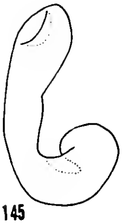
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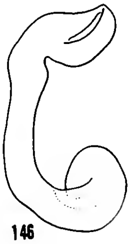
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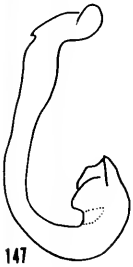
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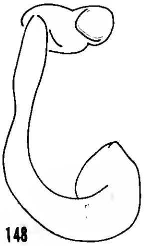
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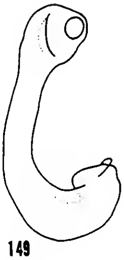
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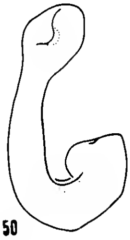
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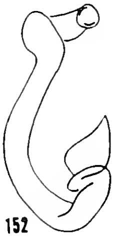
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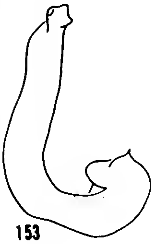
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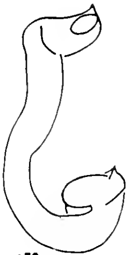
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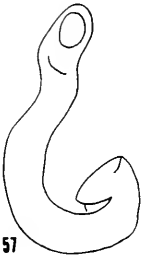
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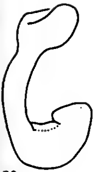
Figures 158–186, *Ptomaphagus* spermathecae. Fig. 158, *P. hirtus*, Mammoth Cave, Kentucky. Fig. 159, *P. hirtus*, Byposs Cave, Kentucky. Fig. 160, *P. hirtus*, Copelin Cave, Kentucky. Fig. 161, *P. hirtus*, Slick Rock Cave, Kentucky. Fig. 162, *P. nicholasi*, Fogelpole Cave, Illinois. Fig. 163, *P. hubrichti*, Cripps Mill Cave, Tennessee. Fig. 164, *P. cocytus*, Roaring Springs Cave, Arizona. Fig. 165, *P. fisus*, Pinal Mts., Arizona. Fig. 166, *P. fisus*, Palm Springs, California. Fig. 167, *P. fisus*, "S. Cal., 1879," (INHS). Fig. 168, *P. fisus*, paratype of *P. inermis*, Mexico. Fig. 169, *P. fisus*, Glenns Ferry, Idaho, view of left side. Fig. 170, same as 169, dorsal surface. Fig. 171, *P. schwarzi*, Alachua Co., Florida. Fig. 172, *P. texanus*, Alachua Co., Florida. Fig. 173, *P. californicus*, Danville, California. Fig. 174, same as 173, view of left side. Fig. 175, *P. giaquintoi*, Cueva Seamay, Guatemala. Fig. 176, *P. nevadicus*, Strawberry Res., Utah. Fig. 177, *P. nevadicus*, Danville, California. Fig. 178, *P. consobrinus*, lectotype, "Ga." Fig. 179, *P. consobrinus*, Lee Co., Texas. Fig. 180, *P. brevior*, Columbus, Texas. Fig. 181, *P. brevior*, Jefferson Co., Missouri. Fig. 182, *P. brevior*, San Antonio, Texas. Fig. 183, same as 182, view of right side. Fig. 184, *P. brevior*, teratology, Round Knob, N. Carolina. Fig. 185, *P. ulkei*, Limeton, Virginia. Fig. 186, *P. ulkei*, Madison Co., Kentucky, view of right side. Scale line at bottom 0.3 mm.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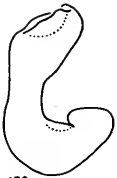
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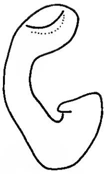
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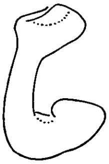
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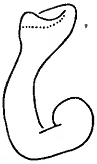
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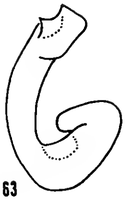
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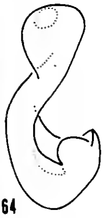
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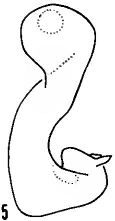
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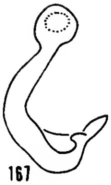
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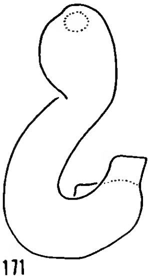
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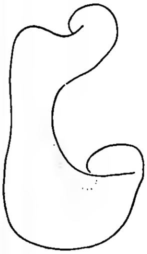
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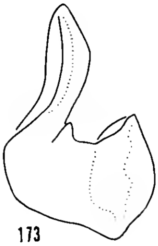
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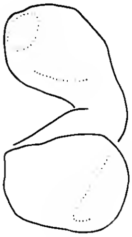
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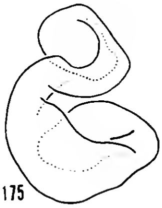
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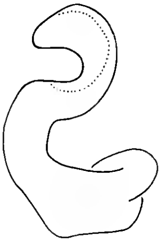
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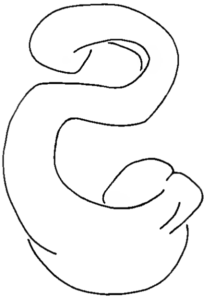
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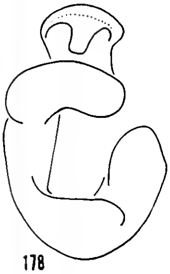
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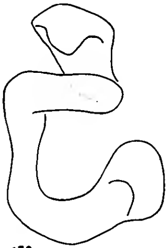
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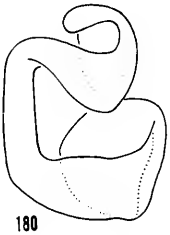
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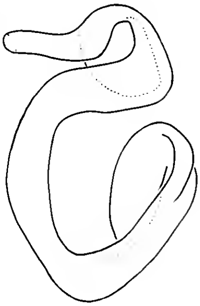
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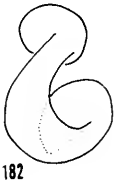
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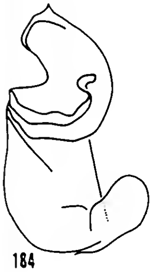
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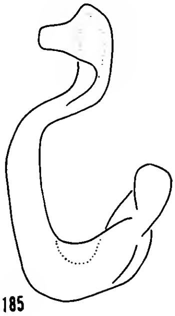
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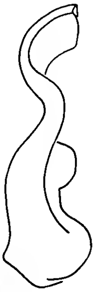
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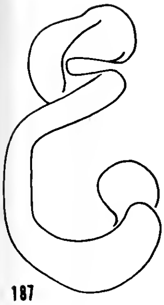
Figures 187–211. Figs. 187–197, *Ptomaphagus* spermathecae; Figs. 198–211, male genital segments. Scale line in lower right 0.3 mm for spermathecae, 0.5 mm for genital segments. Fig. 187, *P. cavernicola*, Benton Co., Arkansas. Fig. 188, *P. cavernicola*, Jackson Co., Florida. Fig. 189, same as 188, view of left side. Fig. 190, *P. troglomexicanus*, Cueva Capilla de la Perra, Mexico. Fig. 191, *P. oaxaca*, Valle Nacional, Mexico. Fig. 192, *P. spelaeus*, Gruta de Acuitlapan, Mexico. Fig. 193, *P. leo*, Chipinque Mesa, Mexico. Fig. 194, *P. altus*, San Cristóbal, Mexico. Fig. 195, *P. newtoni*, Valle Nacional, Mexico. Fig. 196, *P. elabra*, Cueva de El Pachón, Mexico. Fig. 197, *P. jamesi*, San Cristóbal, Mexico. Fig. 198, *Adelopsis mitchellensis*, Mt. Mitchell, North Carolina, s.g. = spiculum gastrale, g.p. = genital plate. Fig. 199, *P. cocytus*, Roaring Spring Cave, Arizona. Fig. 200, *P. fisus*, paratype 2996–5, Arizona. Fig. 201, *P. schwarzi*, holotype, Crescent City, Florida. Fig. 202, *P. texanus*, Alachua Co., Florida. Fig. 203, *P. californicus*, Danville, California. Fig. 204, *P. giaquintoi*, Cueva Seamay, Guatemala. Fig. 205, *P. nevadicus*, Danville, California. Fig. 206, *P. consobrinus*, Alexandria, Louisiana. Fig. 207, *P. brevior*, Middlesex Fells, Massachusetts. Fig. 208, *P. ulkei*, Plummers Island, Maryland. Fig. 209, *P. cavernicola*, Marvel Cave, Missouri. Fig. 210, *P. leo*, Chipinque Mesa, Mexico. Fig. 211, *P. elabra*, Cueva de El Pachón, Mexico.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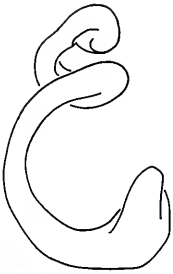
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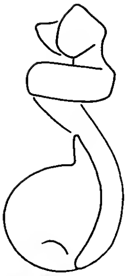
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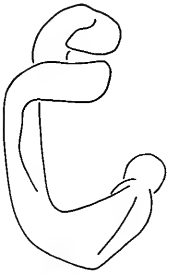
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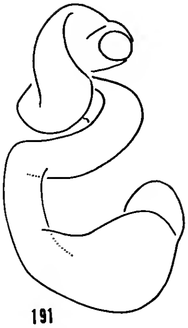
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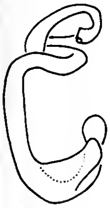
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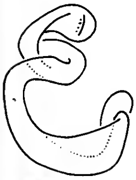
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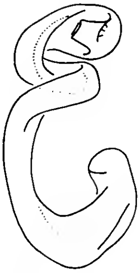
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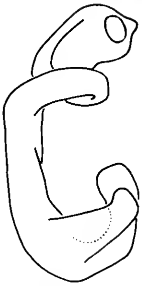
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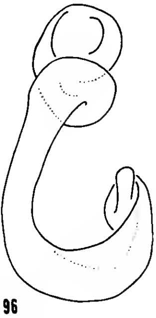
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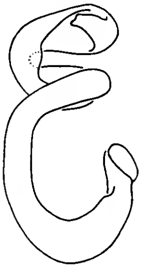
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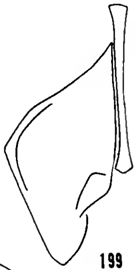
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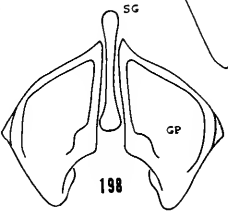

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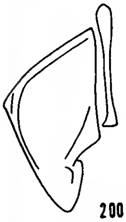
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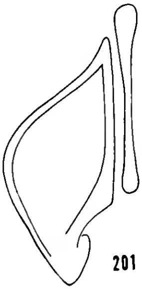
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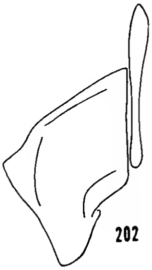
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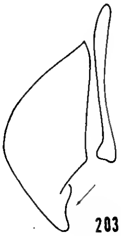
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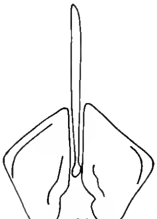
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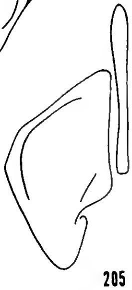
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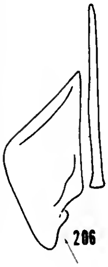
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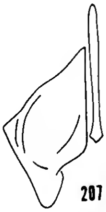
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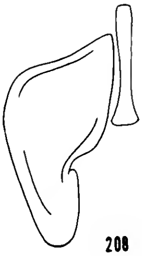
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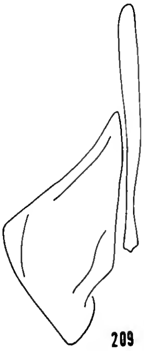
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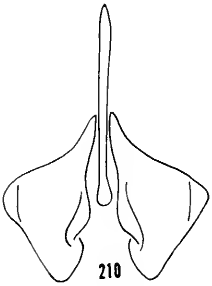
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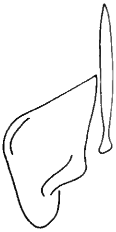
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Ptomaphagus cocytus new species
Figures 16, 39, 40, 117, 164, 199; Map 10

Holotype male and allotype female in MCZ (no. 31893). Type locality: Arizona, Coconino County, Kaibab Plateau, Roaring Springs Cave. Type data: 1.i.1965, Gregory Lane leg. Paratypes, 2 females, same locality, 16.iv.1965, L. Ball and G. T. Lane leg., in SBP.

Diagnosis. The tooth on the male metafemur distinguishes the species from all others except *fisus,* from which it is separated by the reduced wings, elongated appendages, and drawn-out female elytral apex.

Description. Length 3.2–3.4 mm. Width 1.4–1.5 mm. Color pale yellowish brown. Head finely punctured and pubescent. Eyes pigmented, faceted, reduced; horizontal diameter 1.4 times the distance between their anterior margin and antennal socket. Antennae (Fig. 117) not reaching pronotal base when laid back; segments II and III longer than broad; IV and V subquadrate; VI–X wider than long. Pronotum widest at middle, only slightly narrower at base; 1.55 times wider at base than long. Elytra 1.55 times as long as wide at base; slightly wider 1/4 behind base; external apical angles effaced; female apex obliquely truncate, drawn out; male apex obliquely truncate and rounded. Wings reduced to 3/4 the length of elytra. Mesosternal notch present but reduced. Legs elongated, male metafemur with tooth (Fig. 16). Aedeagus (Fig. 39) regularly curved, thin; tip in dorsal view (Fig. 40) sharp. Genital plates anteriorly elongated to enclose most of spiculum (Fig. 199). Spermatheca (Fig. 164) small, central shaft curved, posterior end slightly swollen, anterior end with small crest.

Variation. No variation noted.

Etymology. Cocytus, a noun used in apposition, is the name of the River of Wailing, one of the five rivers of Hades, referring to the type locality, Roaring Springs Cave.

Field notes. I visited the type locality in September 1969, but was unable to collect carefully, and found no beetles. Roaring Springs Cave lies behind Roaring Springs, which is currently being prepared as a water source for the south rim of Grand Canyon National Park. This may restrict future collecting in the cave.

The cave, with its several entrances, and about two miles of mapped passage, lies in the Cambrian Muav Limestone on top of the Bright Angel Shale. It is at an approximate elevation of 5200 feet, or 3000 feet below, and 4.2 miles from, the head of the Kaibab Trail, which is used to reach it from North Rim of Grand Canyon National Park.

Seasonality. If the species is cave-adapted, it should not be expected to show a reproductive seasonality. Larvae are unknown.

Distribution. The species is now known only from the type series of four specimens from Roaring Springs Cave.

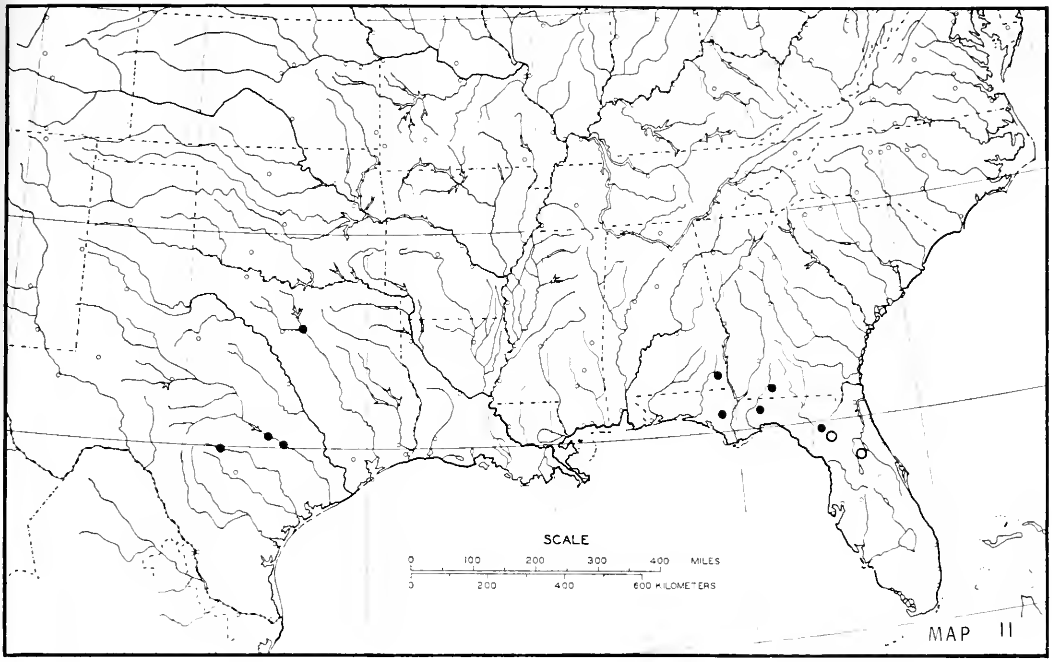
Distributional comments. Several other caves are known in the north rim of Grand Canyon. Roaring Springs Cave is the largest and most accessible. From what little I know of the other smaller and drier caves, it seems less likely that they would be additional localities for this species.

The species may be limited to the type locality. The reduced wings and long legs suggest that it is cave-adapted, and incapable of dispersing in the xeric epigean environment in the bottom of the canyon. It also seems unlikely that there is much chance for extensive underground dispersal. The great depth of the limestone beneath the Kaibab Plateau and its comparative thinness have probably not led to development of extensive and interconnecting systems of air-filled cave passageways.

Ptomaphagus schwarzi Hatch
Figures 43, 44, 119, 171, 201; Map 11

Ptomaphagus schwarzi Hatch, 1933: 203. Holotype male in USNM (no. 43481), seen. Type locality: Florida, Crescent City.

Ptomaphagus (Adelops) schwarzi, Jeannel, 1936: 91; 1949: 97.



Map 11. Distribution of *Ptomaphagus* (*Adelops*) *schwarzi* (open circles) and *Ptomaphagus* (*Adelops*) *texanus* (dark dots).

Diagnosis. The species is distinguished by its fine striae, light brown color, reduced eyes, and the shape of the spermatheca.

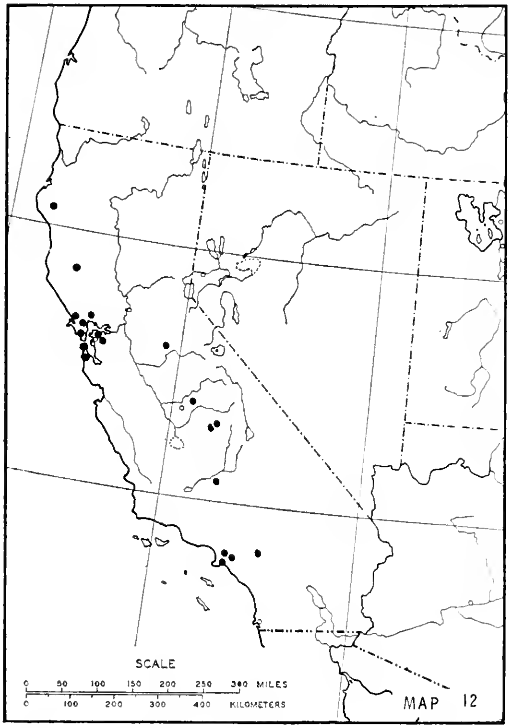
Description. Length 2.7–3.6 mm. Width 1.2–1.7 mm. Color pale yellowish brown. Head finely, densely pubescent. Eyes reduced, pigmented, faceted; their horizontal diameter 1.15 times the width between anterior margin and edge of antennal socket. Antennae (Fig. 119) short, not reaching base of pronotum when laid back; segments II–V longer than broad, VI–X broader than long. Pronotum widest, but only slightly, 1/3 before base; 1.4 times wider at base than long; sides parallel behind, converging in front; hind angles right; hind margin sinuous. Elytra widest 1/4 behind base; 1.5 times longer than wide at base; external apical angles effaced; female sutural angle sharp, apex oblique, sinuous, drawn out; male apex oblique, not drawn out at sutural angle. Mesosternal notch present. Legs with protibial spurs unusually well developed. Aedeagus (Fig. 43) widest near base, curved, gradually narrowing toward tip; in dorsal view tip (Fig. 44) pointed. Spiculum gastrale short and enclosed by slightly anteriorly elongated genital plates (Fig. 201). Spermatheca (Fig. 171) stout; shaft slightly curved, anterior end with low crest, posterior end with curve and bulge.

Variation. No variation noted.

Field notes. The species may be restricted to pocket gopher (*Geomys*) burrows in Florida. Data is not available for the habitat of the holotype, but four of the five other known specimens were taken in *Geomys* burrows.

Seasonality. Only adults are known from January, May, and September collections. The specimen collected in a malt trap in January may indicate the time of dispersal by flight.

Distribution. The species is apparently restricted to pocket gopher burrows in central peninsular Florida. I have seen



Map 12. Distribution of *Ptomaphagus* (*Adelops*) *californicus*.

six specimens from the following four localities: FLORIDA. *Alachua County:* Devils Millhopper (*Geomys* burrow), 2 (FSCA); no locality (B. A. Barrington, *Geomys* burrow no. 11, 13.IX.1939), 2 (UMMZ). *Putnam County:* Crescent City, 1 (USNM).

Distributional comments. The species may belong to the suite of arthropods that diverged and speciated when peninsular Florida was isolated as an island during the higher sea levels of the major interglacials (reviewed *in* Howden, 1969: 47). An extensive report on the fauna of the Florida pocket gopher burrows is that of Hubbell and Goff (1940). The several specimens of *Ptomaphagus* that they report from pocket gopher burrows at Newnans Lake, Alachua County, are probably this species but the location of the specimens is not known.

Since the adults are winged, distribution and dispersal is not necessarily limited to and by pocket gopher burrow systems.

Ptomaphagus texanus Melander
Figures 45, 46, 92, 120, 172, 202; Map 11

Ptomaphagus texanus Melander, 1902: 329. Lectotype here designated as USNM specimen bearing red label "cotype no. 6618," from syntype series; lectotype also bears label "Austin Tx 11.19.1.," seen. Five paralectotypes seen from same locality, 3 collected 11.19.1901, 2 11.16. 1901. Type locality: Texas, Austin. Hatch, 1933: 204.

Ptomaphagus (*Adelops*) *texanus,* Jeannel, 1936: 92.

Diagnosis. The species is partially characterized by its range in the Gulf Coastal States, habits of living in ant nests and vertebrate burrows, large eyes, generally light-colored elytra and darker pronotum, and oblique female elytral apex. It is clearly distinguished by the shape of the spermatheca, and male genital structures.

Description. Length 2.6–3.2 mm. Width 1.0–1.5 mm. Color light to dark brown, generally with elytra lighter than head and pronotum. Head finely punctured and pubescent. Eyes large, their horizontal diameter 3.3 times as wide as the space between their anterior margin and antennal socket. Antennae (Fig. 120) short, reaching to base of pronotum when laid back; segments II–III longer than broad, IV–X broader than long. Pronotum widest at base; 1.6 times wider than long; sides parallel behind. Elytra widest 1/4 behind base; 1.6 times longer than wide; external apical angles effaced; male apex rounded; female apex obliquely truncate. Mesosternal notch present (Fig. 92). Aedeagus (Fig. 45) gently curved, narrowing gradually to tip; tip in dorsal view moderately pointed (Fig. 46). Spiculum gastrale long, 1/2 enclosed by genital plates (Fig. 202). Spermatheca (Fig. 172) with stout, fairly straight central shaft, anterior end broadly hooked, posterior end bilobed with dent.

Variation. Differences have been noticed in the genital segments between Florida and Texas populations. The spiculum is slenderer and the genital plates broader in Texas material. The spermatheca shows only minor differences, being slightly thinner with a slightly broader anterior end in Texas material.

Field notes. Melander (1902) reported taking 10 males and 13 females in simple pitfall traps at the entrances to nests of *Pogonomyrmex barbatus,* harvester ants, at Austin, Texas, in November. Four were taken by H. Howden in malt traps at Kerrville, Texas. Alabama and Georgia specimens were taken in old field mouse nests. All Florida material was taken in gopher tortoise (*Gopherus*) burrows, or in malt-proprionic acid traps in the burrows. I tried Melander's methods in June in central Texas and captured only several thousand *Pogonomyrmex* and several painful stings. Perhaps at this time of year the ants are more active and the beetles less active than those Melander encountered in November.

Seasonality. Vertebrate nest and burrow collections have been made in February, March, and April. Ant nest collections are from November. Malt trap collections are from April. The species may exist as adults in nest-burrow habitats throughout the year. They apparently are active in the winter months, leaving ant nests to disperse or forage, and were probably dispersing by flight when taken in malt traps in April. Larvae are unknown.

Distribution. The species is known only from southern Gulf Coastal Plain localities. I have seen 50 specimens from the following 11 localities:

ALABAMA. *Dale County:* Mobile. Typhus Lab (old field mouse nest), 2 (USNM). FLORIDA. *Alachua County:* "Sta. 6, *Gopherus* burrow," 16 (FSCA); High Springs (4 mi. N, *Gopherus* burrow), 11 (HAHC). *Calhoun County:* Clarksville (tortoise burrow), 3 (HAHC). *Gilchrist County:* Trenton (*Gopherus* burrow no. 5, 14 ft. from entrance), 3 (FSCA). *Leon County:* Tallahassee, 1 (HAHC). GEORGIA. *Thomas County:* Thomasville (old field mouse nest), 2 (USNM). TEXAS. *Bastrop County:* Bastrop St. Pk., 1 (CNCI). *Dallas County:* Dallas, 1 (INHS). *Kerr County:* Kerrville (malt trap), 4 (CNCI). *Travis County:* Austin, 6 (USNM, MCZ, AMNH, FMNH).

Distributional comments. The species probably actively disperses in cooler months. As presently known it generally inhabits ant nests in Texas and not in Florida, and inhabits vertebrate nests and burrows in Florida and not in Texas. I believe this is a reflection of inattention given to these hard-to-collect habitats in both regions. If the beetle can inhabit the nests of *Pogonomyrmex barbatus* throughout the range of this ant, a very large distributional range is possible. Cole (1968: 57) shows the ant to occur throughout most of Mexico, all of Texas and Oklahoma, and westward to Arizona, and north to eastern Colorado. East of the Mississippi River another ant species, *P. badius,* is widely distributed and may be an alternate but as yet unexamined host for the beetle.

Ptomaphagus were reported by Hubbard (1894, 1896) and Young and Goff (1939) as *Gopherus* burrow inhabitants at DeFuniak Springs, and Crescent City, Florida. The specimens they treat as *ulkei* from DeFuniak Springs probably were *texanus.* Two specimens from tortoise burrows at Crescent City were *consobrinus.*

Ptomaphagus californicus (Leconte)
Figures 47, 48, 121, 173, 174, 203; Map 12

Catops californicus Leconte, 1854: 281. Lectotype here designated as female in MCZ (Leconte coll.) bearing red label with "type 3153–3" and a gold disc, seen. Murray, 1856: 458.

Ptomaphagus californicus, Horn, 1880: 263; Hatch, 1957: 42.

not *Ptomaphagus californicus,* Hatch, 1933: 203.

not *Ptomaphagus* (*Adelops*) *californicus,* Jeannel, 1936: 91; 1949: 97.

Ptomaphagus latior Hatch, 1933: 204. Holotype male in CAS (no. 2301), seen. Synonymy implied by Hatch, 1957: 42, and I agree with this.

Diagnosis. The species is known only from California. It can be separated from all others by the shape of the spermatheca. This is the only species besides *consobrinus* having a curve on the edge of the genital plate bordering the genital orifice.

Description. Length 2.4–3.0 mm. Width 1.3–1.5 mm. Color medium to dark brown, head and elytra usually darker than elytra. Head finely striate. Eyes somewhat reduced; their horizontal diameter 1.4 times wider than space between their anterior edge and antennal socket edge. Antennae (Fig. 121) somewhat elongate, reaching base of pronotum when laid back; segments II–V and VIII longer than wide, VI and VIII–X wider than long. Pronotum widest at base 1.6 times as wide as long; sides sub-parallel behind; hind angles right, hind margin straight. Elytra 1.4 times as long as wide at base; female apex obliquely truncate, male apex rounded-truncate. Mesosternal notch as in *consobrinus* (Fig. 94). Aedeagus (Fig. 47) fairly straight, curved down at tip; dorsal view of tip (Fig. 48) bluntly rounded. Genital plates not elongated anteriorly along thin spiculum, which is more than 3/4 enclosed; concavity in edge of plate bordering genital orifice (arrow, Fig. 203). Spermatheca (Figs. 173, 174) very flattened in center and at both ends; twisted.

Variation. No variation noted.

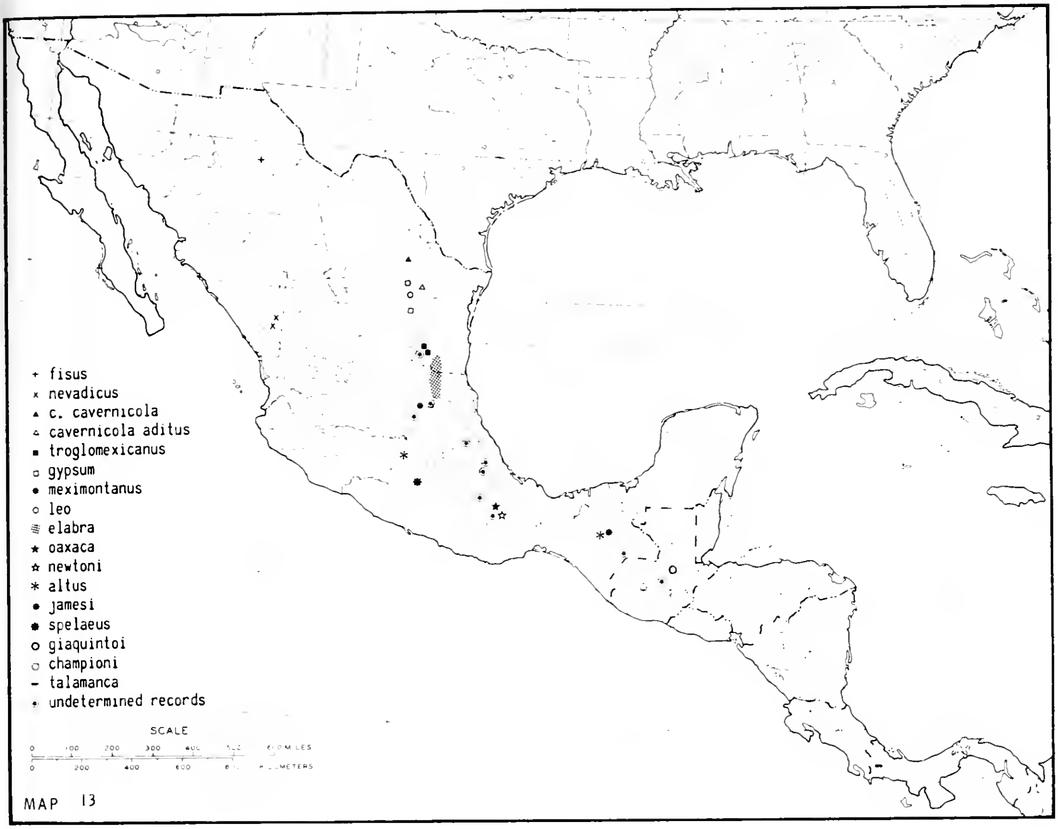
Field notes. The information that is available suggests that the species is a general scavenger in the more mesic areas of California. Many specimens were taken in the debris and nests of ground-dwelling *Vespula* (*pennsylvanica*?, F. X. Williams det.) wasps. Many have been taken at Danville, California: 1 in a shrew nest, 1 at the entrance of a fresh pocket gopher burrow, 3 in a pocket gopher nest, and 1 in a field mouse nest under sheet metal. Two are from a small dirt cave in Napa County, California. Two from Alameda County are from under yellow cup fungi. One was taken from the hair of a *Neotoma* rat (alive?) and a series of 11 described as *P. latior* came from a *Neotoma* nest.

Seasonality. Collections of the species are known from every month except September. There may be no reproductive seasonality in protected sites such as *Neotoma* nests and pocket gopher burrows. Free-living forest inhabitants are probably influenced by the dry California summers, and are more active in the wet winter months. Larvae are not known.

Distribution. The species is known to me only from California, and is probably most abundant in mesic forest habitats. I have seen 60 specimens from the following localities:

CALIFORNIA. *Alameda County:* Oakland (hills back of, under yellow cup fungus), 2 (CAS); No locality, 1 (MCZ). *Contra Costa County:* Danville, 1 in shrew nest, 1 in entrance of fresh gopher burrow, 3 in gopher nests, 1 in field mouse nest, 17 in debris *Vespula* nests, (CAS). *Humboldt County:* Redwood Creek (Blairs Ranch), 1 (USNM). *Kern County:* no locality, 1 (MCZ). *Lake County:* Hullville, 1 (FMNH). *Los Angeles County:* Coquilett, 1 (USNM); Los Angeles, 1 (ANSP); Pasadena, 2 (CAS); Pomona, 2 (MCZ). *Madera County:* North Fork (*Neotoma* nest), 6 (CAS, CUIC) (all paratypes of *P. latior*). *Marin County:* Fairfax, 5 (CAS). *Napa County:* White Cave (4 mi. E St. Helena), 2 (CAS). *San Bernardino County:* San Bernardino Mts., 2 (MCZ). *San Francisco County:* San Francisco, 1 (CAS). *San Mateo County:* Edgemar, 1 (CAS). *Sonoma County:* Forestville (in marsh), 2 (CAS); Sobra Vista, 1 (CAS); "S. Sonoma Co." (*Neotoma* hair), 1 (CAS). *Tulare County:* Kaweah (1 at 1000′), 2 (CAS); Sequoia National Park (Potwisha), 1 (CAS). *Tuolumne County:* Twain-Harte (4000′), 1 (CAS).

Distributional comments. Hatch (1957: 42) records the species from southwestern Idaho. This is based upon the name in a



Map 13. Distribution of Mexican and Central American *Ptomaphagus*. None are known from the West Indian Islands.

list of beetles from Atlanta, Idaho, reported by Leconte in 1878. I believe that the record probably represents another species.

Ptomaphagus giaquintoi Jeannel
Figures 49, 93, 123, 175, 204; Map 13

Ptomaphagus (*Adelops*) *giaquintoi* Jeannel, 1936: 93. Type in MNHN, Paris, seen. Type locality: Guatemala, Sepacuite Cave, near Panzos, Alta Verapaz. Jeannel, 1949: 98.

Diagnosis. This is the only *Ptomaphagus* known from caves in Guatemala. It is the only species known from Guatemala and Mexico, other than *troglomexicanus* and *gypsum*, which shows cave adaptations, having long antennae reaching beyond the pronotum when laid back. The possession of wings and pigmented eyes whose horizontal width equals the space between the eye and the antennal base separates it from *troglomexicanus* and *gypsum*.

Description. Length 2.0–3.0 mm. Width 0.9–1.3 mm. Color light to dark brown. Head faintly punctured. Eyes reduced in size, faceted, pigmented; width of head from antennal base to margin across eyes 2.0–2.3 times width of eyes. Antennae (Fig. 123) elongate, narrow, reaching first third of elytra when laid back; segment III four times as long as wide, longer than II; segments IV, V, and VI subequal, three times as long as wide, longer than II; VII twice as oblong as wide, conical; VIII longer than wide; IX and X longer than wide. Pronotum clearly transverse, at base 1.75 times as wide as long; widest at base, sides widening gradually to base; hind margin slightly sinuous. Elytra widest slightly behind base; 1.6 times as long as wide at base; external apical angles rounded; apex oblique in female, rounded in male. Wings present and large, not observed in flight; but I see no reason to doubt that they function in flight. Mesosternal carina (Fig. 93) high and prominent; notch conspicuous. Aedeagus (Fig. 49) long, slender, slightly curved; in dorsal view tip broadly pointed. Spiculum gastrale very long and thin; projecting more than twice its length beyond genital plates (Fig. 204). Spermatheca (Fig. 175) compact, broad, heavily twisted, expanded and flattened at anterior and posterior ends.

Variation. No variation noted. I do not find the pubescence to be as long and uneven as did Jeannel (1936: 81), nor do the antennae match his description.

Etymology. The species was named for the collector of the type series, Dr. Giaquinto Mira, an Italian physician who studied malaria and sleeping sickness in Guatemala in 1933 (personal communication with Dennis Koester, Finca Seamay).

Field notes. A series of 44 specimens was taken in 1948 on dead bats in Cueva de Lanquin, by R. D. Mitchell (FMNH). I took 41 in Cueva Seamay and 86 in Cueva de Lanquin on dryish guano of insectivorous bats and 36 on moist guano beneath a roost of insectivorous emballonurid bats (*Balantiopteryx plicata*, my determination) in Cueva Sepacuite. The beetles were not attracted to carrion-baited traps in Cueva Seamay, nor found at guano and waste of frugivorous bats. In each cave the beetles were found only in a single small localized area.

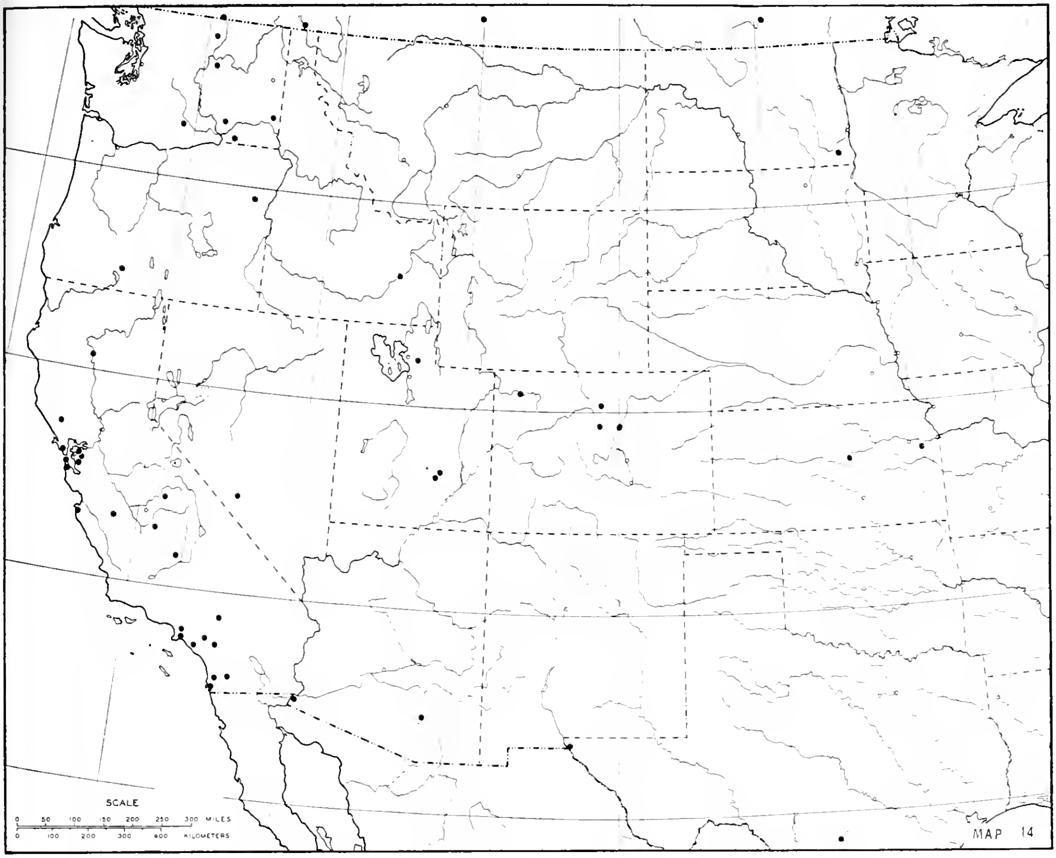
The cave air and soil temperatures were 67°F in Cueva Seamay; Lanquin Cave, 2100 feet lower in elevation, had an air and soil temperature of 74°F and 73°F respectively.

Seasonality. Collections have been made only in June and August. Teneral adults were taken only in Lanquin Cave (10 out of 86 in August and 6 out of 44 in June). Larvae are known only from my August collection in Lanquin Cave. Any seasonality in the species is probably related to the wet-dry season of this section of Guatemala.

Distribution. Known from three limestone caves in the Guatemalan Department of Alta Verapaz. The maximum linear extent of the known range is 20 km. I have seen 207 specimens from the following localities: **GUATEMALA.** *Dept. Alta Verapaz*: Cueva de Lanquin, 1000′ elev. (at Lanquin), 130 (FMNH, SBP); Cueva Seamay, 3100′ elev. (at Finca Seamay, Senahu), 41 (SBP); Cueva Sepacuite (No. 2), 3500′ (?) elev. (at Finca Sepacuite, Senahu), 36 (SBP).

Distributional comments. Doubt exists as to the identity of the type locality. It is reasonable that Cueva Sepacuite is on Finca Sepacuite, 6.1 road miles from the junction 0.9 miles before Senahu. Three caves exist at Finca Sepacuite, and all were explored and collected. Only one was large and contained beetles, and I believe it to be the cave in which Dr. Mira collected. I will treat these caves and their fauna in a later paper, in my series on the faunas of tropical American caves (Peck, 1971a).

The species can be expected to have a larger range than is now known. Its long antennae and reduced eyes suggest cave specialization, but the large wings do not suggest that the species is unable to disperse by flight. Numerous unexplored and uncollected limestone caves exist in the lowlands and highlands of northern Guatemala, and adjacent Mexico and Belice. Sufficient collecting has not been accomplished to know if the species is absent from lowland caves remote from montane regions.



Map 14. Partial distribution of *Ptomaphagus* (*Adelops*) *nevadicus*. Localities not shown are Whitford Lake, 70 mi. ENE of Edmonton, Alberta, Canada, and El Salto, 55 mi. WSW of Duranga, Mexico.

Ptomaphagus nevadicus Horn

Figures 50, 51, 124, 176, 177, 205; Maps 13, 14

Ptomaphagus nevadicus Horn, 1880: 263. Lectotype here designated as female in ANSP (no. 2997), seen. Type locality: "western Nevada." Hatch, 1933: 203.

Ptomaphagus californicus Leconte, Hatch, 1933: 203.

Ptomaphagus (*Adelops*) *californicus californicus* Leconte, Jeannel, 1936: 91; 1949: 97.

Ptomaphagus (*Adelops*) *californicus nevadicus* Horn, Jeannel, 1936: 91.

Ptomaphagus piperi Hatch, 1933: 204. NEW SYNONYMY. Holotype female in USNM (no. 43482), seen. Type locality: Washington, Pullman. Hatch, 1957: 42.

Ptomaphagus (*Adelops*) *piperi*, Jeannel, 1936: 91; 1949: 97.

Ptomaphagus thomomysi Hatch, 1957: 42. NEW SYNONYMY. Holotype female in UBCZ, no number, Stace Smith collection, seen. Type locality: British Columbia, Creston.

Ptomaphagus densus Hatch, 1957: 42. NEW SYNONYMY. Holotype male in Burke Museum, University of Washington, Seattle, not seen. Type locality: Oregon, Forest Grove.

Diagnosis. The species is separated from all others by the long, thin, curved aedeagus, and the shape of the spermatheca.

Description. Length 2.5–3.3 mm. Width 1.3–1.5 mm. Color light to dark brown, head and pronotum darker than elytra, antennal base lighter. Head with faint striae. Eyes normal to slightly reduced, their horizontal diameter 1.3–1.9 times width of space between antennal socket and anterior margin. Antennae (Fig. 124) normal, barely reaching base of pronotum when laid back; segments II–V and VII longer than wide, segments VI and VIII–X wider than long. Pronotum widest at base; 1.5–1.7 times as wide at base as long; sides nearly parallel behind; hind margin straight or slightly sinuous. Elytra 1.3–1.5 times as wide as long at base; apex rounded in males, obliquely truncate in females at suture, little to distinctly drawn out with little to distinct sinuation in margin; striae fine to coarse, transverse to oblique. Mesosternal notch low as in *consobrinus* (Fig. 94). Aedeagus (Fig. 50) long, thin, curved; tip with button; in dorsal view (Fig. 51) finely pointed. Spiculum gastrale long and thin, 2/3 to 1/2 enclosed by genital plates which are not anteriorly elongated (Fig. 205). Spermatheca (Fig. 176, 177) slightly flattened at posterior end, broadly flattened with low knob at anterior end.

Variation. This species possesses the most external variation recognized in *Adelops.* The variation has led to the previous creation of three other specific names. I treat the variation as being within one species because of the uniformity of the internal male and female characters which I believe are better characters upon which to base species recognition.

Greatest noticeable variation is in the elytral striae. In all California material and most of that from the southwestern states, the striae are distinctly transverse to the elytral suture. Material from the Pacific Northwest possesses striae that range from being distinctly oblique to the suture to slightly oblique. Within one population, such as that from Creston, British Columbia, there is a relationship between striae and body width, with the broader individuals possessing striae that are more distinctly transverse. Throughout the range, the larger specimens are generally with finer and more transverse striae.

Using the external characters, the northwestern populations generally can be easily distinguished from those at the southern and eastern edges of the species range. However, geographically intermediate populations are also intermediate in external characters. This, combined with the uniformity of the genitalia, is my reason for uniting the various populations into one species. This problem of taxonomy and variation is like the complex case of *P. subvillosus* in Europe (Sokolowski, 1956).

I have not adequately solved the problem of this variation. Much opportunity remains for additional collecting to observe the patterns of variation. If future studies show that the Pacific Northwest entities with more coarse and oblique striae merit separate taxonomic recognition, it should be either as the subspecific or specific name of *piperi,* because this is the oldest name applicable to these populations.

Other variation is minor. The Mexican population has aedeagi that are thicker in lateral view, and in a dorsal view at the tip, and spermathecae that are thinner and have a slightly smaller anterior end. The spermatheca differs in the same way in Mojave Desert material, and the spiculum is more than 1/2 free from the genital plates. The aedeagus of Medicine Hat, Alberta, males is less elongate and less hooked at the end.

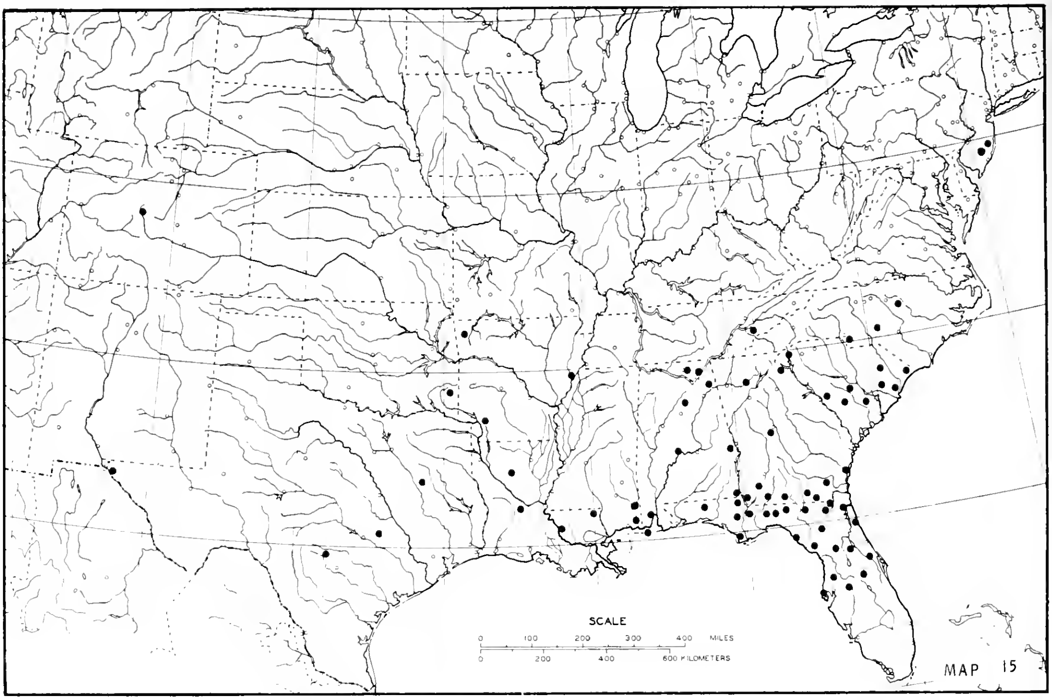
Field notes. Most of the habitat records for the species indicate that it is an inhabitant of nests and burrows of small mammals. It is known from pocket gopher nests in California, Texas (Ross, E. S., 1944), Kansas, North Dakota, British Columbia, and Durango, Mexico; from mouse nests in Utah and California; *Dipodomys* nests in California; marmot burrows in British Columbia; spermophile nests in Alberta and British Columbia; and *Speotyto* (burrowing owl) nests in Washington and Idaho. One was taken from a shelf fungus in California; one at a light in Kern County, California, and one in a malt trap in British Columbia.

Seasonality. Little seasonality would be expected for individuals living in protected nests and burrows. Adults have been collected in every month except August. The greatest numbers are from winter month collections in California, and spring and early summer collections elsewhere. Larvae are unknown.

Distribution. This species has the widest range of any known *Adelops.* It is distributed in southern Canada from British Columbia eastward to Manitoba, and southward through the prairie and mountain states to Texas and California, with one known Mexican population. I have seen 431 specimens from the following localities:

CANADA. ALBERTA. Medicine Hat (spermophile hole), 2 (CAS); Whitford Lake, 1 (CAS). BRITISH COLUMBIA. Creston (47 in gopher burrow, Stace Smith leg; and 16 in *Citellus* burrows), 27 (MCZ, CNCI, CAS, UBCZ); Osoyoos (8 mi. E), 3 (CNCI). MANITOBA. Treesbank, 3 (CNCI). **MEXICO.** DURANGO. El Salto (10 mi. W, 3 in gopher burrow), 13 (CNCI); El Salto (11 mi. SW), 6 (CNCI). **UNITED STATES.** ARIZONA. *Pima County:* Santa Catalina Mts., 5 (CAS, MCZ). *Yuma County:* Yuma, 2 (INHS). CALIFORNIA. *Alameda County:* Castro Valley (gopher nest), 2 (CAS); no locality, 7 (CAS). *Contra Costa County:* Antioch (gopher burrow), 3 (CAS); Danville (18 in gopher nest under board, 2 in debris of ground nest of *Vespula* wasp, 111 in gopher [*Thomomys*] nest, 4 in gopher burrow) (CAS); Mt. Diablo (1800′, field mouse nest), 1 (CAS); Vine Hill, 1 (CAS). *Fresno County:* Fresno, 1 (USNM); Coalinga, 1 (CUIC). *Kern County:* Alta Sierra (5800′, light), 1 (CNCI). *Kings County:* Hanford (shelf fungus), 1 (CNCI). *Lake County:* Blue Lake, 1 (CAS). *Los Angeles County:* Little Rock (Mojave Desert, *Dipodomys* nest), 6 (CAS); Pasadena, 5 (CAS, MCZ); Los Angeles, 1 (USNM). *Marin County:* Novato (*Thomomys* nest), 23 (CAS). *Monterrey County:* Carmel, 3 (CAS, CUIC). *Orange County:* Cypress, 1 (USNM). *Riverside County:* Colton, 1 (INHS); San Jacinto, 1 (USNM). *San Bernardino County:* Victorville (mouse nest), 4 (AMNH). *San Diego County:* Poway, 3 (MCZ, CAS); San Diego, 3 (CAS); Sta. Ysabel, 1 (MCZ Leconte); Jct. to Vallecitas (rodent burrow), 1 (CAS); Trib. to Jamul Cr. near Lower Otay Lake (flood debris), 1 (CAS). *San Francisco County:* San Francisco, 2 (USNM); Lake Merced, 3 (CAS); Presidio (*Thomomys* burrow), 1 (CAS); San Miguel Hills (San Francisco), 1 (CAS). *San Mateo County:* Salada Beach, 1 (CAS); Stanford University, 1 (USNM). *Tehama County:* Red Bluff, 13 (CAS). COLORADO. *Clear Creek County:* Georgetown (8300′–8600′), 1 (USNM). *Denver County:* Denver, 2 (USNM). *Grand County:* Grand Lake, 1 (CAS). *Moffat County:* Craig, 1 (CNCI). IDAHO. *Bingham County:* No locality (*Speotyto* nests), 6 (USNM). KANSAS. *Douglas County:* No locality, 1 (SEMC). *Saline County:* Salinas (*Geomys bursarius* burrow), 3 (CAS). NEVADA. *Esmeralda County:* Goldfield, 11 (CAS, USNM Casey coll., FMNH, MCZ, CNCI). NORTH DAKOTA. *Ransom County:* McLeod (5 mi. SW, *Geomys* burrow), 2 (CNCI). OREGON. *Baker County:* Spring Creek, 1 (GHNC). *Klamath County:* No locality, 1 (FMNH). TEXAS. *Bexar County:* Sommerset (*Geomys bursarius* burrow), 3 (CAS). *El Paso County:* El Paso, 2 (MCZ). UTAH. *Garfield County:* Hanksville (24 mi. S, 7500′), 2 (CNCI); Lonesome Beaver (7500′, mouse nest), 16 (CNCI). *Morgan County:* Strawberry Res. (SE of Ogden, 8000′), 3 (CAS). WASHINGTON. *Adams County:* No locality (*Speotyto* nests), 3 (USNM). *Douglas County:* No locality (*Speotyto* nests), 8 (USNM). *Franklin County:* No locality (*Speotyto* nests), 12 (USNM). *Garfield County:* Pullman, 2 (USNM). *Okanogan County:* No locality (*Speotyto* nests), 17 (USNM). *Walla Walla County:* College Place, 1 (GHNC). *Yakima County:* No locality (*Speotyto* nests), 5 (USNM).

Distributional comments. Hatch (1957:



Map 15. Distribution of *Ptomaphagus (Adelops) consobrinus.*

42) reports as *thomomysi* what may be this species from Corvallis (*Peromyscus* nest) and Medford, Oregon.

Ptomaphagus consobrinus (Leconte)
Figures 1, 4, 52, 53, 94, 125, 178, 179, 206; Map 15

Catops consobrinus Leconte, 1854: 281. Lectotype here designated as female in MCZ (Leconte coll.) bearing red label "type 3151," with a printed label "Ga," and a hand written label "N. Orleans Motsch," seen. Published type locality: Georgia.

Catops strigosus Leconte, 1854: 281. Lectotype here designated as female in MCZ (Leconte coll.) bearing red label "type 3152" and a small white paper square (meaning eastern United States in Leconte's locality code), and a rectangular yellow label marked "7562," seen. Published type locality: South Carolina.

Catops lecontei Murray, 1856: 459. Name proposed for *C. strigosus* Leconte, type and locality the same.

Ptomaphagus consobrinus Leconte, Horn, 1880: 263; Hatch, 1933: 206.

Ptomaphagus (*Adelops*) *consobrinus* Leconte, Jeannel, 1936: 92; 1949: 98.

Ptomaphagus (*Adelops*) *carolinensis* Schweiger, 1949: 1. Holotype male and allotype female in Reichsmuseum, Stockholm, seen. NEW SYNONYMY. Type locality: South Carolina.

Diagnosis. This species is found only east of the Rocky Mountains in Canada and the United States. Its large eyes and dark color separate it from all eastern species except *brevior* and *ulkei* and it is separated from these by the shape of the spermatheca, the long, thin, curved aedeagus, and the genital segment with a long spiculum and genital plates that are both elongated anteriorly and notched on the border of the orifice.

Description. Length 2.5–3.2 mm. Width 1.2–1.5 mm. Color dark brown to piceous. Head pubescent, punctured. Eyes normal, their horizontal diameter 2.2 times width of space between their anterior margin and antennal socket. Antennae (Fig. 125) short, not reaching edge of pronotum when laid back; segments II and III longer than broad, IV and V subquadrate; VI–X distinctly transverse. Pronotum widest at base; sides parallel behind; 1.5 times as wide at base as long; hind margin curved; elytra 1.4 times as long as wide at base, slightly wider 1/3 behind base; female apex obliquely truncate, very slightly drawn out at suture; male apex transversely rounded. Mesosternal keel (Fig. 94) low, notch present. Aedeagus (Fig. 52) regularly curved, long, thin; tip pointed; in dorsal view tip rounded with tooth (Fig. 53). Genital plates (Fig. 206) elongated anteriorly along spiculum gastrale, 2/3 enclosing long thin spiculum; slight concavity in edge bordering genital orifice (arrow in Fig. 206). Spermatheca (Figs. 178, 179) thin, very twisted; anterior end thin, not swollen or flattened in side view.

Variation. The variation in the species is slight. Some variation occurs in the spermatheca when ends of the range are compared (Figs. 178, 179). The spermatheca of the lectotype of *P. strigosus* (Leconte) (=*lecontei* Murray) is identical to that of the lectotype of *consobrinus*. By its description and illustrations it is inseparable from *consobrinus*, which is the only species known from South Carolina, with the exception of one specimen of *P. cavernicola*.

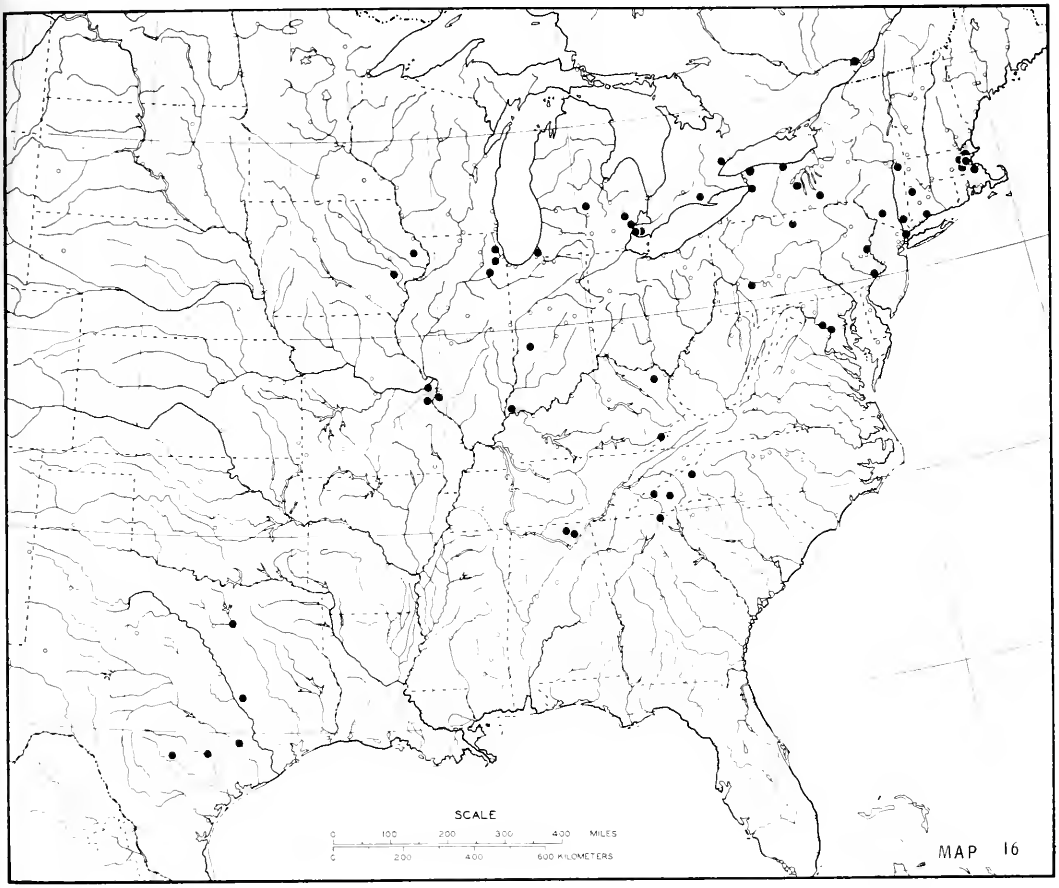
Field notes. The species has been frequently collected on the Coastal Plain in the southeast by using Berlese funnels. In Florida and adjacent states, W. Suter has found specimens in tree forks, tree holes, pine and oak buttresses, log and leaf litter, and palmetto debris. An Alabama collection was from fungus. Malt traps set for scarab beetles have taken large numbers in several Florida localities as well as in North and South Carolina and Georgia. It can be only occasionally taken at carrion, but four traps in Torreya State Park, Florida, captured 42 in a week in early April. A long-term carrion study in South Carolina by Payne and King (1970) found only this species of *Ptomaphagus*, and this only infrequently. Gopher tortoise burrows in Florida yielded two specimens that I have seen (see field notes of *P. texanus* for additional data on tortoise burrows). A. Newton, using human dung and rotted squid as bait in pitfall traps, has taken this species often in pine-oak woods in New Jersey. Additional habitat documentation is found in the distribution section.

Seasonality. Adults have been taken in every month of the year. The winter month collections are from the more southern localities and are mostly from malt traps and litter. Early spring to early summer months probably represent the period of greatest activity since the largest collections are made at this time, usually in baited traps. Nothing is known about reproductive seasonality, but it seems that most reproduction would occur in the spring. Only a few larvae are known from Berlese funnel collections.

Distribution. The species is distributed in the southern Gulf Coastal Plain states from Texas to Florida, northward to Colorado and the pine barrens of New Jersey. I have seen 1356 specimens from the following localities:

ALABAMA. *Blount County:* Inland Lake (rock crevice debris), 1 (FMNH). *Dallas County:* Selma, 3 (USNM). *DeKalb County:* Ft. Payne (in cave), 14 (UANH). *Houston County:* Gordon (log with polypore), 1 (FMNH); Chattahoochee St. Park, 1 in sassafrass tree hole, 3 in 139 lbs. log litter (FMNH, SBP). *Jackson County:* Scottsboro (forest carrion trap), 1 (SBP). *Madison County:* Monte Sano, 2 (HAHC). *Mobile County:* Mobile, 10 (CUIC, UANH); Spring Hill (in fungus), 4 (UANH). Dauphin Island, 7 in pine tree fork, 3 in magnolia tree hole (FMNH). *Russell County:* Seale, 5 (HAHC). ARKANSAS. *Hempstead County:* Hope, 1 (MCZ). *Phillips County:* Helena, 1 (USNM). *Washington County:* No locality, 5 (INHS). COLORADO. *Denver County:* Denver, 1 (USNM). FLORIDA. *Alachua*

County: High Springs (4 mi. N, malt-proprionic acid traps), 15 (HAHC, FSCA); Archer, 28 (CNCI); Gainesville (10 on carrion, 24 in malt traps), 37 (CNCI, FSCA, USNM, PURC); Newnans Lake (malt traps), 31 (FSCA). *Baker County:* McClenny (5 mi. N), 19 in palmetto debris, 14 in bush fork, 229 in malt traps (SBP, FMNH, FSCA); Glen St. Mary (malt trap), 97 (FSCA). *Calhoun County:* Clarksville (1 at light, 1 in malt trap), 12 (HAHC, MCZ); Scotts Ferry (oak litter), 2 (FMNH). *Columbia County:* Suwannee River (pine buttress), 1 (FMNH). *Dixie County:* Steinhatchee, 1 (CNCI). *Duval County:* Jacksonville, 1 (USNM). *Gulf County:* Honeyville (1 at oak log, 3 at pine buttress) (FMNH); Wewahitchka (edge sawdust pile), 8 (FMNH). *Hernando County:* Brooksville (Anataloga Hammock, 1 at log, 5 in maple duff, 1 at oak buttress) (FMNH). *Jackson County:* Florida Caverns St. Park (forest carrion traps), 4 (SBP). *Jefferson County:* Capps (pine buttress), 4 (FMNH); Wacissa (pine buttress), 1 (FMNH). *Lafayette County:* Branford (12.8 mi. NW, malt traps), 2 (FSCA). *Leon County:* Tallahassee, 3 (HAHC); Iamonia (beech log), 17 (FMNH); Woodville (sweetgum litter), 4 (FMNH); Chavies, 5 in pine buttress, 3 in fibrous floor litter (FMNH); Silver Lake (pine buttress), 5 (FMNH); Tallahassee, 2 in gum log, 4 in pine stump, 2 in magnolia bush fork (FMNH). *Levy County:* Bronson (pine-maple pseudofork), 18 (FMNH); Coes Landing (log), 1 (FMNH); near Bronson and "area 3" (malt traps), 19 (FSCA); no locality, 37 (MCZ, CAS, CNCI). *Liberty County:* Torreya St. Park (42 in carrion trap, 1 in 185-liter log Berlese, 10 in malt trap), 53 (SBP, FSCA). *Madison County:* Madison (floor at log), 2 (FMNH). *Marion County:* Ocala (14.5 mi. E, malt), 3 (HAHC); Silver Springs (palm stump), 6 (FMNH); no locality, 3 (MCZ, CNCI). *Orange County:* S. Orlando (pine-cypress stump debris), 1 (FMNH). *Pinellas County:* Dunedin, 38 (TAMU, CUIC, PURC, AMNH, CAS, MCZ); Coachman, 3 (CUIC). *Polk County:* Lakeland, 1 (PURC). *Putnam County:* Crescent City (gopher hole), 2 (USNM); Welaka (Univ. Florida Conserv. Reserve, malt traps), 305 (FSCA). *St. Johns County:* St. Augustine, 2 (MCZ). *Volusia County:* Enterprise, 1 (MCZ). *Walton County*: DeFuniak Springs (dead owl), 4 (HAHC). GEORGIA. *Baker County:* Newton (Emory Univ. Field St., malt traps), 3 (HAHC). *Brantly County:* Nahunta (oak tree crotch), 2 (FMNH). *Brooks County:* Quitman (pine buttress), 2 (FMNH). *Charlton County:* St. George, 5 at log, 1 in magnolia litter, 1 in sawdust, (FMNH). *Clinch County:* Dupont (sawdust under ferns), 2 (FMNH). *Echols County:* Needmore (pine buttress), 4 (FMNH). *Glynn County:* Thalman (pine-oak tree crotch), 2 (FMNH); Jekyll Island (palmetto axil), 1 (FMNH); Brunswick, 1 (USNM). *Grady County:* Calvary, 2 in *Cornus* stump and 1 in pine-sweetgum tree fork (FMNH); Beachton (oak branch litter), 1 (FMNH). *Peach County*: No locality, 1 (USNM). *Seminole County:* Donaldsonville (pine buttress), 2 (FMNH). *Stephens County:* Toccoa (5 mi. W), 1 (CNCI). LOUISIANA. *East Baton Rouge Parish:* Baton Rouge, 1 (USNM). *Rapides Parish:* Alexandria (10 mi. SW), 26 (CNCI). *Washington Parish:* Bogalusa, 2 (USNM, CUIC). *Winn Parish:* Winnfield, 1 (MCZ). MISSISSIPPI. *George County:* Lucedale, 3 (CUIC). *Jackson County:* Lakehurst, 25 (AMNH). *County not located:* Manchester, 2 (CNCI). NORTH CAROLINA. *Moore County:* Southern Pines (12 at malt traps), 23 (CNCI, HAHC, MCZ, USNM Casey coll.). *Union County:* No locality (woods trash), 1 (USNM). *Wake County:* Raleigh (4 at carrion), 5 (HAHC). OKLAHOMA. *Leflore County:* Heavener (10 mi. SW, Winding Stair Watchtower, log litter), 2 (SBP). SOUTH CAROLINA. *Aiken County:* Graniteville (malt traps), 37 (FSCA); Aiken (malt), 25 (HAHC, FSCA). *Bamberg County:* Bamberg (woods



Map 16. Distribution of *Ptomaphagus* (*Adelops*) *brevior.*

trash), 2 (VMKC). *Calhoun County*: No data, 1 (SBP). *Dorchester County*: No locality, woods trash, 2 (VMKC). *Florence County:* Florence (5 in woods trash, 1 in field corn ear, 1 in broom sedge), 20 (VMKC, CNCI, MCZ). *Georgetown County*: No locality, 2 (SBP). *Horry County:* Little River (woods trash and broom sedge), 3 (VMKC). *Pickens County:* Clemson (Payne carrion study), 4 (SBP); Greenville (woods trash), 1 (VMKC). *Williamsburg County:* Kingstree (malt), 1 (HAHC); No locality, 1 (NR) (type male *Pt. carolinensis*). TENNESSEE. *Blount County:* Chilhowee Mt. (malt), 1 (HAHC). TEXAS. *Anderson County:* Elkhart (10 mi. SW), 3 (TAMU). *El Paso County:* Fabens (light), 1 (HAHC). *Lee County:* Fedor (an old locality?), 5 (MCZ, USNM, CAS). *Kerr County*: Kerrville (malt traps), 3 (CNCI).

Ptomaphagus brevior Jeannel
Figures 54, 55, 95, 122, 180–184, 207; Map 16

Ptomaphagus (*Adelops*) *brevior* Jeannel, 1949: 98. Holotype male in MNHN, seen. Type locality: Indiana, Putnam County.

Diagnosis. This species is widespread in the eastern United States, especially in the more northern states. Its range, piceous color, short antennae, and large eyes separate it from all other species except *ulkei* and *consobrinus*. Its deeper and more rounded mesosternal notch, concave margin of the male genital segment, and shorter, thicker aedeagus separate it from *consobrinus*. Its longer aedeagus and broader genital plates separate it from *ulkei*. It is separated from all other species by the shape of the female spermatheca.

Description. Length 2.4–3.1 mm. Color dark brown piceous, antennal base lighter. Head finely punctured, pubescent. Eyes with horizontal diameter 2.8 times width of space between their anterior margin and antennal socket. Antennae (Fig. 122) short, not reaching base of pronotum when laid back; segments II–III longer than broad, IV–X broader than long. Pronotum 1.5 times as wide at base as long, slightly wider 1/3 before base; hind margin slightly sinuous; elytra 1.5 times as long as wide; apex rounded-obliquely truncate in male; obliquely truncate in female, edge not sinuous at suture. Mesosternal notch (Fig. 95) usually very well developed, deep, rounded. Aedeagus (Fig. 54) curved, broader at base, tapering to point with down-curved tooth; in dorsal view (Fig. 55) broadly rounded with terminal tooth. Genital plates broad, anteriorly projected along and 3/4 enclosing long thin spiculum (Fig. 207). Spermatheca variable (Figs. 180–183), central shaft curved, posterior end curved back on itself and usually broadly flattened, anterior end broadly flattened.

Variation. This species has the greatest variation in the spermatheca of any known epigean *Adelops*. The variation is most evident in Texas when eastern localities (Brazos, Colorado, Dallas counties) are compared with central (Bexar, Gonzales) localities. In Bexar and Gonzales County females the spermatheca is smaller and more compact (Figs. 182, 183). Colorado County spermathecae (Fig. 180) are intermediate in shape. The common shape (Fig. 181) is constant throughout the rest of the species' range. Insufficient material is available to determine if the change in spermathecal form in Texas is gradual or sharp. The nature of this variation can be studied only after additional extensive collecting.

This species presented the only recognized case of teratological variation in the spermatheca. This was in one specimen from Round Knob, North Carolina (Fig. 184). Two other specimens from this locality were normal.

All the Texas populations are different in the form of the mesosternal notch, which resembles that of *consobrinus* in that it is not deeply incised and rounded.

Field notes. Most collections are of a few specimens only. They have been taken in Berlese samples and by sifting litter in Ontario, Massachusetts, Texas, and Illinois; in human dung-baited pitfall traps in Texas and Massachusetts; and at carrion in Alabama, Illinois, Kentucky, Massachusetts, Michigan, Missouri, and New York. In Massachusetts they have also been taken in traps baited with skunk cabbage leaves.

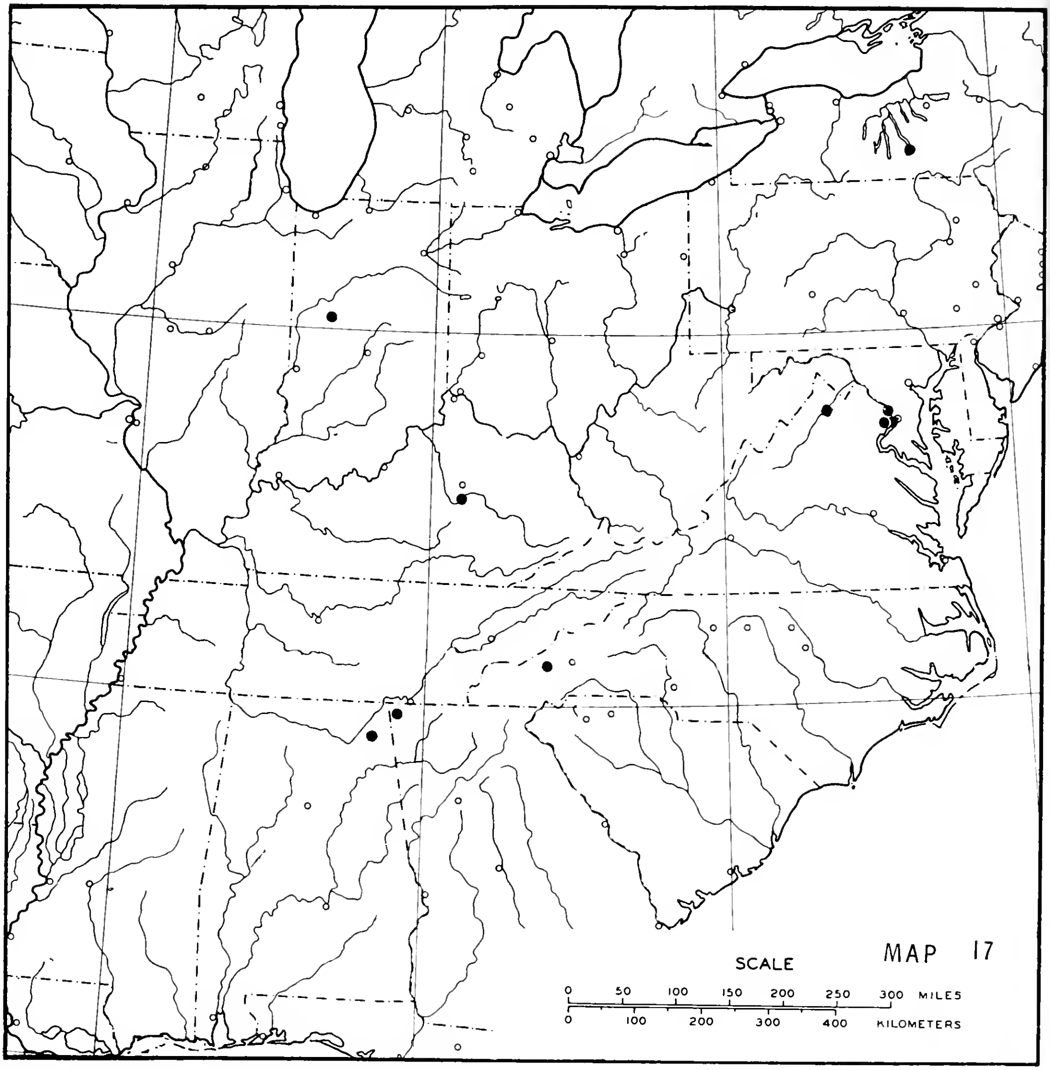
Seasonality. Specimens have been collected in every month except February and December. Records for January and November are from Texas. Records for July and August are from high elevations in Tennessee and North Carolina. The one September record was from a litter sample in New York. The bulk of the specimens were collected from March to June. In Massachusetts trapping by Al Newton and myself showed that the beetles are active from early March until June, and are not trapped in the summertime.

Reproduction is known to occur only in late spring but may occur earlier. Adult females captured in May in Massachusetts produced eggs only until late May, and then died. Males lived until mid-July. Additional data on reproduction will be in a separate paper on the life cycles of *Ptomaphagus*.

Distribution. The species ranges from southern Quebec and southern Ontario, southward through most of the glaciated eastern United States to the southern Appalachians, with a series of peripheral and variant populations in Texas. It is known on the Coastal Plain only in Texas. I have seen 195 specimens from the following localities:

CANADA. ONTARIO. Ancaster, 3 (CNCI); LaSalle (sifting), 9 (KS); Maidstone, 3 (KS); Tillsonburg, 1 (CNCI). QUEBEC. Rigaud, 4 (CCC). **UNITED STATES.** ALABAMA. *Jackson County:* Scottsboro (forest carrion trap), 1 (SBP). *Madison County:* New Market (4 mi. E, carrion trap), 1 (SBP). CONNECTICUT. *Litchfield County:* Washington, 1 (FMNH). *New Haven County:* New Haven, 1 (MCZ). DISTRICT OF COLUMBIA. Washington, 1 (USNM). GEORGIA. *Rabun County:* Clayton (2000–3700 ft.), 1 (CNCI). ILLINOIS. *Cook County:* Des Plaines (Carle Woods, carrion), 17 (SBP). *DuPage County*: Argonne National Lab., 9 (traps) (FMNH). *St. Claire County:* no locality, 1 (FMNH). *Will County:* Joliet, 1 (FMNH). INDIANA. *Posey County:* no locality, 1 (PURC). *Putnam County:* no locality, 2 (PURC, MNHN). IOWA. *Jackson County:* Maquoketa Caves St. Park (Berlese, 297 lbs. leaf litter), 1 (SBP). *Johnson County:* Iowa City, 1 (USNM). KENTUCKY. *Carter County:* Carter Caves St. Park (molasses trap), 1 (SBP). *Harlen County:* Pine Mt. (2 at carrion trap, 4000′), 5 (SBP, ANSP). MARYLAND. *Montgomery County:* Plummers Island, 9 (USNM). MASSACHUSETTS. *Middlesex County:* Cambridge, 2 (MCZ, USNM); Framingham, 1 (MCZ); Lincoln (forest carrion trap), 1 (SBP); Medford (Middlesex Fells Res., carrion and human dung traps), 30 (SBP); Natick, 1 (HAHC); Sherborn, 2 sifting, 1 sweeping, 2 skunk cabbage traps, (MCZ, NYSM); Stoneham (Middlesex Fells Res., carrion, skunk cabbage, and human dung traps), 24 (SBP); Winchester, 2 at human dung (SBP). *Suffolk County:* Dorchester, 1 (MCZ). MICHIGAN. *Barrien County:* Warren Woods (carrion traps), 2 (SBP); Mud Lake Bog (carrion trap), 3 (SBP). *Clinton County:* Rose Lake (pitfall traps), 5 (SBP). *Oakland County:* No locality, 1 (MCZ). *Wayne County:* Detroit, 9 (ANSP, USNM). MISSOURI. *Jefferson County:* High Ridge (sinkhole forest-carrion trap), 18 (SBP). *St. Charles County:* No locality, 3 (MCZ). NEW YORK. *Bronx County:* Bronx Park, 4 (USNM). *Erie County:* Buffalo, 2 (CAS). *Monroe County:* Rochester, 1 (SBP). *Niagara County:* Olcott, 1 (CUIC). *Rensselaer County:* Berlin (under board with rodent runways), 1 (SBP); Valley Falls, 1 (NYSM). *Richmond County:* Staten Island, 1 (USNM). *Orange County:* Mountainville, 1 (NYSM); West Point, 2 (USNM). *Tompkins County:* Ringwood Forest (7 mi. E Ithaca, carrion), 1 (SBP); Ithaca, 2 (CUIC). *Westchester County:* Peekskill, 1 (CNCI). *Yates County:* Penn Yan, 1 (CUIC); unlocated locality, Danby, 1 (CUIC). NORTH CAROLINA. *Haywood County:* Black Mountains (Mt. Mitchell), 7 (AMNH, CAS, MCZ); Round Knob, 3 (USNM). *Jackson County:* Whiteside Mt., 2 (TCB). *Swain County:* Great Smoky National Park (Heintooga Overlook, Mollies Gap, carrion trap, 5000′), 1 (SBP). PENNSYLVANIA. *Northampton County:* Easton, 1 (CAS). *Philadelphia County:* Frankford, 1 (USNM). *Tioga County:* Arnoto, 1 (SBP). *Westmoreland County:* Chestnut Hill, 1 (MCZ); St. Vincent, 1 (USNM). TEXAS. *Bexar County:* San Antonio, 3 (MCZ, USNM). *Brazos County:* College Station, 1 (TAMU). *Colorado County:* Columbus, 12 (USNM, CAS). *Dallas County*: Dallas, 1 (USNM); No locality, 1 (GHNC). *Gonzales County:* Palmetto St. Park, 2 in leaf litter, 2 in human dung trap, (SBP).

Distributional comments. A gap in the distribution exists between the Texas populations and those of the northern and eastern states (Map 16). Insufficient collecting has been done to state whether or not this gap is real.



Map 17. Distribution of *Ptomaphagus (Adelops) ulkei.*

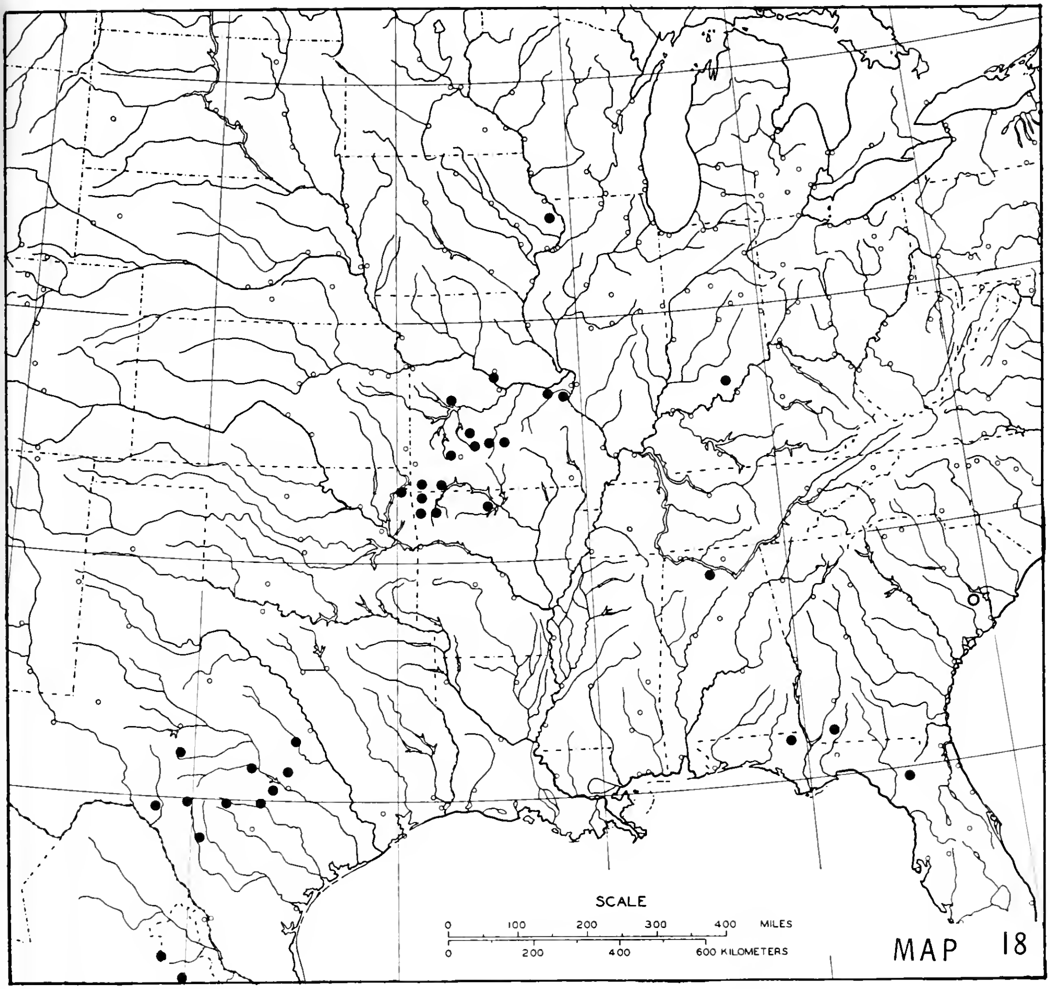
Ptomaphagus ulkei Horn
Figures 56, 57, 96, 127, 185, 186, 208; Map 17

Ptomaphagus ulkei Horn, 1885: 137. Lectotype here designated as male in ANSP (no. 2998), seen. Type locality: District of Columbia. Hatch, 1933: 205.

Ptomaphagus (Adelops) ulkei, Jeannel, 1936: 92; 1949: 98.

Diagnosis. This species is difficult to distinguish from *brevior* and *consobrinus,* which also occur in the southeastern United States. It is best distinguished by the aedeagus and unique form of the female spermatheca.

Description. Length 3.3–4.3 mm. Width 1.5–2.2 mm. Color dark brown. Head finely punctured, pubescent. Eyes normal, their horizontal diameter 3 times the width of the space between their anterior margin and antennal socket. Antennae (Fig. 127) short, not reaching base of pronotum when



Map 18. Distribution of *P.* (*Adelops*) *cavernicola*. The symbols represent only county records. This troglophilic species is known from 55 cave localities (dark circles) and one epigean locality (open circle) in South Carolina.

laid back; segments II and III longer than broad, IV–X transverse, VI–X strongly so. Pronotum widest by slight amount 1/3 before base; 1.5 times as wide at base as long; hind margin sinuous. Elytra 1.3 times as long as broad at base; apex transversely truncate and slightly rounded in both sexes. Mesosternal notch distinctly and deeply incised (Fig. 96). Legs in large males with metatibiae strongly curved, less so in smaller males. Aedeagus (Fig. 56) short, stout, curved in posterior half, tip narrow; in dorsal view tip broad with terminal tooth (Fig. 57). Genital plates elongate, enclosing 3/4 of normal spiculum (Fig. 208). Spermatheca narrow in side view (Fig. 186), in dorsal view (Fig. 185) thin, shaft curved, posterior opening facing right.

Variation. The size variation of this species is the greatest for any known *Adelops*. Some individuals are the largest specimens known for the genus in the United States. A female from Georgia showed variation in the spermatheca in that the posterior end was more curved over in an anterior direction.

Field notes. I took four in a forested ravine at decaying fish bait in Madison County, Kentucky, and one at a carrion pitfall trap in a forested sinkhole in Georgia. A Virginia specimen was found on a dead snail. Data is not available for other specimens but they probably came from forested habitats.

Seasonality. Adults have been taken in April, May, June, July, and September, with 13 of the 21 adults being captured in May and June. Larvae are not known.

Distribution. The species is known from central New York, westward to central Indiana, and southward to northwestern Georgia (Map 17). I have seen 24 specimens from the following 11 localities:

ALABAMA. *DeKalb County:* Manitou Cave (at Fort Payne), 2 (AMNH). GEORGIA. *Dade County:* 4.5 mi. NE Rising Fawn (outside Johnson Crook Cave), 1 (SBP). INDIANA. *Montgomery County:* Crawfordsville, 1 (INHS). KENTUCKY. *Madison County:* Clays Ferry, 4 (SBP). MARYLAND. *Montgomery County:* Plummers Island (Cabin John), 9 (USNM). NEW YORK. *Tompkins County:* Six Mile Creek (Ithaca), 1 (PISZ). NORTH CAROLINA. *Haywood County:* Cosby Knob, 1 (KS); Round Knob, 1 (USNM). VIRGINIA. *Alexander County:* No data, 2 (USNM). *Fairfax County:* Dead Run, 1 (USNM). *Warren County:* Limeton (on dead snail), 1 (USNM).

THE *CAVERNICOLA* GROUP

Diagnosis. Spermatheca shaped like a reversed "S" in anterior end but with posterior end curved around in a coil and then bent to the left; anterior end expanded and flattened (Figs. 187–197).

Description. Shape elongate oval. Color light to dark brown. Eyes large to reduced, pigmented or unpigmented. Antennae short to long. Pronotum with hind angles acute, striae distinct. Elytra with external angles rounded, apex oblique or rounded-truncate in females, and rounded in males; sutural angles of females rounded or sharply acute; some female elytral tips with pruinose area. Wings normal or reduced. Mesosternal carina medium or low. Legs normal or elongated. Aedeagus elongate, gently curved; pointed at tip in lateral view; dorsal view of tip pointed to broad.

The group contains ten named species and seven recognized but unnamed species. All but one of the above are limited in distribution to Mexico and Guatemala. The exception is the troglophile *cavernicola,* which ranges from northeastern Mexico into and across much of the central and southern parts of the eastern United States. Two subspecies are recognized. Of the named species, two troglobites and two troglophiles are known from Mexico. The remaining five are epigean in middle- and high-elevation Mexican forests.

Ptomaphagus cavernicola cavernicola Schwarz

Figures 58, 59, 97, 126, 187–189, 209; Maps 13, 18

Ptomaphagus cavernicola Schwarz, 1898: 57. Type in USNM (No. 1424), seen. Type locality: Missouri, Stone County, Marble (=Marvel) Cave. Hatch, 1933: 204.

Ptomaphagus (Adelops) cavernicola, Jeannel 1936: 92; 1949: 101; Sanderson, 1939a: 117; Barr, 1963: 54; Peck, 1970b (Florida records).

Diagnosis. The large size and large eyes, elongate antennae with segments III–VII longer than wide and IX–X quadrate, produced female elytral tips, and the thin and twisted spermatheca serve to distinguish this cave-inhabiting species, which ranges from northeastern Mexico to the Ozarks of the United States and southeast to Florida. Antennal segments II and III are subequal, separating it from *oaxaca* which has II distinctly shorter than III. The eyes are larger in *oaxaca.*

Description. Length 3.0–4.0 mm. Width

1.4–1.7 mm. Color piceous to brown, head blackish, mouthparts and basal half of antennae testaceous. Head very finely, not densely punctate; eyes large, width of head from antennal base to margin, across eye, 1.7 times width of eye; width of eye 2.0–2.9 times width of space between antennal base and front margin of eye (except in Cueva de la Boca population with smaller eyes). Antennae (Fig. 126) slender and distinctly longer than head and thorax; segments II and III each nearly three times longer than wide; IV, V, and VI sequentially decreasing in length but VI still slightly longer than wide; VII longer than wide; VIII slightly narrower than the adjoining segments and half the length of VII; IX and X quadrate; terminal segment longer than wide, acuminate. Prothorax at base 1.4–1.7 times wider than long; slightly wider 1/3 before base; sides arcuately narrowing in front, nearly straight behind; hind margin slightly sinuate; surface transversely strigose and extremely finely punctulate, the striae much finer and denser at the sides than in the middle. Elytra at base as wide as thorax; 1.6 times as long as wide at base; gradually narrowing to apex; external apical angles more rounded in males than in females; females with acute (but not sharp) sutural angle and oblique apex. Wings normal, their length 1.6 times length of elytra from base to tip in Florida populations. I have observed them functioning in flight only in the Florida populations. Mesosternal carina low, notch conspicuous (Fig. 97). Aedeagus (Fig. 58) thickest in middle, narrowing gently to both ends, more curved in anterior end; left edge of tip raised in side view; gently tapering to apex in dorsal view (Fig. 59). Spiculum gastrale (Fig. 209) long and thin, half enclosed by genital plates that are slightly produced anteriorly. Spermatheca (Figs. 187–189) completing full spiral, small knob on posterior end; broad and flattened knob on anterior end when viewed from side (Fig. 189) and thin in dorsal view (Figs. 187, 188).

Variation. A species having this wide a range and which is apparently restricted to caves could certainly be expected to have variation. However, none of a major extent has been noted except the variation in eye size, which is used to characterize the subspecies *cavernicola aditus.* No difference was found in a study of the measurements and proportions of pronotal and elytral lengths and widths in a series of selected populations. Careful examination of aedeagi and spermathecae from many populations throughout the range showed no differences except in aedeagal mean length. Populations from Missouri and Texas have an aedeagus with a mean length of 1.26 mm (1.20–1.30 mm, n = 32). The Mexican population in Gruta Palmito has a mean aedeagal length of 1.04 mm (1.01–1.12 mm, n = 26). Alabama and Florida populations have a mean of 1.08 mm (1.04–1.12 mm, n = 11). The ranges of the aedeagal lengths of the Texas-Missouri group of populations do not overlap with the ranges of the Mexican or Alabama-Florida populations. These last two groups do overlap. I do not see any obvious evolutionary meaning or adaptive significance in this aedeagal length variation.

However, obvious evolutionary significance does occur in variation in the size of the eyes. In all populations, except that in Cueva de la Boca, the eyes are large, with an eye width of 2.0–2.9 times the width of the space from the anterior margin of the eye to the edge of the antennal socket. The eyes are reduced in the Cueva de la Boca population, which has eyes with a width of 1.5–1.75 times the width of the space between the anterior eye margin and the antennal socket. This population is formally treated below as a distinct subspecies. This one feature strongly suggests that the Cueva de la Boca population has been isolated for some time from the other populations of the species. The Cueva de la Boca population may be cave-limited, and selection for large eyes has either been relaxed, or active selection is tending to reduce the eyes. In either case, genetic resistance to the reduction has not been recently provided by interbreeding with large-eyed populations. As a corollary to this, in all other populations of the species, either active or relaxed selection is not reducing the eyes, because the beetles are not cave-limited, or the cave limitation is so recent that not enough time has elapsed for morphological differentiation to appear.

That the species is not cave-limited in the southeastern United States is suggested by the single January collection of one female from litter in South Carolina, a state entirely free of caves.

Collecting notes. Barr (1963) reported the species from raccoon feces and dead bats. I have taken it on human dung and in bat guano in Texas, Florida, and Mexico. I have baited and trapped it with both carrion and human dung in Florida and Ozark caves. Sanderson (1939a) reported the beetles in Arkansas by the hundreds, where they crawl "over the cave floor, in bat guano and raccoon dung, in decayed vegetable debris washed and carried into caves, and . . . . to ground beef and banana peel when allowed to decay." It can also be found on old moist cigarette and cigar butts left in caves. Occasional lone specimens are found in debris and under rocks. The one specimen from an epigean locality was taken from woods trash in late January in South Carolina.

Seasonality. The species seems not to be seasonal, but to be active and breeding all year round. Barr (1963) collected larvae in January in Missouri. Another Missouri population was found in January exposed to a cold, dry current of air blowing in from a cave entrance. Florida, Ozark, and Texas collections have been made in both winter and summer months. The Mexican populations have been collected only in March and June. A few populations may have seasonality of some sort. In June 1964 I took 63 individuals in Devils Sinkhole, Texas, but in February 1965 James Reddell could find none.

Distribution. The nominate subspecies is known from 55 cave localities and one epigean site. It ranges from Florida, South Carolina, and Alabama, to the Ozarks and Iowa, southwestward to Texas and Mexico (Maps 13, 17). Localities for the Ozarks are given in Barr (1963), most of which are included below. I have seen 845 specimens from the following 56 localities:

MEXICO. NUEVO LEÓN: La Gruta Palmito (near Bustamante, W of Sabinas Hidalgo), 45 (SBP). **UNITED STATES.** ALABAMA. *Morgan County:* Inge Cave, 1 (2.v.1959, T. Barr) (TCB); Talucah Cave, 12 (19.vi.1942, W. B. Jones) (UANH). ARKANSAS. *Benton County:* Cave Spring Cave (Keith Lake Fish Hatchery), 7 (SBP); Tom Danford Cave, 1 (INHS). *Madison County:* Dinneys Cave (Huntsville), 6 (USNM). *Stone County:* Rowland Cave (Fifty-Six), 2 (SBP). *Washington County:* Carroll Cave, 2 (INHS); Devils Den Cave (Devils Den State Park), 1 (SBP); Finchers Cave, 2 (INHS); Granny Dean Cave (Corkscrew Cave), 299 (CNCI, FMNH, INHS, MCZ, SBP, TCB); Stephenson Cave, 5 (CNCI, MCZ). *Unknown county*: Davis Pit, 33 (SBP). FLORIDA. *Alachua County*: Warren Cave, 15 (SBP). *Jackson County*: *Millers Cave* (Florida Caverns St. Park), 201 (FSCA, SBP); Gerards Cave, 29 (SBP). GEORGIA. *Grady County*: Waterfall Cave (near Cairo), 1 (FSCA). INDIANA. "Wash. Co. Ind," 6 (CMNH), a questionable record. IOWA. *Jackson County*: Hunters Cave, 2 (SBP). MISSOURI. *Benton County:* Lish Estes Cave, 2 (SBP). *Boone County:* Devils Icebox Cave, 3 (TCB); Hall Cave, 1 (USNM); Hunters Cave (5 mi. NNW Ashland), 4 (USNM). *Camden County:* Carrol Cave, 7 (TCB). *Franklin County:* Fisher Cave, 3 (TCB). *Greene County:* Low Water Bridge Cave, 3 (SBP). *Jefferson County:* Pleasant Valley Cave, 8 (SBP); Rices Cave (3 mi. NE Goldman), 32 (USNM). *Laclede County:* Mary Lawson Cave, 2 (TCB). *McDonald County:* Henson Cave, 3 (SBP). *Phelps County:* Granny Baker Cave, 1 (INHS); Spencer Cave (7 mi. NW Rolla), 7 (TCB). *Pulaski County:* Inca Cave, 3 (TCB). *Stone County:* Dillo Cave, 1 (TCB); Fairy Cave, 2 (TCB); Marvel Cave, 16 (AMNH, USNM, TCB). *Texas County:* Bat Cave (7 mi. NE Success), 4 (USNM). SOUTH CAROLINA. *Orangeburg County:* Holly Hill, 1 (V. M. Kirk leg., woods trash, VMKC). TEXAS. *Burnett County:* Longhorn Caverns, 4 (SBP). *Comal County:* Brehmer-Heidrich Cave, 1 (SBP); Little Gem Cave, 2 (SBP). *Coryell County:* Shell Mt. Bat Cave, 2 (SBP); Tippets Cave, 1 (SBP). *Edwards County:* Deep Cave, 2 (SBP); Devils Sinkhole, 63 (SBP); Hughes Cave, 1 (SBP). *Kerr County:* Wilsons Cave, 4 (CNCI). *Schleicher County:* Ogleby Ranch Cave, 4 (SBP). *Travis County:* Tooth Cave, 1 (TCB). *Uvalde County:* North Well, 1 (SBP). *Val Verde County:* Fawcetts Cave (36 mi. N Del Rio), 1 (SBP). *Williamson County:* Chinaberry Cave, 1 (TCB); Coffin Cave, 1 (SBP); Laubach Cave, 2 (SBP).

Distributional comments. Notable disjunctions exist in the range (Map 18) of the species. Some of these are in areas with no caves, such as the region between central Texas and the Ozarks. The absence from caves in Illinois, Kentucky, and Tennessee is significant. These states have been fairly well collected for cave fauna by myself and others. This gap must be considered as real, and not an artifact of poor collecting. I have collected in 184 caves in Alabama alone, and the lack of more than two localities in this state shows the beetle to be indeed scarce there. The Iowa locality is also disjunct. This record is based on two specimens I collected in a pitfall trap in 1957. This population may no longer exist, for repeated baiting in this and other nearby Iowa caves has not led to the capture of additional specimens. The Indiana record is questionable. The specimens are old and adequate data does not accompany them.

The preference for caves must be for physiological or behavioral reasons. Dispersal by flight is possible for all populations in that they have fully developed wings, and I have seen them used in flight by the Florida populations. Only one collection is known from a noncave habitat, but we may assume that the species can now actively disperse. The one epigean collection from South Carolina was taken in late January, which may be a reflection of the activity season of the species in forests. The dispersal and cave occupation of more xeric areas such as the Edwards Plateau of Texas may date from a cooler and more moist time during or shortly after the Wisconsin glacial maximum.

Ptomaphagus cavernicola aditus new subspecies

Maps 13, 18

Holotype male and allotype female in MCZ (no. 31961). Type locality: Mexico, Nuevo León, Cueva de la Boca (near Santiago, 20 mi. SSE Monterrey). Type data: 22.vi.1969, S. & J. Peck. Paratypes: 50 with above data, 9 from same locality, 4.xii.1966, T. Raines; 15 from same locality, 22.vi.71, S. Peck and D. Bright.

Diagnosis. The subspecies is distinguishable from *cavernicola cavernicola* only by the smaller eyes and shorter wings. The eye horizontal diameter is 1.50–1.75 times the width of the space between the antennal socket and the anterior eye margin. The eye of *c. cavernicola* is 2.0–2.9 times the width of the eye-antennal space. The wing is 1.2–1.3 times the length of the elytra in *c. aditus* and 1.6 times the elytral length in *c. cavernicola.* Otherwise the description is that of *c. cavernicola* given above, including appendages and male and female genitalia. Measurements of the other structures of this population have not been made to determine if other detectable differences exist.

Etymology. The name *aditus,* Latin, is used as a noun in apposition and refers to the impressive entrance, from which the cave received its name.

Field notes. The 1969 series was taken in the back of the cave in an area with moist bat guano covered with a dense mat of white fungal hyphae. The beetles were abundantly crawling both on the fungal mat and on rocks. The fungal mat was absent in 1971. Human feces were present here and nearby in dryer lower passages but no beetles were found on them. The fauna of the cave is fairly rich and includes a *Nicoletia* thysanuran, collembola, numerous mites, flies, spiders, *Oxidus gracilis* millipedes, histerid and staphylinid beetles, and the carabid beetles *Tachys* and *Rhadine.* The cave is described with a map in Russell and Raines (1967).

Seasonality. Collections have been made only in June and December. Larvae are unknown from either collection.

Distribution and evolution. The subspecies is known only from Cueva de la Boca. This population is 125 air km SSE of the nearest known population at Gruta del Palmito at Bustamante (west of Sabinas Hidalgo). Both caves lie in the limestones exposed in the eastern front of the El Abra Reef Trend.

Both the Gruta del Palmito and Cueva de la Boca *cavernicola* populations exist in similar xeric scrub habitats, and both would seemingly be equally isolated from the Texas populations (the nearest in Val Verde County lying 200 or more air miles to the north) by the low desert between the Mexican and the Texas cave areas. Both Mexican populations were probably in genetic contact with the populations in the rest of the species' range during the Wisconsin glaciation, though Martin and Harrell (1957) find no indication that the arid south Texas region was more favorable for dispersal of mesic fauna in the Wisconsin than now. In the Recent, genetic isolation of the Mexican populations has probably occurred, but only the Cueva de la Boca population has diverged morphologically.

Ptomaphagus gypsum new species
Map 13

Holotype female in MCZ (no. 31960). Type locality: Mexico, Nuevo León, Resumidero de Pablillo (at Pablillo, 55 km SW Linares, 32 km S Galeana). Type data: 4.vi.1966; J. Reddell, D. McKenzie leg.

Diagnosis. The species is characterized by its reduced and unpigmented but distinctly faceted eyes, its wings, which are reduced to 3/4 the length of the elytra, and its habitat in a gypsum cave in the mountains of the Mexican state of Nuevo León. Its eyes are less reduced than in *troglomexicanus* but more than in *cavernicola aditus.* Its antennae and legs are less elongate than in *troglomexicanus* but are more so than in *cavernicola aditus.*

Description. Length 4.0 mm. Width 1.5 mm. Color medium brown. Head finely punctured; eyes reduced, unpigmented, about 30–35 facets indistinctly visible, greatest width on axis at 45° angle from head margin behind eye, maximum length 1.75 times maximum width, space between antennal socket and anterior eye margin equal to maximum length of eye; antennae of medium length, extending to first 1/4 of elytra when laid back, segment II shorter than III and IV, II equal to V and longer than VI, VII longer than broad, VIII transverse, IX and X broader than long. Pronotal sides almost parallel, slightly converging behind, 1.31 times as wide at base as long, hind margin slightly sinuous. Elytra 1.85 times as long as wide at base, external apical angle rounded. Wings reduced to 3/4 length of elytra. Mesosternal carina and notch as in *cavernicola.* Legs slender and elongate. Aedeagus unknown. Spermatheca as in *cavernicola* (Figs. 187–189) but with thinner anterior end when seen in dorsal view.

Etymology. The name is a noun in

apposition referring to the gypsum cave in which the specimen was collected.

Field notes. The type locality cave lies in a dry interior mountain valley. The cave is in Jurassic (?) gypsum with other gypsum caves nearby, and to the north in the vicinity of Galeana. All these could contain the species. A photograph of the area, a description, and a map of the cave is given by Russell and Raines (1967). I searched for the cave in 1969 and was unable to find it with the published information, and I could find no one in Pablillo who knew about a resumidero (a sink at the downstream end of a water course).

Ptomaphagus troglomexicanus Peck
Figures 60, 131, 190; Maps 13, 19

Ptomaphagus (*Adelops*) *troglomexicanus* Peck, 1968: 92. Holotype male in MCZ (no. 31653), seen. Type locality: Mexico, Tamaulipas, Cueva de la Perra, 15 miles NW of Gómez Farías.

Diagnosis. This is the only cave-specialized *Ptomaphagus* known from Mexico. Its tiny unpigmented eyes and very elongate antennae with all segments longer than wide serve to distinguish it.

Description. Length 3.6–4.0 mm. Width 1.7–1.9 mm. Color yellowish to dark brown. Head finely punctured. Eyes reduced to depigmented, faceted spot; head width from antennal base to margin across eye 3 times width of eye. Antennae (Fig. 131) very slender and long, slightly flattened, reaching into first third of elytra when laid back; segment II 2.5 times as long as wide; II and IV subequal, 3.5 times as long as wide; V, VI, and VII sequentially shorter and wider; VII 1.8 times as long as wide; VIII longer than wide; IX 1.3 times longer than wide; X 1.1 times longer than wide. Pronotum widest at base, 1.55 times wider than long; sides slightly divergent behind; hind margin straight. Elytra widest 1/3 from base; 1.55 times as long as wide at base; external apical angles rounded; apex slightly oblique in female, with acute sutural angle. Wings reduced to tiny scale, elytra fused. Mesosternal keel of medium height, notch present. Aedeagus (Fig. 60) long, straight, thin, curved only in basal quarter, tip narrow; in dorsal view, narrowing to broadly sharp tip. Spiculum gastrale long and thin, 2/3 enclosed by genital plates, which are anteriorly elongate and pointed. Spermatheca (Fig. 190) with straight central shaft; twisted at posterior end with 1 1/2 turns; anterior end broad in lateral view, narrow with knob in dorsal view.

Variation. No variation noted.

Field notes. I made collections in Cueva Chica on *Neotoma* (?) dung, on insectivorous bat guano in Cueva Capilla, and carrion bait near the entrance of Cueva de la Mina. The temperature of the first cave is 13°C and that of the third is 15°C. In Cueva Capilla all specimens came from a large mud-flat near the back of the cave. The beetles were feeding on a light sprinkling of guano, in association with troglobitic *Mexisphodrus* and *Paratrechus* carabid beetles. These three caves and others at medium and high elevations in the Sierra de Guatemala of the state of Tamaulipas in Mexico contain a remarkably rich and diverse assemblage of cave-adapted invertebrates. The fauna and the caves are further discussed by Mitchell (1968) and Reddell and Mitchell (1971b). The region, with its cloud forest, is of general biogeographic interest and is discussed by Martin and Harrell (1957), and Martin (1958).

Seasonality. Reproductive seasonality may not occur in this cave species. Adults have been collected only in January, March, and July. Teneral adults are known only from July collections (2 from Cueva de la Mina, and 3 from Cueva Capilla). Larvae are known from a July collection in Cueva Capilla.

Distribution. The species is known only from three caves at an elevation of 5000–7000 feet in the Sierra de Guatemala in Southern Tamaulipas, Mexico. The caves are six air km distance from each other. I have seen 49 specimens from the following three localities: **MEXICO.** TAMAULIPAS. Cueva Chica de la Perra, 7000′ elev., 11 air km NW Gómez Farías, 6 (SBP); Cueva de la Perra, 7000′ elev., 11 air km NW Gómez Farías, 34 (SBP, MCZ); Cueva de la Mina, 5000′ elev., near Rancho del Cielo, 7 air km NNW Gómez Farías, 8 (SBP).

Distributional comments. The type locality is undoubtedly Cueva Capilla de la Perra. Upon inquiring of inhabitants of the small lumbering town of Charco de la Perra (also called El Porvenir), I was led to two caves. The two caves are less than a quarter of a mile apart. I chose the name Chica to distinguish the small cave from the large cave (which, I was told, was locally known as Cueva Capilla).

It is difficult to reach these caves without a four-wheel drive vehicle. We packed in with burros and supplies to Rancho del Cielo and its caves in one day, where we stayed and worked as guests of Texas Southmost College of Brownsville, Texas, and into La Perra and its caves on a later day. Future workers wishing to collect in the caves and cloud forest of the Sierra de Guatemala should bear these difficulties in mind.

Ptomaphagus oaxaca new species
Figures 64, 65, 135, 191; Map 13

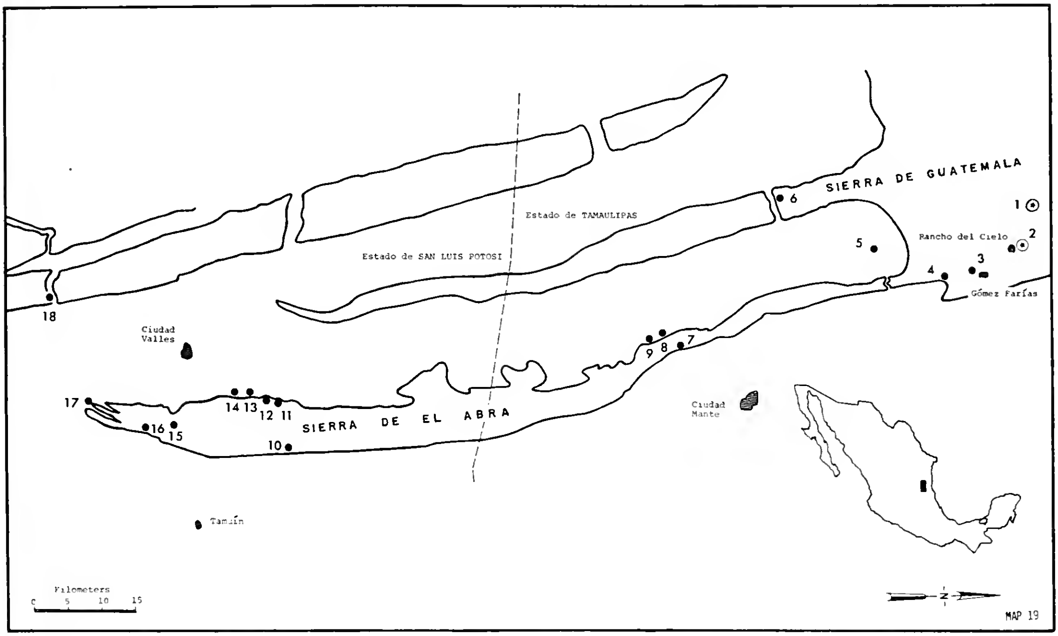
Holotype female and allotype male in MCZ (no. 31965). Type locality: Mexico, Oaxaca, 30 mi. S Valle Nacional on Highway 175. Type data: SE mountain slope, 6800′ elev., cloud forest remnant, 10–13. viii.1970, A. Newton, human dung trap No. 5. Paratypes: all with same date and collector; 5 with above exact data; 5 from 25 mi. S Valle Nacional, W slope, 6350′, rich cloud forest, human dung trap No. 4; 4 from 23 mi. S Valle Nacional, W slope, 5750′, dense cloud forest, human dung trap No. 3; 1 from 35 mi. S Valle Nacional, SE slope, 8000′, low mossy woods, broad-crowned thick-leaved oaks, human dung trap No. 6.

Diagnosis. The species is very similar to *P. cavernicola* and is diagnosed in the same way except for differences in the spermatheca, eyes (larger than in *cavernicola*), and antennae (shorter in *oaxaca*, which has segment II distinctly shorter than III; II, and III are subequal in *cavernicola*).

Description. Length 3.5–3.9 mm. Width 1.8–1.9 mm. Color medium brown, antennal club darker, antennal base lighter. Head finely, densely punctured; eyes large, their horizontal diameter 3.8 times the width of the eye-antennal socket space; antennae long, reaching beyond pronotum when laid back, segment III longer than II, II and IV equal length, V shorter than IV and longer than broad, VI 1.5 times as broad as long; VII 1.15 times wider than long; VIII twice as wide as long. Pronotum widest at base, sides slightly diverging to base, 1.5 times as wide at base as long, hind margin sinuous. Elytra 1.15 times wider than pronotum, widest at middle, 1.65 times as long as wide at base, apex obliquely truncate and sutural angles pointed (Fig. 135) in female. Mesosternal carina low, notch rounded and distinct. Legs long and thin. Spermatheca (Fig. 191) with flattened anterior end and very curved posterior end. Aedeagus long, thin, curved in lateral view (Fig. 64), tip pointed (Fig. 65). Genital segment with long thin spiculum about half enclosed by lateral plates.

Etymology. The name is a noun in apposition and is the name of the mountain range (Sierra Madre de Oaxaca) and of the Mexican state in which the species was collected.

Field notes. The collecting data is given in the type and paratype data. The species was taken in traps along with 26 *Ptomaphagus newtoni,* and 1 female of an unnamed species. Some collecting areas along the road from Valle Nacional to the city of Oaxaca are discussed by Ball and Whitehead (1967).



Map 19. Distribution of *Ptomaphagus troglomexicanus* (circles with stars) and *P. elabra* (solid black spots) in northeastern Mexico. 1 Cueva Capilla de la Perra and Cueva Chica de la Perra, 2 Cueva de la Mina, 3 El Sótano de Gómez Forías, 4 La Cueva del Nacimiento del Rio Frio, 5 El Sótano de las Abejas, 6 La Cueva del Puente, 7 Grutas de Quintero, 8 La Cueva de la Florida, 9 La Cueva de El Pachón, 10 Ventana Jabali (Cave), 11 El Sótano del Tigre, 12 La Cueva de los Sabinos, 13 El Sótano de la Tinaja, 14 El Sotanito de Montecillos and el Sótano de Pichijumo, 15 La Cueva de Valdosa, 16 Las Cuevas de Taninul, 17 La Cueva Chica, 18 Cueva de Puente de Dios. Copied in part from privately distributed base map of William H. Russell and Robert W. Mitchell, 1969, and maps in Reddell and Mitchell 1971a, 1971b.

Distribution and evolution. The species is known only from the above collections made in middle and high elevation temperate forests in the Sierra Madre de Oaxaca. This species is probably similar to the ancestor from which *cavernicola* and its derivatives arose.

Ptomaphagus elabra Peck
Figures 62, 63, 128, 196, 211; Maps 13, 19

Ptomaphagus elabra Peck, 1971b: 9. Holotype male and allotype female in MCZ (no. 31895). Type locality: Mexico, Tamaulipas, Cueva de El Pachón, 16 km SSW Ciudad Mante.

Diagnosis. The species is known only from caves at low elevations in the states of Tamaulipas and San Luis Potosí. Its large eyes, short antennae, relatively short and thick aedeagus, and shape of the spermatheca serve to characterize it.

Description. Length 2.6–3.2 mm. Width 1.2–1.5 mm. Color dark brown. Head finely punctured. Eyes normal, their diameter 2.7 times the distance from their anterior margin to antennal base. Antennae (Fig. 128) short, stout, flattened; not reaching pronotal base when laid back; club darker; segments gradually increasing in width from base to apex; segments II–V longer than wide, VI and VIII–X transverse; VII quadrate. Pronotum widest at base; 1.4 times as wide as long; sides gently diverging; hind margin sinuous; pubescence abundant. Elytra elongate; 1.5 times as long as wide as base; widest 1/3 behind base; apex weakly rounded-oblique in female. Wings normal; observed in flight in

Grutas de Quintero. Mesosternum with low keel, notch distinct. Legs medium; mesotibiae bent outward; metatibiae slightly bent inward. Aedeagus (Fig. 62) relatively short and stout, slightly curved; tip fairly blunt in lateral view, in dorsal view (Fig. 63) more blunt, with terminal button. Spiculum gastrale (Fig. 211) long and thin, half enclosed by genital plates, which are not anteriorly elongated. Spermatheca (Fig. 196) with fairly straight and thin central shaft; anterior end with shaft bent posteriorly, then ventrally and curving to anterior flattened end; posterior end somewhat laterally flattened, thin in dorsal view.

Variation. Variation is noticed in slide mounts of the aedeagus in which the tip is rotated to appear more broad.

Etymology. The name *elabra* is used as a noun in apposition. It refers to the Sierra de El Abra, which contains most of the caves from which the species is known.

Field notes. The species was found abundantly in dryish insectivorous bat guano in Cueva del Nacimiento del Rio Frio, and in Cueva Ventana Jabili. In Grutas de Quintero 134 were found in the felt lining of a severed toe of a boot. In Cueva de El Pachón 119 were taken from pools of liquid vampire guano. The beetles walked freely and rapidly on the liquid guano, showing no tendency to get stuck in the viscous mess. The beetles show no unusual tarsal features that would account for this ability. No other species has been observed on the surface of liquid vampire guano.

The cave temperatures are 24–25°C. The elevations are all under 800 m.

Seasonality. Reproduction probably occurs throughout the year. Adults have been collected in every month except May, August, and October. Teneral adults are known from Cueva de El Pachón (8 out of 119), Grutas de Quintero (27 out of 138), Cueva del Nacimiento del Rio Frio (9 out of 31), and Ventana Jabili (2 out of 24). All were collected in late June and early July. Larvae have been found in two caves in June and July.

Distribution. The species is known only from lowland caves in and near the Sierra de El Abra, a north-south trending low range in the Mexican states of Tamaulipas and San Luis Potosí. I have seen 475 specimens from the following 19 localities:

MEXICO. SAN LUIS POTOSÍ. Cueva Chica (2 1/2 km NE El Pujal), 1 (SBP); Cueva de Puente de Dios (30 km SSW Valles), 3 (SBP); Cueva de los Sabinos (12 1/2 km NE Valles), 3 (SBP); Cueva de Taninul No. 1 (13 1/2 km SE Valles), 1 (SBP); Cueva de Valdosa (10 1/2 km SE Valles), 9 (SBP); Sótano de Manuel (3 km NE El Pujal), 1 (SBP); Sótano de Montecillos (10 km NE Cd. Valles), 1 (SBP); Sótano de Pichijumo (8 km NE Valles), 1 (SBP); Sótano del Tigre (14 km NE Valles), 9 (SBP); Sótano de la Tinaja (10 1/2 km NE Valles), 9 (SBP); Ventana Jabili (20 km E Valles), 27 (SBP). TAMAULIPAS. Bee Cave (19 km NW Limon), 13 (SBP); Cueva de la Florida (8 1/2 km NE Antiguo Morelos), 19 (SBP); Cueva del Nacimiento del Rio Frio (7 km S Gómez Farías), 31 (SBP); Cueva de El Pachón (7 1/2 km NE Antiguo Morelos, type locality), 119 (SBP); Cueva de los Vampiros (20 km NW Limon), 23 (SBP); Grutas de El Puente (9 km SE Ocampo), 6 (SBP); Grutas de Quintero (Quintero, 13 km SW Cd. Mante), 178 (SBP); Sótano de Gómez Farías (2 1/2 km SW Gómez Farías), 2 (SBP); Sótano de Santa Elena (9 km SE Antiguo Morelos), 19 on vampire guano (SBP).

Distributional comments. Though the species is now known only from lowland caves, I do not think it is restricted to them. Though we were unable to collect it in epigean habitats, it should be expected in moist and forested situations in the Sierra de El Abra or other lowland or midmontane localities.

It is conjectural as to whether the species is presently dispersing overland between caves of the Sierra de El Abra. I have seen individuals in flight, so this dispersal method is available to them.

The general area of the Sierra de El Abra is xeric. The vegetation is mostly a lowland tropical thorn forest, with protected ravines and streamsides possessing a tropical deciduous forest. Under certain climatic conditions, such as damp nights, dispersal may occur between caves and favorable noncave situations.

An alternative but less likely explanation is that the species is now completely restricted to the caves because of moisture or other requirements. The restriction may have occurred with changing climatic conditions of the Pleistocene, most likely following the Wisconsin glacial retreat.

A discussion of the El Abra caves and their fauna, with emphasis on cave evolution, is that of Mitchell (1969). A list of the total El Abra cave fauna is given by Reddell and Mitchell (1971a).

Ptomaphagus jamesi new species
Figures 70, 71, 197; Map 13

Holotype female and allotype male in MCZ (no. 31963). Type locality: Mexico; Oaxaca, 5 km W San Cristobal de las Casas. Type data: 16.viii–2.ix.1969, S. & J. Peck, 8000′ elev., pine-oak forest, carrion bait trap. Paratypes: 1 female and 1 male same as above, 6 males as above but 13–16.viii.1969, carrion trap.

Diagnosis. The species is characterized by the spermatheca with a thin anterior profile, broadly pointed (ogival) aedeagus tip, large finely faceted eyes, and rounded nonpruinose sutural angles of the female elytra.

Description. Length 2.9–3.4 mm. Width 1.4–1.6 mm. Color medium-dark brown, head and antennal club darker. Head with large, finely faceted eyes, their horizontal diameter 2.3–2.9 times the width of the eye-antennal socket space; antennae medium length, reaching just beyond pronotal base, segment III 6/7 as long as II, IV 3/4 as long as III, V as long as IV, and 8/9 as wide at apex as broad, VI 7/9 as long as wide, VII longer than wide, VIII–X transverse, VIII twice as wide as long. Pronotum with sides slightly diverging at base, 1.5 times as wide at base as long, hind margin sinuous. Elytra widest 1/3 from base, 1.5 times as long as wide at base, sutural angles and apex rounded in both sexes, no pruinose areas on female elytral tips. Mesosternal carina low, notch normal. Wings present. Legs robust. Aedeagus (Fig. 70) curved, thin, tip (Fig. 71) broadly pointed. Spermatheca (Fig. 197) with narrow anterior part, twisted posterior end. Genital segment as in *P. altus.*

Etymology. The species is named for my brother, James Peck, in recognition of his assistance to me in field work in the summers of 1965 and 1969.

Field notes. The above 10 specimens were taken in a temperate forest along with 69 specimens of *P. altus.* The forest is described with this later species.

Distribution and evolution. The species should probably be expected in other high elevation pine-oak forests of southern Mexico and perhaps Guatemala. Because of its larger eyes it may not be as old or as obligate a montane inhabitant as is *P. altus* to which it is generally similar.

Ptomaphagus altus new species
Figures 68, 69, 129, 137, 194; Map 13

Holotype female and allotype male in MCZ (no. 31962). Type locality: Mexico; Chiapas, 5 km W San Cristobal de las Casas. Type data: 16.viii–2.ix.1969, S. & J. Peck, 8000′ elev., pine-oak forest, carrion bait traps. Paratypes: 29 males and 14 females with same data; 7 males and 9 females from same locality but 13–16.viii.1969 in carrion-baited traps.

Diagnosis. The species is recognized by the combination of characters of the aedeagus, spermatheca, rounded female sutural elytral angles, and somewhat reduced and more coarsely faceted eyes.

Description. Length 3.0–3.4 mm. Width

1.4–1.5 mm. Color dark brown. Head sparsely punctured; eyes reduced and with coarse facets, their horizontal diameter 1.9–2.0 times the width of the eye-antennal space; antennae short, not reaching base of pronotum when laid back, segments (Fig. 129) II and III equal, IV–VI successively shorter and broader, VII quadrate. Pronotum widest 1/3 before base, sides slightly converging to base, 1.2 times as wide at base as long; hind margins sinuous. Elytra wider than pronotum, 1.45 times longer than wide at base; hind margin, and sutural angles rounded in both sexes (Fig. 137); elytral tips with pruinose patch along suture in females. Wings present. Mesosternal carina medium, notch large and rounded. Legs average length. Aedeagus thin and curved with button at tip (Fig. 68), tip in dorsal view pointed (Fig. 69). Genital segment with spiculum mostly enclosed by lateral plates. Spermatheca (Fig. 194) with broad anterior margin.

Etymology. The name (Latin, *altus*, high) is used as a noun in apposition and refers to the high-elevation forests in which the species was collected.

Field notes. The type series was captured in traps at the edge of a wooded ravine, at the oak forest at the sharp bend in the main highway west of San Cristobal. The ravine vegetation was of temperate aspect and included *Quercus*, *Pinus*, *Arbutus*, *Rubus*, *Crategus*, *Carpinus*, and *Alnus*. Ten specimens of *P. jamesi* were taken at the same locality.

Variation and distribution. Another specimen that is assigned to this species is a female bearing the following data: Mexico: Michoacan, 40 km E Morelia at Mil Cumbres, 8–10.ix.1969, S. & J. Peck, 9000′ elev., pine-oak forest, carrion-dung traps. It agrees with the Chiapas specimens in most characters. However, its elytra are less rounded and its mesosternal notch much smaller and narrower. This record suggests that the species or other reduced-eyed ones close to it may be distributed in other high elevation localities with pine-oak forests in the southern and western mountains of Mexico.

Ptomaphagus newtoni new species
Figures 66, 67, 136, 195; Map 13

Holotype female and allotype male in MCZ (no. 31964). Type locality: Mexico; Oaxaca, 25 mi. S Valle Nacional on Highway 175. Type data: W slope of mountain, 6350′ elev., rich cloud forest, 10–12.viii. 1970, A. Newton, human dung trap No. 4. Paratypes: 5 females and 7 males with above data; 2 males with above data but from 23 mi. S Valle Nacional, W slope, 5750′, dense cloud forest, human dung trap No. 3; 4 males and 5 females as above but from 30 mi. S Valle Nacional, SE slope, 6800′, cloud forest remnant, human dung trap No. 5.

Diagnosis. The species is characterized by the spermatheca, pointed aedeagus tip, rounded female elytral sutural angles, large eyes, and short antennae.

Description. Length 2.9–3.5 mm. Width 1.4–1.6 mm. Color medium brown, head and antennal club darker. Head with eyes large, their horizontal diameter 3.5 times the width of the eye-antennal socket space; antennae short, reaching only base of pronotum when laid back, segment III longer than II, IV 3/4 length of II, IV and V equal length, V 9/11 as long as broad at apex, VI 2/3 length of V, VII broader than long, VIII 3.5 times as wide as long, IX and X broader than long. Pronotum widest at base, sides parallel behind, 1.45 times as wide at base as long, hind margin sinuous. Elytra wider than pronotum, widest 1/3 from base, 1.6 times as long as wide at base, sutural angles and apex rounded in both sexes (Fig. 136), not pruinose along suture at apex in females. Wings present, normal. Mesosternal carina medium, notch medium. Legs short, robust. Aedeagus (Fig. 66) pointed and curved in lateral view, tip pointed in dorsal view (Fig. 67). Genital plates half enclosing spiculum. Spermatheca (Fig. 195) with broad, shallowly grooved anterior end, straight middle piece, and moderately twisted posterior end.

Etymology. The species is named for Al Newton in recognition of his help in the field and his making available to me his collections and data.

Field notes. The species was taken at the same montane forest trap sites as *P. oaxaca,* and one female of an unnamed species.

Distribution. The species is known only from the above collections in the middle- and high-elevation temperate forests of the Sierra Madre de Oaxaca.

Ptomaphagus leo new species
Figures 61, 130, 193, 210; Map 13

Holotype male and allotype female in MCZ (no. 31894). Type locality: Mexico; Nuevo León, Chipinque Mesa (5400′ elev., at Monterrey). Type data: 21–25.vi.1969, S. and J. Peck leg., human dung traps in forest. Paratypes: 28 with same data.

Diagnosis. The species is characterized by the small, thin aedeagus; very twisted spermatheca; and especially by the genital plates, which are projected anteriorly along the spiculum gastrale but enclose only half of the long and thin spiculum.

Description. Length 2.5–3.2 mm. Width 1.2–1.4 mm. Color dark brown. Head with numerous punctures forming faint striae; eyes normal, large; 5 times as wide horizontally as space between antennal base and anterior eye margin. Antennae (Fig. 130) normal, short, flattened; segment II longer than III; IV and V subquadrate; VI–X transverse. Pronotum widest at base; 1.4 times as wide at base as long; sides slightly divergent; hind margin sinuous. Elytra widest 1/3 behind base; 1.5 times as long as wide at base; apex oblique in females, sutural angle slightly rounded. Wings normal. Mesosternal carina low, notch present. Legs normal; mesotibiae bent outward; metatibiae slightly bent inward. Aedeagus (Fig. 61) small, thin, curved; tip blunt; in dorsal view tip with sides evenly converging to narrowly truncate point. Spiculum gastrale (Fig. 210) long and thin, half enclosed by genital plates which are elongated anteriorly. Spermatheca (Fig. 193) thin, twisted; posterior end turning once then turning back and over to end; anterior end thin in dorsal view; broad in lateral view.

Variation. No variation noted.

Etymology. Latin, *leo,* lion, a noun in apposition referring to the Mexican State of Nuevo León, from which the species is known.

Field notes. The species has been taken only at two localities. At Chipinque Mesa ten were taken in malt traps (by H. Howden), 30 in three human dung, and 5 in two canned dog food baited traps, 7 in a Berlese extraction of 176 liters (166 pounds) of forest soil and leaf litter, and one in a small cave. Three were taken near guano in both entrance and dark zones of Cueva de Chorros de Agua.

Seasonality. Only dark adults are known from collections made in June and August. Larvae are not known.

Distribution. Presently it is known only from two localities separated by 80 air km in the state of Nuevo León. I have seen 56 specimens from the following two localities: **MEXICO.** NUEVO LEÓN. Chipinque Mesa, 5400′ elev. (at south edge of Monterrey), 53 (CNCI, MCZ, SBP); Cueva de Chorros de Agua (13 mi. W Montemorelos), 3 (SBP).

Distributional comments. Chipinque Mesa is the northernmost locality in the Mexican Sierra Madre Oriental containing mesic forest. We noticed several plants common to the southeastern United States (redbud, *Cercis;* poison oak, *Rhus;* hickory, *Carya;* and catbrier, *Smilax*) that have distributional disjunctions, being absent from xeric south Texas and the adjacent lowlands of Tamaulipas and Nuevo León. In insect distributions, Chipinque Mesa is the northern locality of mesic Mexican species (Howden, 1966).

Ptomaphagus spelaeus (Bilimek)
Figures 72, 73, 138, 192; Map 13

Choleva spelaea Bilimek, 1867: 902. Type in Museum Vienna, not seen. Type locality: Mexico, Guerrero, Cueva de Cacahuamilpa.
Choleva cacahuamilpensis Herrera, 1891: 218. Type repository unknown, not seen. Type locality: Mexico, Guerrero, Cueva de Cacahuamilpa. Synonymized *in* Peck, 1971b: 11.
Dissochaetus spelaea, Jeannel, 1922: 41.
Ptomaphagus (*Adelops*) *spelaeus,* Jeannel, 1936: 93; 1949: 98. Peck, 1971b: 11.

Note on deposition of type. Although Jeannel has stated that the type of the species is in Vienna, Dr. F. Janczyk of the Zoologische Abteilung, Naturhistorisches Museum Wien, has searched the collection and cannot find it (in litt.).

Diagnosis. The species is characterized by the shape of the spermatheca, the aedeagus tip which is bluntly pointed in dorsal view, and with a ventral button in lateral view, the rounded female elytral tips, medium antennae, large eyes, and cave habitat in west-central Mexico.

Description. Length 2.6–3.2 mm. Width 1.2–1.5 mm. Color dark brown. Head with eyes large and prominent, their horizontal diameter 2.7 times width of eye margin-antennal socket space. Antennae slightly lighter in color at base, medium length, scarcely surpassing pronotal hind margin when laid back, segment II 5/12 as wide as long, III 1/2 as wide as long, IV and V slightly longer than wide, VI and VII wider than long, VIII 5/12 as wide as long. Pronotum with sides slightly converging behind, widest at middle, 1.8 times as wide at base as long, hind margin sinuous. Elytra 1.5 times as long as wide at base, sutural angles and hind margin rounded in males and females (Fig. 138), pruinose at tip along suture in females. Fully winged. Legs medium, metatibiae bent inward. Mesosternal carina medium, notch distinct. Aedeagus thin, curved, with terminal ventral button in lateral view (Fig. 72), tip bluntly rounded in dorsal view (Fig. 73). Genital plate half enclosing spiculum. Spermatheca as in Figure 192.

Field notes. From the type locality, Cueva de Cacahuamilpa, Bilimek reported the beetles as running rapidly over cave flowstone. Herrera found one near "Agua bendita." I visited this cave in 1969 but could not collect. It has been commercialized and is heavily visited by tourists. The commercialization may have altered conditions so that the beetles no longer live there. James Reddell (in litt.) found none in a collecting visit to the cave in 1965. In Gruta de Acuitlapan 18 were collected in the first gallery and 12 in the second gallery.

Distribution. I have examined the following material: **MEXICO.** GUERRERO. Gruta de Acuitlapan (12 km E Taxco), 1 (9.iv.1968, W. Calvert, SBP), 30 (2.vi.1963, C. Bolivar, J. Hendrichs, J. Urquijo, SBP, JHSC, ENCB). Resumidero del Rio San Geronimo, near Michapa, 1 (18.x.1942, C. Bolivar, D. Pelaez, ENCB).

Distributional comments. Though I have not seen material from the type locality for comparison, there is no doubt that the above collections represent the species. The type cave, and the two listed above, are all near one another in the same karst region. These caves possess the same general fauna. Several other caves exist in the vicinity (Fish, 1966) and probably contain the species. As evidenced by the distributional data, there is no doubt that Herrera's species is a synonym.

The region possesses rugged topography with a scrubby vegetation. It is xeric in appearance. That the beetle also exists in noncave habitats in the region is conjectural. It does not possess a cave-adapted morphology. Both surface and cave collecting are needed in this section of Mexico.

CAVERNICOLA GROUP INCERTAE SEDIS

The following material represents collections of *Ptomaphagus* in the *cavernicola* group from Mexico and Guatemala. I tentatively judge them to be new species but believe my material is inadequate to serve as the basis for distinctive and complete descriptions and characterizations of new species. I am taking this conservative position to prevent the possibilities of future taxonomic problems arising from names based on inadequate material. I encourage future workers to be as cautious when dealing with this complex fauna in Mexico and Central America, and to try to work seriously only with good population samples of the difficult species in this group. I am providing the following list to make available the seasonal, ecological, and distributional data and to encourage further collecting efforts in these areas.

SPECIES 1

Mexico: Oaxaca; 23 mi. S Valle Nacional on Highway 175, 5750′ elev., dense cloud forest, 9–12.viii.1970, A. Newton, human dung trap No. 3, 1 female; taken with *P. oaxaca* and *P. newtoni.*

SPECIES 2

Guatemala: Alta Verapaz; Patal, 5 km S Tactic, 24–27.viii.1969, S. & J. Peck, 4500′ elev., cloud forest, 1 in trap; taken with following species.

SPECIES 3

Mexico: Chiapas; Lagunas de Montebello, near Comitan, 14–17.viii.1969, S. & J. Peck, 4500′ elev., tropical montane forest, 4 in trap. Guatemala: Alta Verapaz; Patal, 5 km S Tactic, 24–27.viii.1969, S. & J. Peck, 4500′ elev., cloud forest, 1 in trap, 1 on dead millipede.

SPECIES 4

Mexico: Veracruz; Cordoba, 4–6.viii.1969, S. & J. Peck, tropical evergreen forest, 1 in trap. Fortin, 5–8.viii.1969, S. & J. Peck, tropical evergreen forest, canyon Rio Metlac, 2 in trap. Huatusco (1.2 mi. S), 1344 m elev., 5–8.viii.1969, S. & J. Peck, cloud forest, 5 in trap. Hidalgo; 10 mi. SW Jacala, 1–3.viii.1960, H. Howden, 1 in malt trap, CNCI.

SPECIES 5

Mexico: Querétaro; 25 mi. E Landa de Matamoros, 5000′ elev., 14–17.vii.1969, S. & J. Peck, *Liquidambar* forest, 1 in trap. Pueblo; Nuevo Necaxa, 25–28.vii.1969, S. & J. Peck, 1200 m, sycamore forest, 1 in malt trap.

SPECIES 6

Mexico: Tamaulipas; Gómez Farías, Rancho del Cielo, 5000′, Cueva de la Mina, 1.vii.1969, S. & J. Peck, 2 in debris at cave entrance. 3700′, 1–4.vii.1969, S. & J. Peck, cloud forest, 2 in trap.

SPECIES 7

Mexico: Oaxaca; Huatla, 1700 m, 9.iv.1969, forest litter, K. Kowalski leg., 7 (PISZ).

INCERTAE SEDIS

The following three species are known only from male material and cannot be reasonably placed in species groups based upon female characters. Two of the species are new, but I believe they are distinct enough that no future problems will be encountered in recognizing them.

Ptomaphagus championi Jeannel
Figure 133; Map 13

Ptomaphagus consobrinus, Matthews, 1888: 100.
Ptomaphagus (*Adelops*) *championi* Jeannel 1936: 93. Type male in British Museum (Natural History), seen. Type locality: Guatemala, in mountains near Santa Cruz del Quiché. Jeannel, 1949: 98 (systematics).

Diagnosis. Known only from the type, from Guatemala. Its eyes are reduced, the antennal segments II and III are twice as long as wide, and the pronotum is widest at the base.

Description. The description is based

upon those of Matthews (1888) and Jeannel (1936) as well as my inspection of the type (which exists in a fragmented condition, missing the prothorax, most of the head, and the abdomen). Length 2.50 mm. Width at elytral base 1.2 mm. Color medium brown (castaneous); clothed with long sparse pubesence. Head with eyes rather small, not prominent; antennae (Fig. 133) moderate, first two segments lighter color, segments II and III twice as long as wide, IV and V a little longer than wide, VI and VII only slightly wider than long, VIII 3 times as wide as long, IX and X transverse. Pronotum widest at base, sides slightly curved, hind angles acute, striae distinct. Elytra rather attenuated posteriorly, scarcely broader but twice longer than the head and thorax, widest at base; sides scarcely rounded; external apical angles rounded; apex obtuse; striae oblique. Winged. Legs moderately elongate. Mesosternal carina prominent, notch large, quadrangular. Genitalia unknown.

Notes on the type. The type specimen does not exist in sufficiently good condition to clearly characterize the species. The prothorax is missing, but one prothoracic leg and all other legs are present. The head is partially missing so that I cannot measure the eye size, but both antennae are present and glued to the mounting card. A bit of wing is visible beneath the elytra but the elytra were not relaxed and lifted to accurately observe the wing condition. The abdomen is missing, so the genitalia are unavailable.

Distribution and ecology. The type was taken near Santa Cruz del Quiché (Dept. of El Quiché) in the Quiché mountains (a western part of the Sierra de Chuacús) at an elevation of from 7–9000 feet. No other data is available. The Central America (Coban quadrangle) map 1:250,000 shows these mountains with a summit at 2607 m with a road (from Santa Cruz to Santa Rosa Chujuyub) going to 2558 meters. This is the logical place to look for forests in the future in an attempt to secure the species. It may exist, however, at other localities, at lower elevations. In my 1969 collecting in Guatemala I was not able to collect in the Chuacús Mountains. I do not believe any of the three specimens I collected in Guatemalan forests in the Dept. of Alta Verapaz represent this species.

Ptomaphagus meximontanus new species
Figures 75, 76; Map 13

Holotype male in MCZ (no. 31959). Type locality: Mexico; Querétaro, 9 mi. NW Pinal de Amoles, 4 mi. NE Rio Blanco (17 mi. W Jalpan). Type data: 9.vii.1967; J. Reddell, J. Fish, B. Russell; 9000′ elev., broad forested draw. Paratype (SBP) data: one male; Mexico; Querétaro, Tejamanil (3.0 mi. SW of Pinal de Amoles); 9.viii.1966, J. Reddell, J. Fish, D. McKenzie, 3000 m elev., under rock.

Diagnosis. The species is characterized by its winglessness, its eyes whose width is equal to the width of the space between their inner margin and the antennal insertion, and its habitat in high montane Mexican forests.

Description. Length 2.7 mm. Width 1.2 mm. Form elongate oval. Color dark brown. Head shining, with a few punctures; eyes reduced, pigmented, with about 45 facets, their horizontal width less than vertical width, horizontal diameter equal to the space between their anterior margin and the antennal socket. Antennae normal, medium length, flattened; segments II and III equal; IV–VI sequentially shorter; VI transverse. Pronotum widest at middle, 1.47 times as wide at base as long, narrowing slightly at base; striae distinct. Elytra slightly wider 1/4 behind base; 1.25 times as long as wide; external apical angles rounded; apex obliquely truncate; sutural angle rounded in males. Wings absent. Mesosternal carina low, notch small. Legs normal; mesotibiae bent outward, metatibiae slightly bent inward. Aedeagus (Fig. 75) slightly curved, narrowing slightly to apex, tip thin; in dorsal view (Fig. 76) tip wide. Spiculum gastrale normal, slightly over half enclosed by genital plates, which have slight concavity on edges forming border of genital aperture. Spermatheca unknown.

Variation. No variation noted.

Etymology. The name is a noun in apposition referring to the known habitat of the species, high montane forests in the Mexican state of Querétaro.

Field notes. The known habitat data is given for the specimens. In 1969 and 1971 I briefly and unsuccessfully searched for the species at Tejamanil. The forests are of pine and oak on limestone.

Distribution and evolution. The species is known only from two specimens taken in the same high forested mountains at Pinal de Amoles. The reduced eyes and wingless condition suggest that the species has limited dispersal capabilities and may be limited to these particular mountains in western Querétaro.

The male genital structures and the beetles' size suggest membership in the *consobrinus* species-group. With no known females this can not now be certain. It will be of evolutionary interest to learn if this montane edaphophile is a relict species of the *hirtus* or *consobrinus* groups, which do not now inhabit eastern Mexico. Its size and shape, the male genital structures, and the small eye suggest relationship to *californicus*. The eye of *californicus* is also smaller than normal in the genus, but is still larger and more distinctly faceted than in *meximontanus*.

Ptomaphagus talamanca new species
Figures 74, 132; Map 13

Holotype male in CNHM. Type locality: Panama, Chiriquí Province, Finca Lerida, near Boquete. Type data: trail below "Casita Alta," alt. 68–6900 ft., 18 March 1959. G. A. Solem leg.

Diagnosis. This is the only *Ptomaphagus* known from south of Guatemala except for the *Ptomaphagus* (*Tupania*) of Brazil. It is distinguished by its elongate antennae, with only segment VIII being wider than long, and the eye whose horizontal diameter equals the space between the eye and the antennal insertion. The antennal segments are broader than in the cave-inhabiting *giaquintoi* of Guatemala.

Description. Based solely on the unique holotype. Length 3.6 mm. Width 1.9 mm. Form elongate oval. Color dark brown. Head finely sparsely punctured. Eyes reduced, faceted, pigmented; head width across eye from margin to antennal insertion 2.0 times eye width. Antennae (Fig. 132) elongate, flattened and stout; reaching into first quarter of elytra when laid back; all segments but VIII longer than broad; II, III, and IV twice as long as broad; III longer than II and IV; VII elongate conical, 3/4 as wide as long; VIII 1.25 times as wide as long; IX and X 1.1 times as long as wide. Pronotum 1.2 mm long, 1.85 mm wide; widest 1/3 before base; sides arcing weakly behind to acute hind angles; hind margin straight; striae distinct. Elytra narrower than pronotum, widest 1/3 behind base; 2.4 mm long; 1.75 mm wide at base; external apical angle rounded; apex truncate; sutural angle slightly rounded; striae strong, weakly oblique to suture. Wings absent, elytra fused. Mesosternal carina low, notch distinct. Legs with only mesotibiae curved. Aedeagus (Fig. 74) long, slightly curved, blunt at tip; in dorsal view tip very blunt, rounded. Spiculum gastrale long and thin, half enclosed by genital plates, which are somewhat produced anteriorly. Spermatheca unknown.

Etymology. The name *talamanca* is used as a noun in apposition. It refers to the mountain range of western Panama and southeastern Costa Rica in which the beetle was collected.

Distribution. The species is known only from the type locality. It is probably a forest litter inhabitant of high and medium elevations in the Talamanca mountain range.

Distributional comments. Although the species is now known from only one specimen, it seems useful to describe it at this time. The collection serves to partially fill the distributional gap existing between the *Ptomaphagus* of Guatemala and those of northern and southern Brazil.

PHYLOGENY AND ZOOGEOGRAPHY

As is true in most other groups of terrestrial invertebrates, consideration of the phylogeny and distributional history of the Ptomaphagini must be based upon living species because of a very limited or nonexistent fossil record. I know of only one reported fossil for this group of beetles, *Ptomaphagus germari* Schlechtendal (1888) from the Baltic Amber.

For purposes of historical perspective, the ideas of Jeannel on the evolution and distribution of the tribes will be presented first. I will then present the contrasting evolutionary scheme of Szymczakowski, with which I agree, and will add new details and interpretations on the history of the genera. I will then present my own ideas of the evolutionary and distributional history of the New World species of *Ptomaphagus*.

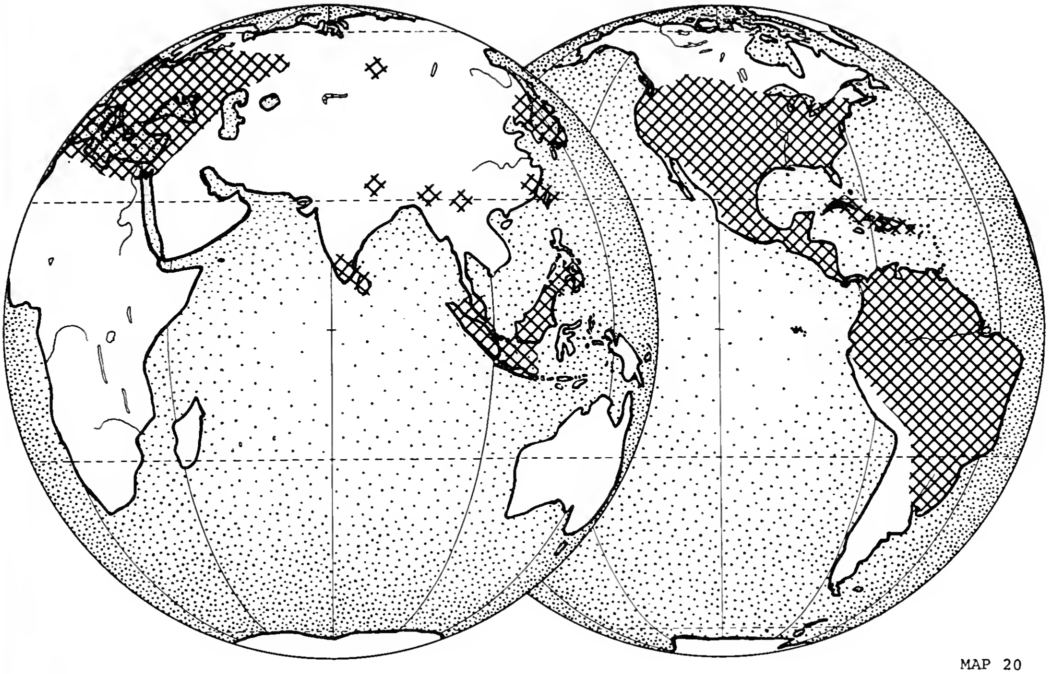
The ideas of Jeannel trace (with modifications) through quite a series of papers (1922: 35; 1936; 1942: 28; 1961: 55; 1964). Jeannel's line of reasoning sprang from a belief in the truth of three major initial assumptions. 1) The origin of the tribe was in tropical America, because this is the region of greatest present diversity. 2) He utilized the Wegenerian concepts of continental drift. I am not here arguing for or against drift, but I believe simply that it is not necessary for understanding the history of the Ptomaphagini. 3) The last assumption, with which I agree, has to do with the evolutionary modification of the morphology of the male aedeagus of members of the tribe. It is as follows: In the tribe Ptomaphagini there has been selection for a migration of the position of the apical genital orifice, the orifice through which the internal sac is everted at the tip of the aedeagus. The tendency is for the orifice to shift from the ventral and median (primitive) position to the dorsal surface of the aedeagus. Jeannel gives no explanation for the selective or adaptive advantage of a dorsal genital orifice, and I can offer none. When this migration has occurred, it has done so by cutting across either the right side or the left side of the aedeagus.

The rest of the story, as interpreted by Jeannel, is found in his most recent papers (1961: 55, 1964), and the following is a summary, in which I use my supra-generic categories.

The primitive ancestors of the Ptomaphagini arose on the Gondwana land mass in the Jurassic. By the Cretaceous, these ancestral populations were displaced to two extremities of Gondwana by "centrifugal segregation." One displaced population would come to occupy those areas that are today the Indo-Malayan region. These species possessed an aedeagus having a tendency to shift the apical orifice so that it cut across the right side of the organ (dextrogyral). This dextrogyral group was to become the subtribe Ptomaphaginina and the genus *Ptomaphaginus*.

On the other side of the ancient Jurassic continent other lines differentiated in the Brazilian massif, which by the Cretaceous was thought to stretch to the north through the lands of Archiguyane and the lands of the Caribbean. In the Cretaceous stocks in South America, the migration of the orifice was effected by cutting across the left side of the aedeagus (sinistrogyral). These sinistrogyral stocks established the subtribe Ptomaphagina and were predecessors of the genus *Adelopsis*.

Jeannel continues by thinking that throughout the Cretaceous, the ancestors of the genus *Adelopsis* experienced many attempts at a successful sinistrogyral migration of the copulatory orifice. In some, the orifice migration occurred near the apex, and often resulted in hyperplastic



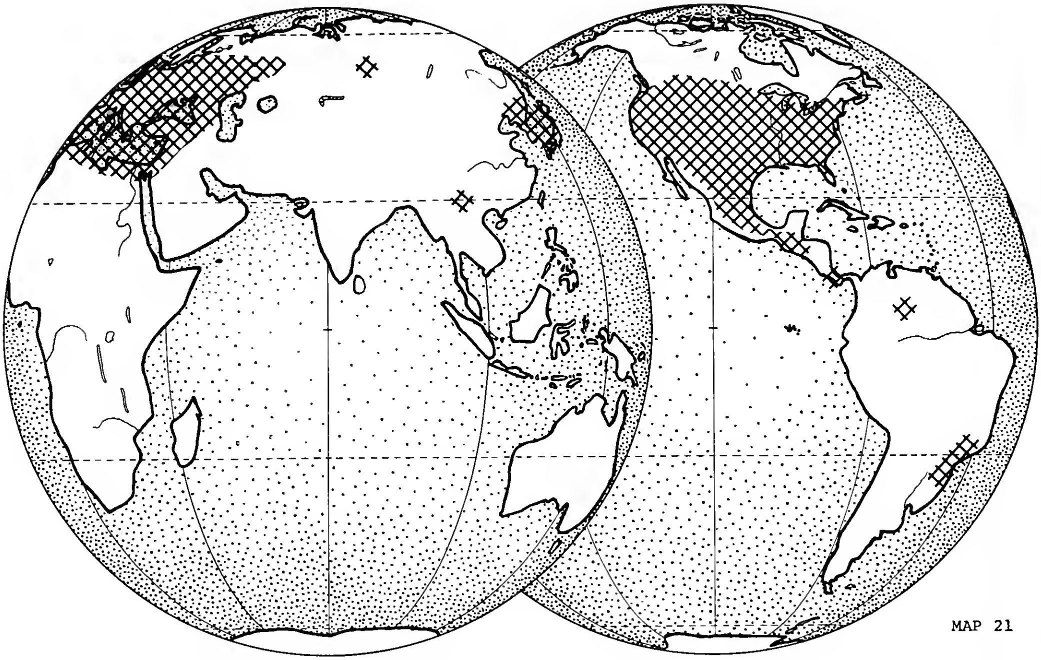
Map 20. Present distribution of the tribe Ptomaphagini.

and monstrous morphologies. In others, the orifice migration passed far from the apex. From these there evolved a new type of sinistrogyral aedeagus which was "successful and harmonious." This later successful stock migrated northward during the Eocene into North America, and from there eventually into all of the Palaearctic region via Europe. The ancestors that successfully distributed themselves throughout the Holarctic region were to become the genus *Ptomaphagus*.

The myrmecophilous *Synaulus* of North Africa are descendants from the first *Ptomaphagus* immigrants to Europe (in the Eocene?, Jeannel, 1922). This earlier paper is also interesting for comparing Jeannel's earliest and latest ideas on dispersal routes. In 1922 he believed that the European *Ptomaphagus* were directly descendant from an ancestral migration of *Adelopsis* from South America via a trans-Atlantic land bridge. The European *Ptomaphagus* then recrossed the Atlantic into North America, giving rise to the subgenus *Adelops* and the cave-inhabiting species.

With Jeannel's earlier concept of continental drift, he believed it was not unreasonable that two trans-Atlantic crossings were more probable than one crossing of the water gap, which is wider in the drift concepts, between North and South America.

In support of this, there are now plausible biogeographic arguments that can be developed to support the hypothesis that eastern North America and Europe were joined early in Tertiary time by a land connection extending across the North Atlantic through Greenland, Iceland, the Faeroes, and the British Isles (Löve and Löve, 1963; Kurten, 1966). The plausibility of these arguments are greatly strengthened by the recent application of paleomagnetic data to demonstrate that the ocean floor



Map 21. Present distribution of the genus *Ptomaphagus*.

has apparently been actively spreading, widening the gap between the continents, for at least several million years (Vine, 1966). However, even though the above considerations allow the possibility of trans-Atlantic connections, faunal studies (Lindroth, 1957) have concluded that the land connections can not have operated with any impact on the fauna of North America and Europe after the early Tertiary.

The zoogeography of the higher groups of the Catopinae as viewed by Szymczakowski (1964) is more reasonable than that of Jeannel. The movements of the beetles are related to geological and paleoclimatic events that have a demonstrable basis in fact. Two later papers (Szymczakowski, 1968; and Peck, 1970a) add more data, which, when considered with the data in this paper, lead me to propose the following history of the Ptomaphagini and its included groups. I think this history accounts for the present facts of distribution of the tribe (Map 20) and the genus (Map 21) when considered in conjunction with the phylogeny proposed in Figure 212.

History of Ptomaphagini. The following speculations on generic divergence are presented in Figure 212. I use the clues and their interpretations suggested by Darlington (1957: 31) as an operational basis for my model.

The tribe originated in the Americas in subtropical or mildly seasonal warm temperate forests. This climatic region presently is the area with the highest numbers and diversity of genera and species. This broad American region presently contains four genera in the two subtribes, compared with two genera in one tribe in the Oriental Region and two genera in one tribe in the Palearctic Region. The nearest related tribe is the Eucatopini, containing only one genus, in which all species are Neotropical. The greatest present generic and specific diversity in

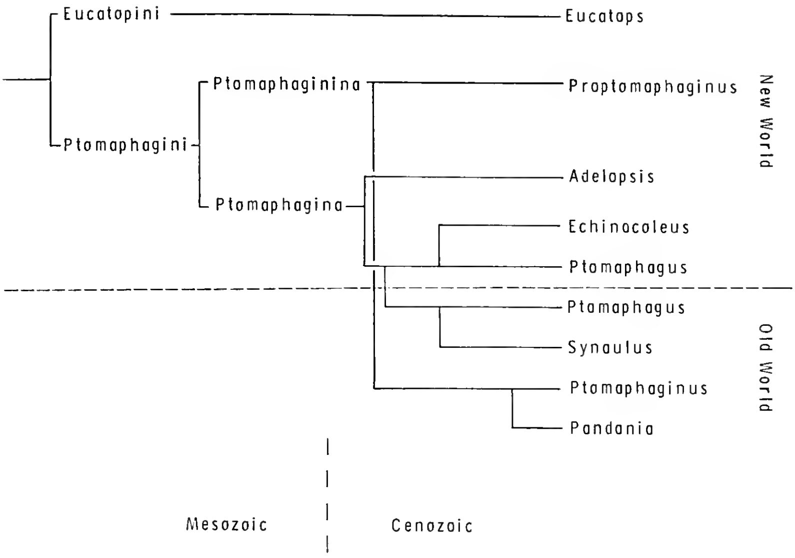


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Figure 212. Hypothetical phylogenetic diagram of generic diversification in the tribe Ptomphogini. Degree of generic difference not inferred.

the Americas is in the broad climatic band where north warm temperate and tropical environments merge. This region, grouped as North and Central America including the West Indies, contains four genera, while South America contains only two genera in the tribe. In the past, tropical and subtropical climates existed over much of the North and Central American land masses. These northern lands, rather than South America, were probably the major theaters of early diversification in the Ptomaphagini.

The proto-Ptomaphagini were derived as a line of specialization from the proto-Eucatopini. The aedeagus of the proto-Ptomaphagini became thinner, more elongate and tubular, with the basal blade becoming reduced and fused to the aedeagus.

Within the North or Central American tropics or subtropics, two sublines diverged, perhaps in the late Mesozoic or early Tertiary. The first line, the proto-Ptomaphaginina continued to retain the primitive character of full protibial spination found in Eucatopini. Within the proto-Ptomaphaginina the tendency became established for the migration of the genital orifice to cut the right side of the aedeagus. The second line, the proto-Ptomaphagina, lost the characters of spination on the outer protibial margin. Within this group the tendency became established for the migration of the genital orifice to cut the left side of the aedeagus.

The proto-Ptomaphaginina. While either tropical or subtropical forest conditions prevailed in the early Tertiary, some proto-Ptomaphaginina migrated and spread into the Oriental region, most likely via the continental connection of Siberia and Alaska. These migrant proto-Ptomaphaginina became the genus *Ptomaphaginus*, which spread and speciated moderately throughout the Oriental region. It vanished from more northerly lands in the Old and New Worlds, and a minor lineage led to the development of the monotypic genus *Pandania*. The proto-Ptomaphaginina of the New World undoubtedly were once widespread. Their descendants, in the genus *Proptomaphaginus*, have since become restricted to islands of the West Indies, with only one known species surviving on the mainland (an undescribed cave or soil inhabitant from Mexico). This genus lost the widespread catopine sexual characteristic of dilated protarsi in the males before occupying the West Indies.

The proto-Ptomaphagina. This group was also spreading throughout the tropical or subtropical forests of the early Tertiary in the New World. Selection was acting to perfect the shift of the genital orifice to the left side of the aedeagus. One subgroup, the proto-*Adelopsis* (the *Adelopsis* of today) spread through Central and much of North and South America. They have descended to today with either little shift in the genital orifice, or with a shift on the left side but at the very apex of the aedeagus. This shift at the aedeagal apex has led to almost monstrous complexities in the aedeagal tip in some species. Jeannel (1964) interpreted four species with a median orifice (that is, showing little or no shift in the aedeagus orifice to the left) as remnants of a primitive lineage. These four species have a collective distributional center in Colombia and Venezuela, in the northern Andes. Jeannel thought these were evolutionary relicts, which were isolated in their distributional center from Central and South America by Paleocene seaways. Range expansions into South America were possible with the uplift of the Bolivar geosyncline in the late Oligocene. Jeannel did not know of Central American *Adelopsis* and so did not consider when they may have moved out of northern South America into Central America. If proto-*Adelopsis* arose on Central or North American land masses as I suggest, they moved into South America long enough ago to acquire the high amount of diversity the genus exhibits in South America. South American occupation may have been in the Cretaceous as Jeannel suggests, or even as late as the Tertiary. If the latter, dispersal was across one or more barriers of sea water, because there is no evidence to indicate the presence of continuous land connections at this time (Maldonado-Koerdell, 1964).

*The proto-*Ptomaphagus. In the other subgroup of the proto-Ptomaphagina, the proto-*Ptomaphagus,* the orifice shift occurred on the left side of the aedeagus at a distance from the aedeagal tip. This group apparently acquired a dominance (as Jeannel suggested) that allowed it to spread throughout South and North America, and into the Palearctic Region.

Although Jeannel favored a trans-Atlantic crossing, I believe that the shallow seas separating Alaska and Siberia in and near the Bering Strait seem to be a more likely site for Eurasian-North American land connections. It is well documented (Hopkins, 1967) that the Bering Strait region lay above sealevel throughout most of the early and middle Tertiary, and was a region without pronounced climatic zonation. As late as from the late Oligocene to the middle Miocene Beringia lay at the apex of a continuous region of a broad-leaf deciduous (mixed mesophytic) forest encircling the North Pacific Ocean from Japan through Alaska into the northwestern United States. Paleobotanical evidence suggests that a climatic decline in late Miocene broke this forest band. Climatic factors and the opening of the Bering Strait in the late Miocene led to this disjunction and it has continued to the present (Wolfe and Leopold, 1967). However, fossil mammal data suggests that late Tertiary conditions may have been suitable for *Ptomaphagus* movements. Pliocene (Hemphillian) land-bridge conditions were warm temperate, humid, and forested. Early Pleistocene (Blancan) times were temperate, humid, and forested, with some grasslands present. Middle Pleistocene interglacial (Irvingtonian) conditions were an even division between temperate open grasslands and forest (Repenning, 1967).

In summary, conditions were seemingly suitable on many occasions for the exchange of *Ptomaphagus* between North America and Eurasia. If more than one movement did occur is not now evident and will not be so until the Eurasian *Ptomaphagus* are reviewed. It is noteworthy that I have interpreted the movement as being from North America into Eurasia. This is contrary to the general zoogeographic observation that net faunal movements have been from Eurasia into North America.

No matter what else happened, the presence of *Ptomaphagus germari* in Baltic Amber, if correctly determined, indicates that the genus had differentiated and reached northwestern Europe by the Oligocene. This is the only nonspeculative statement that I can make in the entire model of the history of the tribe.

There is only one other paleontologically based statement that can be made about evolution and differentiation in the entire subfamily Catopinae. It is that another Baltic Amber catopid is indistinguishable from *Nemadus colonoides,* which today inhabits much of Europe (Jeannel, 1942: 192). The genus today has only this and one other (Japan) Old World species. Elsewhere, only eleven species are known from the United States and Canada.

The genus *Synaulus* of North Africa may have originated with a middle Tertiary entry of a European *Ptomaphagus* into the habitat of ant nests. Another invasion of ant nests by an early *Ptomaphagus* stock occurred in North America and led to the development of the genus *Echinocoleus.*

The subgenera. The Palaearctic *Ptomaphagus* have been isolated from those of the Nearctic since the time when the Bering Bridge became unsuitable for *Ptomaphagus* dispersal. This may have been in the late Miocene as indicated above. Under present climatic conditions, the northern limits of the range of the genus lie far to the south of Beringia (Map 21). Past Pleistocene interglacials may or may not have been favorable for *Ptomaphagus* migrations between the two regions, depending on the suitability and continuity of forests. Any conclusions about the relationships of Old and New World *Ptomaphagus* can not now be firmly made. A comparative study of Palearctic *Ptomaphagus* is needed.

At present it seems that differentiation in the Palearctic Region has occurred to such an extent that subgeneric separation is possible, but with difficulty. The Eurasian group differentiated into the subgenus *Ptomaphagus* after its isolation from North America. The ancestral stock that invaded Eurasia is indicated below. No evidence is yet at hand to indicate either more than one dispersal into Eurasia or any reinvasion into North America. The difficulty of distinguishing the Eurasian subgenus *Ptomaphagus* from the North American subgenus *Adelops* may indicate a relative recency of separation. The distinct European subgenus *Merodiscus,* now restricted to the Balkans, probably came from Eurasian *Ptomaphagus* before they themselves had been separated from the New World *Ptomaphagus.*

In North, South, and Central America two subgenera are recognized. One of these, *Adelops,* is probably the ancestor of the other three subgenera. *Adelops* has three species groups, each with a more complex spermatheca. I interpret the increasing complexity as an evolutionary trend from primitive to advanced condition. The most advanced species group of *Adelops* is the *cavernicola* group, which today is most abundant in Mexico. The similarity of the spermatheca of the Eurasian *Ptomaphagus* (the few species I have examined) to *cavernicola*-group *Adelops* suggests that *cavernicola*-group *Adelops* were ancestral to the stocks that migrated into Eurasia and differentiated into the subgenera *Ptomaphagus* and *Merodiscus.* The spermathecal similarity between *cavernicola*-group *Adelops* and the Neotropical subgenus *Tupania* (of Mexico and Brazil) similarly suggests that *Tupania* originated from this group of *Adelops.*

Species groups. I have based my species

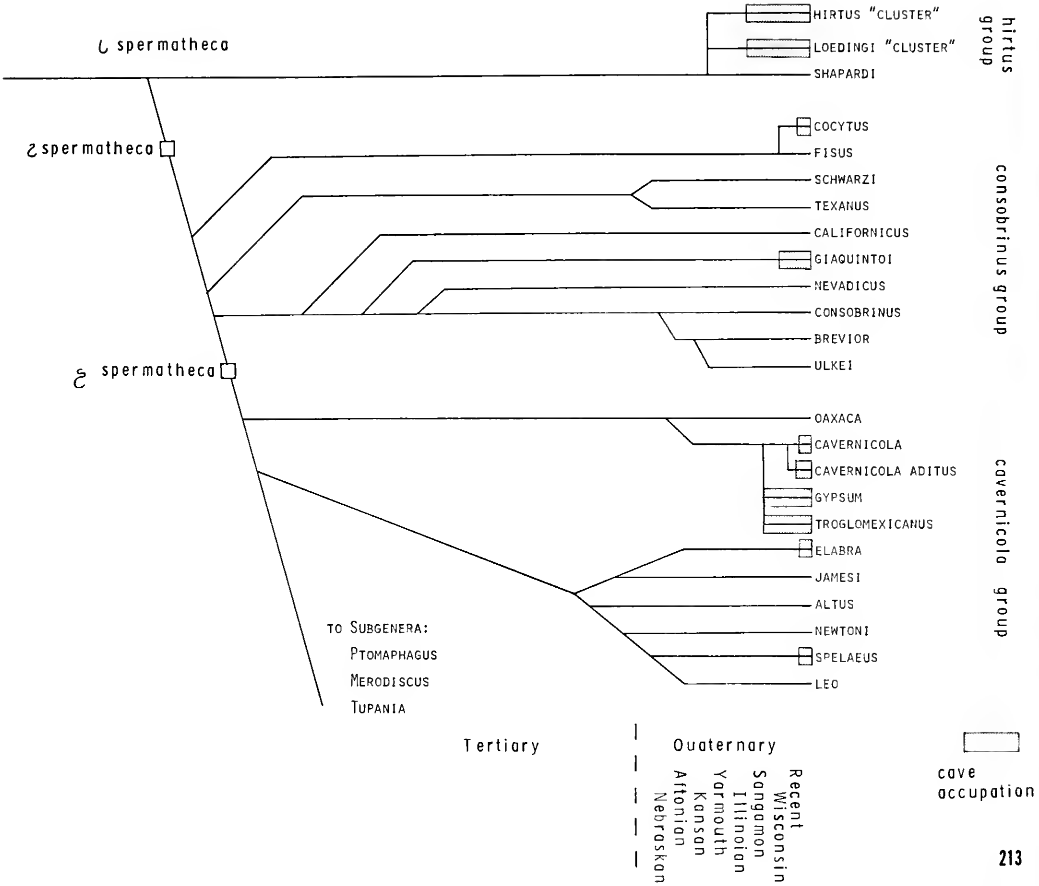

Figure 213. Hypothetical phylogenetic diagram of specific diversification in *Ptomaphagus* (*Adelops*). Degree of specific difference not inferred. Rates of divergence in Tertiary not inferred.

groups in the subgenus *Adelops* upon the female spermatheca, their characters and complexities. This is the only character I found that provided me with data I could use in interpreting a phylogeny for major events within the subgenus. In the discussion to follow only North and Central American events will be considered.

I want to caution here against a too ready acceptance of the chronologic implications of the following discussion. Where I suggest, for instance, that two related events occurred in the Illinoian and Wisconsin respectively, more definitely "earlier" and "later" are being indicated. This is based upon the assumption that greater differences take a longer time to develop than lesser ones. I offer definite times only as appealing possibilities that seem to be logically consistent within an overall framework of combinations of fact, theory, and circumstantial evidence. Figure 213 presents a summary of the following discussion.

I believe the *hirtus* group to be the most primitive, and I base this belief solely upon the observation that within this group the female spermatheca is the most simple, and is closest in form to the other genera in the Ptomaphagina (*Echinocoleus* and *Adelopsis*). The *hirtus* group is hence the oldest of the species groups of *Adelops*, and I interpret it as being the oldest in the entire genus. At some time, one line of epigean ancestors in the *hirtus* group underwent extreme morphological specialization after occupying deep (montane) forest litter environments. This line acquired behavioral, physiological, and morphological characteristics frequently found in montane soil beetles (edaphophiles). Some of the latter are reduction in pigmentation and cuticle thickness, loss of wings, and reduction of eyes. Selection for these are considered by Darlington (1943, 1970). This line is the only one of the *hirtus* group that has survived. The original epigean species and perhaps several edaphophilic species became extinct. The epigean extinctions may have been in the Tertiary and the edaphophilic extinctions during the warm-dry interglacials of the Pleistocene. Only one edaphophile in the group (*shapardi*) exists today. At a time in the Pleistocene, I suggest the Yarmouth interglacial, two edaphophilic species entered into cave habitats where they underwent further selective change. These have survived until today as troglobites. This cave occupation will be considered below. No species are now known that can be considered close to the ancestral species from which the *hirtus*-group troglobites descended. The possibility exists that continued searching in the southern Appalachian Mountains may uncover an extant edaphophilic species whose ancestors gave rise to the troglobites in the Pleistocene. This would parallel the recent discovery of an epigean *Pseudanophthalmus* carabid which led to a strengthening of conclusions regarding some of the cave species (Barr, 1967b).

Probably early in the Tertiary the *consobrinus* group arose with a spermatheca of intermediate complexity from the *hirtus* group (Fig. 213). The *consobrinus* group spread over North and Central America (or at least into Guatemala), and may have migrated into Eurasia (judging only from the external similarity of *brevior* and *consobrinus* to some European species). The group at least spread over all of the range of the older *hirtus* group and may have been instrumental in the extinction of *hirtus*-group species from the epigean habitats that they undoubtedly occupied. Speciation and range adjustments in the group were undoubtedly intensified during the increased continental drying in the Pliocene and the climatic fluctuations of the Pleistocene. Probably during the drying some species in the west took up their association with various other animals, at first using the nests and burrows of these animals in a facultative way as favorable microclimatic retreats. The group became dominant in America north of Mexico and still is so. Perhaps as late as the Pleistocene it was eliminated from Mexico and Central America except for *nevadicus* and *fisus* in arid western Mexico, and for *giaquintoi*. This last species first persisted in the mid-montane forests of Guatemala, and was eventually restricted to caves in the limestone mountains of eastern Guatemala. The elimination of *consobrinus*-group species from mesic forests in Mexico and Guatemala was possibly related to the rise and spread of the third species group in this region.

The third group, the *cavernicola* group, with the most complex spermatheca evolved from the *consobrinus* group, perhaps in the United States and perhaps in the early Tertiary (Fig. 213). I have already suggested that the other three subgenera of *Ptomaphagus* arose from this group. If this is true, the origin, evolution, and dispersal occurred early enough in the Tertiary to allow their occupation of the Baltic Amber forests. Lately, one species, *cavernicola*, under the opportunities offered by fluctuating Pleistocene (Wisconsin glacial) climates, extended its range from Mexico into and through much of the eastern and southern United States.

Speciation. My attitudes on insect species in the Pleistocene are conservative. They are mostly based upon recent liter-

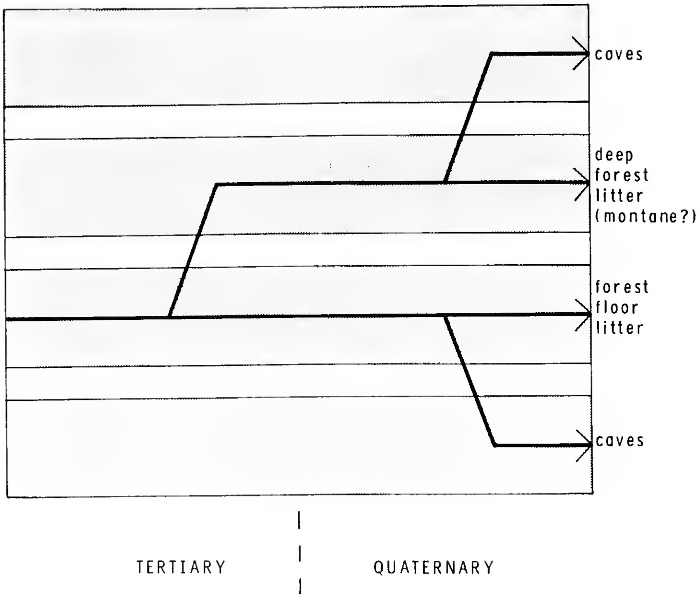

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Figure 214. Hypothetical shifts in adaptive zones in the evolution of *Adelops,* demonstrating the two pathways to cave occupation and specialization. From the ancestral forest floor litter habitat early *hirtus* group ancestors became specialized to deep forest litter, probably in montane situations. Specializations to the new zone resulted in loss of wings and a reduction in the eyes. The morphological and ecological specializations for deep montane litter preadapted the beetles for survival in caves. The deep litter species lived in the cave regions during the Illinoian glaciation. The caves became refuges during the increasing heat and aridity of the Sangamon interglacial. Speciation in the cave populations followed the Sangamon extinction of local epigean populations. The second route of cave occupation (lower zone) involved only ecologically preadapted ancestors in the *consobrinus* and *cavernicola* groups. This lower zone also includes cavelike situations such as mammal burrows.

ature on the problem such as H. H. Ross (1965), Frey (1965), Howden (1969), Coope (1970) and other papers referred to in these works. Generally, these authors agree that insect speciation in the Pleistocene has been of limited extent, except where a combination of unusual ecological requirements and situations has allowed the splitting of populations into smaller isolated units as a consequence of climatic fluctuations. The invasion of caves by *Ptomaphagus* has been one of these unusual situations and has resulted in considerable speciation. There is little that suggests to me that speciation occurred in epigean *Ptomaphagus* in the Pleistocene, but I do accept its possibility, especially for the difficult complex of species in the *cavernicola* group in Mexico.

Speciation in the hirtus *group.* In this group, no wide-ranging, epigean species have survived. The only nontroglibitic species is *shapardi,* a small-eyed, wingless, soil inhabitant of the southwestern Ozark region. This species can be taken as representing the level of morphological specialization possessed by at least two other edaphophilic species of the group in the Tertiary. During the Pleistocene, or before, all epigean species became extinct, one edaphophile survived as such, and two others became cave inhabitants. The route of cave occupation, from preadapted edaphophilic ancestors, under the influence of climatic changes in the Pleistocene, is adequately presented by Barr (1967a, 1968). Figure 214 shows the proposed shifts in adaptive zones experienced by the

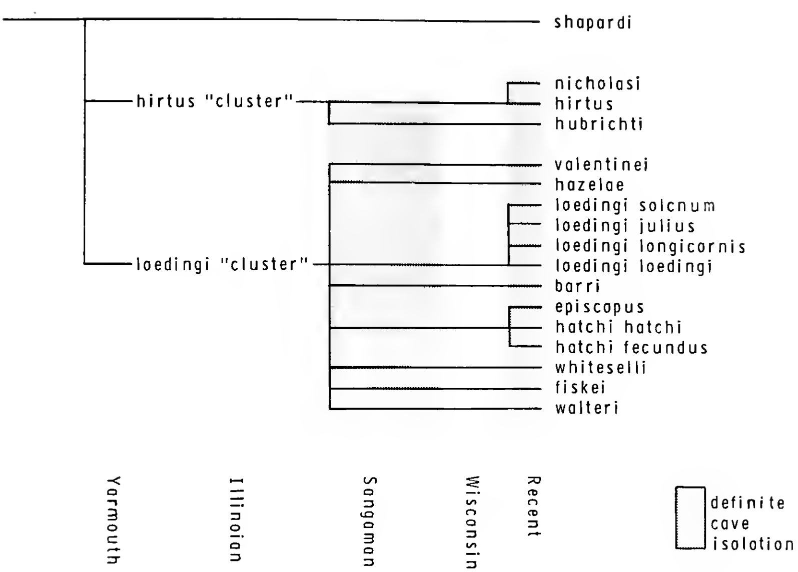

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Figure 215. Hypothetical diagram of specific diversification in the *hirtus* group of the subgenus *Adelops*. See text for explanation of possible periods of alternoting cave restriction and overland dispersal. Degree of specific difference not inferred.

hirtus group, from the primitive zone as a general forest litter inhabitant into an obligate inhabitant of the zone of deep (montane?) forest litter. As they became specialized for this second adaptive zone, *hirtus*-group members became preadapted (in the sense of Mayr, 1963: 593) for the cave occupation which occurred later in the Pleistocene, just as Barr (1965, 1967b) proposed for the cave occupation of trechine carabid beetles.

When did the cave occupation occur? Only three observations lead me to believe that the *hirtus* group did not invade caves before or after being forced to by the drying-warming trends of the Sangamon interglacial. All the cave species have eye remnants. I think these would have disappeared if the cave occupation had been in the earlier Yarmouth or Aftonian interglacials. Secondly, I would expect surviving montane populations of ancestral descendants if the cave occupation had been early in the present interglacial, but none have been found. Lastly, range sympatry does not exist and it might be expected to occur from additional dispersal opportunities if the initial cave invasion was in the Yarmouth.

Within the *hirtus* group, there are two distinct clusters of troglobitic species (Fig. 215). One, the *hirtus* cluster, is composed of *nicholasi, hirtus,* and *hubrichti* from Illinois, Kentucky, and Tennessee. The second group of troglobites, the *loedingi* cluster, is composed of the remaining species in Tennessee, Alabama, and Georgia. I think these species clusters represent cave occupation by two separate ancestral species. The ancestor of the *hirtus* cluster was more northern in distribution than the ancestor of the *loedingi* cluster.

The former ranges of the ancestral species of the *hirtus* and *loedingi* clusters is a problem. It might be expected that they inhabited the higher forests of the Appalachians, and were able to extend their ranges over the cave-containing lowlands during the Illinoian glacial maximum.

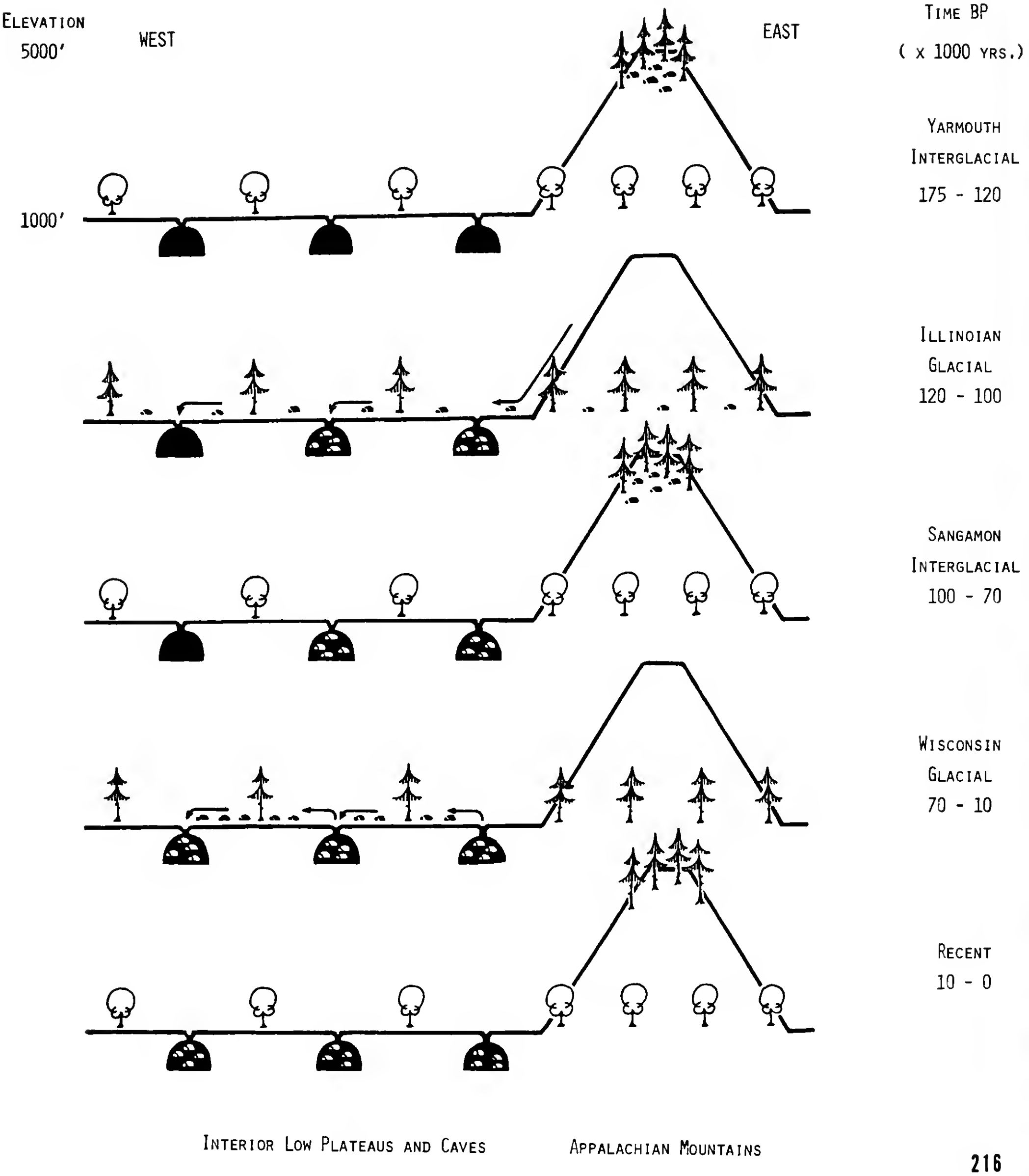

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Figure 216. Pictorial diagram of *Adelops* populations movements in the southeastern United States in response to climatic changes in the Pleistocene. This model uses fluctuating Pleistocene climates as a mechanism to introduce the preadapted montane ancestors to cave areas and caves and then to isolate them there. The isolation permitted the development of troglobitic species, which seemingly later underwent range adjustments by overland dispersal in the Wisconsin. Further explanation in text and with Fig. 214. Application of names is a fit of the model to the classical divisions of the continental North American Pleistocene. Times of glacials and interglacials from Emiliani (1971), based on oceanic sediments. This application is controversial, and simplistic. Its effect here is to perhaps make too rapid the speciational and adaptational events. Biologists often do not appreciate the fact that, for purposes of interpreting evolutionary events and biogeography in a framework of Pleistocene history, the use of a time scale matched with climatic conditions and classical Pleistocene division names preceding 150,000 years BP is presently very questionable (see Broecker, 1965).

But this seems less likely when compared with the distribution of the carabid trechine *Pseudanophthalmus* beetles. These beetles probably did move down from higher elevations in the glacials and did occupy the caves at the early stages of the interglacials (Barr, 1967a, 1968). But these carabids occupied caves not only in the flat limestones of Illinois, Kentucky, Tennessee, Alabama, and Georgia where cave *Adelops* occur, but also the flat limestones of Ohio and Indiana, and in even greater regions of Kentucky, Tennessee, and Alabama where cave *Adelops* do not occur. They also occupied the folded-faulted limestones of the Appalachian Valley of Alabama, Tennessee, Virginia, and West Virginia, where troglobitic *Adelops* do not occur. This great difference of geographical ranges of cave occupation between the two genera must lie in one or several of the following comparative reasons. 1) The cave-occupying ancestors of the *hirtus* group came from a different geographic area, perhaps from west of the Appalachians during the Illinoian glaciation. 2) There was a great dissimilarity in the overland dispersal abilities of the ancestral beetles. 3) If ancestral *hirtus*-group species did occupy caves in a greater geographic area than they now occupy, they have now vanished (especially in the folded-faulted limestones of the Appalachian Valley) because their ecological requirements and/or population structure were unsuitable and insufficiently adaptable. This last seems to me to be less likely than the first two.

Distributional events in the *loedingi* cluster were undoubtedly complex, and have led to the complicated speciation and distribution now found in Tennessee, Alabama, and Georgia, while the *hirtus*-group events were less complex and led to the speciation and distribution in Illinois, Kentucky, and Tennessee (Fig. 215 and Map 2).

The following model that I propose is summarized in Figure 216. The species ancestral to the *loedingi* and *hirtus* clusters were edaphophiles that may have become isolated at high elevations in forest litter in the Appalachians during the Yarmouth interglacial. During the Illinoian glacial, with a depression of life zones, the wingless edaphophiles spread into the cave-containing lowlands.

What were the Illinoian climatic conditions like? Virtually no information is available from the southeastern United States. Although the climatic conditions in the cave regions of the interior low plateaus during the Illinoian are unknown, they may be inferred from what is known of a nearby Wisconsin site in Bartow County, Georgia, about 40 air miles from the nearest *Adelops* cave and 100 air miles SE of Huntsville at the western edge of the range of cave *Adelops* in Alabama. Watts (1970) found that in a full glacial (Wisconsin) environment of 20,100 and 22,900 years BP Bartow County harbored a floral assemblage characteristic of sites today lying 1,100 km to the north in New England. It seems reasonable to assume that the climate, causing the vegetational changes, might have been similarly changed in the nearby cave region of northeastern Alabama and adjacent states that is comparable in elevation and latitude to the Bartow County site.

Even if the Illinoian climate was not comparable to the Wisconsin, the beetles distributed themselves into at least parts of the cave-containing regions of the interior low plateaus. Some populations entered caves, found conditions suitable for survival, and became facultative troglophiles. As the Illinoian ice vanished and the warmer and drier conditions of the Sangamon interglacial came into being, the epigean environment became increasingly unsuitable for the lowland epigean populations. Perhaps some of them moved back up the mountains. At this time in the early Sangamon the opportunities were restricted for overland dispersal and gene flow between cave-inhabiting populations, and then they were eliminated by a gradual extinction of the epigean populations. The populations of facultative troglophiles then became isolated genetic entities, and each could genetically try to respond in its own way to the selective pressures of the caves. The "genetic size" of each population depended on the availability of food to support its individuals, and the extent of continuous underground dispersal corridors. At this time some or most of the cave populations may have become extinct. However, some persisted, and in the process of meeting the rigors of survival as small cave-limited populations they became obligate troglophiles. As divergence and adaptation proceeded throughout the Sangamon, the troglophiles progressed to the troglobitic level of specialization, sometime before the Wisconsin glaciation.

At the beginning of the Wisconsin, then, the *hirtus*-cluster ancestor had split into *P. hirtus* occupying caves in Kentucky, and *P. hubrichti* in caves in Tennessee. The *loedingi*-cluster ancestor had split into *P. barri* in central Tennessee, and *P. valentinei, hazelae, loedingi, whiteselli, fiskei, hatchi*, and *walteri* in caves along parts of the edge of the Cumberland Plateau in Tennessee, Alabama, and Georgia. The caves occupied at the beginning of the Wisconsin are judged to be close to or the same caves as are occupied now for the simple reason of the observed tight distributional pattern now observed. A more confused or elaborate distribution would seem likely if the Sangamon distribution was much different from that of today. Thus, the major features of distribution and speciation in the cave *Adelops* of the southeast were established by the beginning of the Wisconsin.

However, some minor features of distribution and morphological differentiation may have been acquired more recently. It seems possible that the full Wisconsin glacial climatic conditions in the cave regions may have been suitable for the overland dispersal of the recently evolved troglobites (see the above discussion of the full glacial environment in Bartow County, Georgia). Such minor features might be the spreading of *P. loedingi* eastward across the Flint River into Keel Mountain, and then eastward across the Paint Rock River into July Mountain and Tater Knob, leading to the later geographic isolation and subspeciation of these populations in the present interglacial. Similarly, *P. hatchi* may have spread northwestward into Caney Hollow Cave, to become later isolated, thereby accounting for its acquisition of subspecific differentiation. *P. episcopus* is close enough to *P. hatchi* that it may represent the descendants of a *hatchi* occupation of Bishop Mountain during Wisconsin range expansions. Also, the complex pattern of spermathecal forms in *hatchi* may date from multiple dispersals and colonizations at this time. This may also be the time that *P. whiteselli* dispersed across Wills Creek in Lookout Valley, but no morphological differences exist between populations from both sides of the valley.

The wide range of *P. hirtus,* on both sides of two major rivers potentially acting as dispersal barriers in Kentucky, may date from Wisconsin overland dispersal. The lack of differentiation between *hirtus* and *nicholasi* may represent a migration of *hirtus* from Kentucky into Illinois during the Wisconsin. Conditions in caves in Illinois in the Wisconsin may have been too rigorous during the glacial maximum for the survival of descendants from a Sangamon colonization because of the proximity of the ice front (Map 2). Cave occupation by *hirtus* in Illinois was probably during the Wisconsin glacial recession.

Distributional data supporting the Wisconsin overland dispersal of *Ptomaphagus* is also available for *Pseudanophthalmus* carabid beetles. Close morphological similarity and great geographical separation occur in these carabids in several species pairs such as *englehardti* and *loedingi* (Krekeler, 1959), *hoffmani* and *petrunkevitchi* (Barr, 1965), and *illinoisensis* and *barberi* (Barr and Peck, 1966).

Although I think the possibilities were good for overland dispersal of the cave species during the cooler (perhaps more moist) climates of the Wisconsin glacial maximum, the hypothesis is somewhat weakened by the fact that no remnant population from this dispersal is now known to exist in a noncave habitat. I think this is somewhat strange, because the southern and middle Appalachian Mountains harbor a wealth of cavelike habitats in their cool, wooded, wet and rocky gorges and ravines. If the post-Wisconsin altithermal (or hypsithermal) affected the Cumberland Plateau, it may have helped to eliminate any such remaining epigean populations. The possibility of discovering a relict population from this dispersal is brightened by the recent discovery of a remnant epigean population of *Pseudanophthalmus* in West Virginia (Barr, 1967b).

Of great ecological interest is the observation that divergence in the troglobitic *Pseudanophthalmus* of the eastern United States has led to the development of about 165 species (Barr, 1969), contrasted with the 12 cave species of *Adelops* in the same area. In many cases two and up to five (in Mammoth Cave) species cohabit single cave systems. Ecological problems of niche separation and resource division may be pertinent to these trechines, but are not pertinent to cave *Adelops,* because no specific sympatry is known for them. This observation again argues for the greater multiplicity of speciational and distributional events over a greater time period for *Pseudanophthalmus* than for *Adelops.*

If overland dispersal was possible for the troglobitic *hirtus*-group *Adelops* in the cooler Wisconsin climates, it is not now possible. Present dispersal is limited to subterranean routes. The availability of such pathways and avenues is dependent upon the previous courses of ground-water solution in the cave-bearing limestones. For the *loedingi* species cluster these dispersal avenues are now only in limestones at the flanks of the Cumberland Plateau and the Highland Rim. Subterranean dispersal is not possible for these beetles through the water-filled spaces in the limestones underlying lowlands and river valleys. Likewise, dispersal is generally not possible under the Cumberland Plateau through the limestones underlying the Pennington and Pottsville shales and sandstones, but exceptions may exist. I know of no geological references on this point, but it seems to be a widely held geological assumption that groundwater flow in the limestones under the Pennington and Pottsville of the Cumberland Plateau is virtually nonexistent. If groundwater flow (not deep artesian flow) has formed solution channels under the Pennington-Pottsville, these channels have not yet been discovered. Thus, my range maps show the Cumberland Plateau as a dispersal barrier. However, the situation is different in Kentucky where large cave systems such as Mammoth Cave have been developed under a sandstone caprock.

Active dispersal by these wingless cave-beetles is, of course, limited to walking through their subterranean corridors. Passive dispersal in the caves seems likely only by means of flood waters, which usually occur in the winter and spring. Floods probably only infrequently carry individuals to as yet uncolonized sections of the same cave system. The chances for flood waters carrying an individual to a new and uncolonized cave system are even lower. That this is nevertheless a possibility, and that its success depends upon the beetles ability to withstand submersion, is discussed by Barr and Peck (1965) in their consideration of a cave carabid beetle found washed from an Alabama cave.

Speciation in the consobrinus *group.* Little can be offered as a series of speciation and distributional events for this group (Fig. 213). Perhaps more than one species adapted to the Pliocene drying of the western United States by entering protected habitats such as animal burrows. This is seen in the wide western distribution of *fisus* and *nevadicus* in moderate to very xeric regions. In the late Pleistocene (Sangamon interglacial?) a population of *fisus* became isolated in, and adapted to, a cave in Arizona, differentiating into *cocytus*. Some type of isolation probably acted to produce the elytral variation in *nevadicus*, with the Pacific Northwest populations retaining striae typically oblique to the elytral suture, while the populations over the rest of the range diverged toward striae that were transverse to the suture. The disruption of the transcontinental mesic forests which began in the Miocene probably separated *californicus* from the rest of the *consobrinus* cluster of species. This progressive drying also led to the restriction of the ancestor of *giaquintoi* to the more moist parts of Mexico and Central America. It is now restricted to caves and probably entered the cave-adaptive zone without experiencing much morphological specialization but with at least some ecological specialization acquired in the deep forest litter adaptive zone (see Fig. 214). An early Pleistocene event (interglacial?) may have separated the ancestor of *consobrinus* from that of *brevior* and *ulkei*, these last two diverging later. Variation in *brevior* comes from a later Pleistocene event.

Speciation and dispersal in the cavernicola *group.* The story in this group is more complex than is here indicated (Fig. 213), because of the number of species in the group not yet described. Its distribution is presently in association with the moist mid-montane forests of Mexico and Guatemala, with only one species known from outside this tropical region. Members are unknown from lowland tropical forests. For reasons given above, this group is the most advanced, the youngest to develop, and the ancestor from which arose the other three subgenera of *Ptomaphagus*. As previously indicated, the time of origin must have been in the early Tertiary if not before. Up to mid-Tertiary times there were forest corridors for migration between the north and the forests at the edge of the Mexican Plateau. Probably the *cavernicola*-group ancestors moved southward with the warm-temperate forest element that had reached Mexico by the mid-Tertiary (Martin and Harrell, 1957). This montane Mexican forest today has a marked affinity to the flora of the eastern United States (and also to a lesser degree to that of southeastern China). The disjunction of the flora by the Pliocene development of an arid zone in southern Texas and northeastern Mexico also marked the disjunction of the *cavernicola* group and it perished to the north of this arid zone, leaving no hint about a possible region of origin in the form of relict species.

The oldest cluster of species in the group is the *cavernicola* cluster. It originated from a montane ancestor that had become morphologically and ecologically adapted to montane forest litter. A survivor of this ancestor is the species *oaxaca* living in the eastern mountains of the Mexican State of Oaxaca. An undeterminable speciation event gave rise to what was to become the species *cavernicola*. At least two populations of early *cavernicola* were isolated in cave habitats in the early Sangamon interglacial. One of them, *troglomexicanus*, became more modified for cave existence than the other, *gypsum*. During the Wisconsin glaciation, *cavernicola* itself spread northeastward out of Mexico across the arid zone of northeastern Mexico and southern Texas. This zone had become ameliorated enough so that savanna conditions existed (Martin and Harrell, 1957). Temporary use of animal burrows may have aided the crossing of this barrier, since caves are absent here. When *cavernicola* reached central Texas it encountered mesic forests and caves, and the way was clear for it to disperse to at least the extent of its present range. This present range is undoubtedly one of (altithermal?) contraction, because the species is now known mostly from caves, which are undoubtedly being used as some sort of refuge. Temperate forests may presently be inadequate in some way for permanent occupation. The lack of material from forests may also indicate an unusual seasonality of overland flight and dispersal, judging from the one South Carolina forest collection made in the wintertime. One population of *cavernicola* has been out of the mainstream of genetic contact long enough that it has acquired enough differences to be treated as the subspecies *cavernicola aditus*, inhabiting Cueva de la Boca, south of Monterrey, Mexico. This probably results from a longer period of population isolation, beginning with the early return of the present arid conditions in northeastern Mexico. It is interesting that the other known Mexican population from Gruta del Palmito, north of Monterrey, has not diverged, although it has seemingly also suffered the same isolation.

Little or nothing of a positive nature can be offered concerning the times and places of speciation events in the remaining six named species in the group. The position of *elabra* is isolated because of the unusual shape of the anterior end of the spermatheca. The species *jamesi* is closer to *altus* in features of the spermatheca and aedeagus than it is to *newtoni*, but *newtoni* and *jamesi* are not pruinose near the rear of the female elytral suture, which *altus* is. The species *leo* and *spelaeus* have similar spermathecae but are different in aedeagal characters, with *spelaeus* females having the pruinose elytral tip, which is absent in *leo*.

The cave occupation of *elabra* and *spelaeus* probably dates from the Wisconsin. At that time populations moved down from higher elevation forests. With the Wisconsin recession the lowland populations were left in cave refuges as the climate became drier or hotter. The species undoubtedly exist today somewhere in nearby epigean environments.

There are certainly more than the present ten named and seven unnamed species in the *cavernicola* group. This is evident simply because so few collectors in Mexico have used the specialized methods necessary for collecting Catopinae. How can we account for the production of this close-knit group of at least 17 species with its center of abundance in the mid-montane forests of eastern Mexico? It might be viewed simply as a manifestation of the generalization of a higher species diversity in tropical regions compared to temperate regions. However, this cannot be the case, because the mid-montane forests are actually temperate in their physical and biological characteristics. As a model for explaining the high species diversity I suggest a modification of that offered by Martin (1955). He noted that an isolated patch of Mexican cloud forest (at Rancho del Cielo, Tamaulipas) did not have any vertebrate species that were limited to it. He suggested that if any obligate cloud forest vertebrates did inhabit it in the past, they may have been eliminated by reduction of forest size under different climatic circumstances. However, the forest reduction (or reductions) were not severe enough to reduce the richness of the floral components. If there was such a period of fluctuating boundaries with disjunctions and reunions in the mid-montane forests, this offers an excellent model for multiple geographic isolations in the insect fauna. It suggests that much endemism can be expected by future students investigating the terrestrial arthropod fauna of these forests. However, if this fauna is to be known, active and intense efforts must be made now to collect it, because the destruction and disruption of these forests for domestic and agricultural purposes is proceeding at a very rapid rate.

Conclusion and prospectus. In closing the discussion of the phylogeny and zoogeography, I believe it is useful to restate three of the major operational assumptions I have used. 1) That the group that I call the tribe Ptomaphagini arose in tropical-subtropical America, probably on the land mass that is now North or Central America. 2) That the morphology of the spermatheca of *Ptomaphagus* is useful for uniting species into groups. 3) That I have correctly interpreted the progression of evolution in the spermatheca from simple to complex as an indicator of the relative ages of the species groups. Proceeding from this basis, I have constructed the above past history for the group in a manner that I believe is internally consistent for the data available. I offer the history as a model that can be continually tested as new data become available, in the form of new taxa, characters, and distributional information.

I believe it will be an interesting future exercise to test the phylogenetic scheme with phenetic (numerical) and cladistic methodologies. In the former the anticipated difficulty will be the discovery of a sufficient number of unit characters that can be coded as "0" or "1." The difficulty of the latter will be in making decisions on the primitive and advanced conditions of each character. In such an endeavor the greatest aid comes from comparing conditions in the unit under study with those in allied groups. This I have already done in many instances in arriving at the above reconstructed evolutionary history.

Lastly, it is interesting to note as a general summary and conclusion that multiple cave occupation and specialization has occurred in all three species groups of *Ptomaphagus* and occurred to at least nine ancestral species which resulted in nineteen cavernicolous species. Some of these nineteen are more cave adapted than others. None of the original cave occupations occurred before the beginning of the Sangamon interglacial. The levels of adaptation and specialization in troglobitic *Ptomaphagus* are far below the levels achieved by the troglobitic Bathysciini of Europe.

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Valid generic names and specific combinations in italics; only major discussions listed for species

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Host Preference in Ciid Beetles (Coleoptera: Ciidae) Inhabiting the Fruiting Bodies of Basidiomycetes in North America

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HOST PREFERENCE IN CIID BEETLES (COLEOPTERA: CIIDAE) INHABITING THE FRUITING BODIES OF BASIDIOMYCETES IN NORTH AMERICA

JOHN F. LAWRENCE

CONTENTS

Abstract. Host records are summarized for 74 species of North American ciid beetles occurring in the fruiting bodies of 117 species of basidiomycete fungi, and the data are analyzed to determine patterns of host preference. The morphology and classification of the host fungi are reviewed and the life history and ecological role of the Ciidae are discussed. For species with five or more breeding records, an attempt is made to determine degree of host specificity, using a modified equation for "niche breadth." Few North American ciids are monophagous and probably none are indiscriminate, but most appear to be group-specific, preferring to breed in one or two hosts but occurring in several more, which are often phylogenetically related. The majority of host fungi may be placed into one of four host preference groups, on the basis of shared ciid inhabitants. These groups and their associated Ciidae are not mutually exclusive, but, with the exception of a few eurytrophic species, the beetles rarely breed in fungi of the "wrong" group. Each host preference group is discussed with respect to its faunal composition in each of four major geographical regions of North America. Speculations are made on the possible mechanisms of host selection, and certain zoogeographical and evolutionary factors are discussed.

INTRODUCTION

Beetles of the family Ciidae are the most common, if not the most conspicuous, arthropods inhabiting the relatively large and often woody or leathery fruiting bodies of the Polyporaceae and related higher fungi. Within this habitat, the Ciidae are represented by many more species than other inhabitants, such as tenebrionid beetles or tineid moths, and, although the individual size is small (usually 1 to 3 mm), the large populations constitute a major portion of the consumer biomass and contribute significantly to the breakdown of fungus conks (Matthewman and Pielou, 1971). This paper deals with patterns of host preference in 74 species of American Ciidae occurring north of the Mexican border, and is based on over 2000 host records gathered by myself and various colleagues.

Previous works on the inhabitants of fungi vary in scope and approach, and fall into four major categories: a) general compilations of host data for all organisms (or one large group) recorded from fungi within a certain geographic area; b) more detailed studies of one family or genus of fungus feeders, with an emphasis on host specificity; c) faunal analyses of a single host species; and, d) biological studies involving a single mycetophagous organism.

In the first category belongs the work of Benick (1952), which covers all beetles known from fungi in the Palaearctic region and includes 1116 species from 286 different hosts. Other more restricted studies include Donisthorpe (1935) [beetles, England]; Graves (1960) [all inhabitants, Chicago area]; Graves and Graves (1966 and in preparation) [all inhabitants, North Carolina]; Roman (1970) [beetles, France and Switzerland]; Scheerpeltz and Höfler (1948) [beetles, Austria]; and Weiss and West (1920, 1921a, 1921b) [insects, eastern United States].

Information on the feeding habits of particular families or genera are usually included within taxonomic papers and are not readily available to the general biologist or ecologist. Host preference in the Ciidae has been discussed by Paviour-Smith (1960a) [England], Ackerman and Shenefelt (in press) [Wisconsin], and Lawrence (1967a, 1967b, 1971, in press) [United States]. Papers on the inhabitants of a single host species include those of D. Pielou and his group (Pielou, 1966; Matthewman and Pielou, 1971; Pielou and Matthewman, 1966; Pielou and Verma, 1968) on *Fomes fomentarius* and *Piptoporus betulinus* in eastern Canada; Borden and McClaren (1970 and in press) on *Cryptoporus volvatus* in western Canada; and Paviour-Smith (1960b) on *P. betulinus* in England. Among the numerous examples of individual life history studies are those of Paviour-Smith (1963, 1964, 1965a, 1965b) on *Tetratoma fungorum* (Fabricius) and those of Heatwole and Heatwole (1968), Liles (1956), and Pace (1967) on *Bolitotherus cornutus* (Panzer).

The main purposes of the present paper are 1) to discuss the classification of the Polyporaceae and related Basidiomycetes in order to establish a sound basis for studies of host preference in Ciidae and other fungus-feeding arthropods; 2) to examine possible structural and chemical characteristics of the fruiting bodies which may serve as clues in host selection or at least account for the discriminate use of host species; and, 3) to present host records gathered to date for North American ciids and to explore methods of analyzing this data which may be of use in future ecological studies.

Methods

The host records cited in this paper are based on the following types of data: 1) Samples of Ciidae extracted in the field or laboratory from fungus fruiting bodies collected by me personally. 2) Samples extracted in the laboratory from fruiting bodies collected by colleagues in the field. 3) Samples extracted from dried fruiting bodies in a herbarium (mainly the U.S.D.A. herbaria at Beltsville, Maryland). 4) Collections made by R. C. Graves and H. S. Dybas from both field and herbarium specimens. 5) Insect specimens bearing pieces of dried fruiting body on the pin. 6) Insect specimens with host data on the label. 7) Host records from the literature.

Samples extracted by me were either pinned or placed in fluid (usually 80% ethanol) and stored in my personal collection or that of the M.C.Z. All specimens from a single collection (one fruiting body or several growing together) were given the same lot number. Specimens of the host fungus were either sent out to specialists or identified by me. Voucher specimens were retained in most instances, but with certain common fungi this was not done. Collections made by Graves were identified by L. R. Hesler, while those of Dybas were determined by J. A. Stevenson, with voucher specimens placed in the Field Museum.

Host records in categories 1 through 5 are considered to be the most reliable, since the ciids were examined by me and the fungus identifications are relatively certain or at least capable of verification. These verified or verifiable records are the only ones used in the analysis of the host data. The records in categories 6 and 7 may be mentioned in the text, but are referred to as unverified (UV).

Verified records are further divided into those which definitely represent a breeding population and those which may be accidental. A breeding record consists of any one of the following: 1) Ten or more fully pigmented adults. 2) Two or more teneral adults. 3) One teneral and two or more fully pigmented adults. 4) One or more larvae and/or pupae (when these can be identified). This breakdown is somewhat arbitrary, but it tends to eliminate accidental records, which are common enough, especially in situations where several very different host fungi (such as *Phellinus gilvus*, *Bjerkandera adusta*, *Hirschioporus pargamenus*, and *Coriolus versicolor*) grow on a single log. Cross-contamination in shipment may also account for a certain percentage of accidental occurrences. The added weight given to the presence of teneral individuals is based on the assumption that dispersal flights occur only after full pigmentation (and thus hardening of the cuticle) has been attained. Thus, a teneral adult (if it does not represent a contaminant from an adjacent fruiting body) has almost certainly developed *in situ*.

In the main data section (pp. 190–207), for each ciid species known from fungi, a brief statement of geographic distribution is given, and this is followed by a summary of host data containing the following information: 1) number of fungus species from which the ciid has been recorded; 2) number of breeding hosts (in parentheses); 3) total number of host records; 4) number of breeding records (in parentheses); 5) "niche breadth" for those species with five or more breeding records (*see* p. 181); 6) host preference group (*see* pp. 182–187); 7) number of records (nonbreeding, breeding, and total) and percentage of breeding records for each host species; and, 8) discussion, which may include host data on related extralimital species.

In Table 1, this data is further condensed and summarized. The Ciidae are arranged according to Lawrence (1971) and each is given a number that is used in the host index on page 207. A rough idea of distribution is given by indicating which adjacent geographic sectors (NW, NE, SE, SW) are included within the greater part of the range (excluding disjunct montane populations). These sectors, which are also referred to in Table 2, are based on figure 87 in Lawrence (1971). The SW sector includes southern California, Arizona, New Mexico, Texas (west of the Pecos River), and western Mexico, while the NE sector is bordered by Manitoba, the Dakotas, Nebraska, Kansas, Missouri, Kentucky, and Virginia.

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THE HOST FUNGI

North American species of Ciidae have been recorded from the fruiting bodies of 117 host fungi, nearly all of which are wood-rotting members of the advanced basidiomycete order Polyporales and are usually referred to as polypores or bracket fungi. Spores of these fungi usually germinate in dead wood, in the wounds of living trees, or in trees that have been weakened by insect attack. In some instances, access to the wood is gained through the entrance and exit holes of xylophagous insects, such as bark beetles. The mycelium of the fungus penetrates the woody tissue and causes "white rot" if cellulose and lignin are hydrolized, or "brown rot" if cellulose alone is affected. The location of the rot varies with the fungus species, and may be restricted to sapwood, heartwood, roots, or branches. Although a number of polypores are parasitic, most of those considered here are saprobes and occur primarily on dead trees and logs.

Structure and Development of the Fruiting Body

The primary mycelium, which develops from a single spore, consists of branches or hyphae that are composed of uni-nucleate cells. When anastomosis occurs with another primary mycelium, the resulting bi- or pluri-nucleate hyphae are referred to collectively as the secondary mycelium. When environmental conditions are proper, this secondary mycelium gives rise to a fruiting structure.

The fruiting body of a basidiomycete fungus is usually called a sporophore, basidiocarp, or hymenophore, and in the Polyporaceae it is often referred to as a bracket or conk. In gross structure, it usually consists of two main parts: the sterile upper portion or pileus and the reproductive layer or hymenium, which contains the spore-bearing basidia and associated cells. In most higher Basidiomycetes, the lower part of the pileus is produced to form gills, spines, or tubes, each of which is lined by hymenial surface; these structures are often called the dissepiments. The major part of the sterile tissue making up the pileus is called the context, while that forming the dissepiments is known as the trama. In some polypores, the tubes are sharply separated from the pileus, but in others the context and tramal tissue cannot be distinguished.

The form of the fruiting body varies considerably, even within a single species. In some groups it may be resupinate, that is, lying flat against the substrate with no true pileus and only the hymenial surface free. In most species, it forms a definite pileus, which may be stipitate or broadly attached to the substrate. Other modifications include a central core or a specialized upper surface, consisting of various kinds of hairs or a solid cuticle. In the majority of species, the fruiting body is annual, but in certain groups new layers of tubes are formed each year.

In most of the fungi considered here the dissepiments consist of tubes, so that the lower surface is poroid. In a few groups, however, these pores are irregular and maze-like (daedaloid), in others they break down, forming spines (irpiciform), and in certain species they are elongate so that gills are formed. In some groups, the dissepiments are lacking and the hymenial surface is flat. Although the form of the dissepiments is more constant than that of the pileus, it is notoriously variable in certain polypore species (*Daedaleopsis confragosa*) and is a poor indicator of generic or familial relationships (see below). (Bessey, 1950; Cunningham, 1965; Overholts, 1953; Snell and Dick, 1971; Teixeira, 1962).

The first undifferentiated and indefinitely growing hyphae of the secondary mycelium are called generative hyphae (Corner, 1932a,b), and they, in turn, may produce specialized branches or special microstructures, such as setae, cystidia, or basidia. Pinto-Lopes (1952) refers to all modified hyphae as tertiary hyphae, but most authors use a different terminology, discussed below. The generative hyphae are thin-walled and septate, and they usually have nodose septa or clamp connections. The loss of clamp connections (simple-septate condition) is considered important in classification, although it is thought to have occurred several times (Nobles, 1958; Teixeira, 1962).

In some species, the generative hyphae grow and branch, forming the context, surface, and dissepiments, but they never form special branches of limited growth, and normally their walls do not become thickened or discolored; Corner called this type of fruiting body monomitic, since it contains only generative hyphae. In other fungi, the generative hyphae produce a number of thick-walled and commonly aseptate specialized branches, which are of two main types: skeletal hyphae, which are broader and unbranched, growing parallel to one another, and binding hyphae, which are narrow and much-branched, forming an intricate network, and of limited growth. Fruiting bodies with skeletal or binding hyphae in addition to the generative hyphae are said to be dimitic, while those with all three types are trimitic (Corner, 1953). It is usually the skeletal hyphae that have very thick and darkly pigmented walls. Although Corner's system is an excellent descriptive tool, it has caused difficulties when applied uncritically by taxonomists (see below). The skeletal hyphae of the bovista type described by Cunningham (1947) are considered to be binding hyphae by Corner (1953), while Teixeira (1962) mentions several terms (arboriform, vermiform, etc.) used to describe individual hyphal types. One of the main difficulties in using such terms as dimitic and trimitic is that the hyphae do not remain the same in all parts of the fruiting body. In species of *Ganoderma*, for instance, the context is trimitic and the dissepiments are dimitic (Hansen, 1958), whereas in *Laetiporus sulphureus* the context is dimitic with binding hyphae and the trama monomitic (Corner, 1953).

Classification of the Host Fungi

Since this paper will serve as a basis for further studies of host preference in fungus-feeding arthropods, the classification of the polypores and their relatives will be treated in some detail. The necessity for this is partly due to the fact that American mycologists working on higher Basidiomycetes have until recently used an extremely conservative generic classification, which allows one to make very few generalizations about feeding preferences and renders useless generic determinations, such as *Fomes* sp. or *Polyporus* sp. The fact that a particular gall maker is restricted to the genus *Quercus* or that certain adult bees prefer the flowers of *Clarkia* is a useful piece of biological information. In contrast, the fact that a fungus beetle prefers species of *Fomes* is almost meaningless, since that genus in Overholts' manual (1953) contains a number of unrelated forms whose only character in common is a tendency for the fruiting body to be perennial, adding new hymenial layers each year.

The earliest generic concepts in this group date back to Fries, whose work spanned more than fifty years, beginning in 1821 and culminating with "Hymenomycetes Europaei" in 1874. Fries and his followers recognized about ten segregates based on gross structure of the fruiting body and form of the dissepiments; these include *Polyporus, Fomes, Daedalea, Poria, Trametes,* and *Hexagona,* among others. According to Donk (1971), the first real break with the Friesian system was made by Patouillard (1900), who made use of microstructural details and proposed a strongly modified classification of the Hymenomycetes. It is unfortunate that the contemporary American specialists represented two extreme schools. The conservative Lloyd ridiculed the work of Patouillard, while Murrill, a radical splitter, proposed many monotypic genera for the New World polypores. The result was that Overholts (1953) retained the old Friesian system advocated by Lloyd, and the same treatment with few modifications is found in recent manuals by Lowe (1957, 1966), and Lowe and Gilbertson (1961a,b). In Europe, on the other hand, Patouillard's system was further modified and eventually gave rise to the modern classifications of Donk (1933) and Bondarzew and Singer (1941).

The classification adopted here for the North American host fungi (see below) follows Bondarzew and Singer for the most part, but also incorporates recent changes made by Kotlaba and Pouzar (1957), Donk (1966), and others. Murrill's genera have been used for certain New World forms not treated in European manuals. Further notes on the placement of individual species are given in the next section.

Detailed reviews of the methodology used in polypore taxonomy are given by Teixeira (1962) and O. Fidalgo (1968). Excluding gross structure of the fruiting body, the following classes of characters are most frequently used: (1) generative hyphae and clamp connections, (2) modified hyphae and hyphal systems, (3) surface characters of the pileus, (4) hymenial structures, (5) spores, and (6) cultural characters.

Examples of gross habitus characters used by the early workers are resupinate condition of the sporophore (*Poria*), perennial sporophore with layers of tubes (*Fomes*), uneven tube depth (*Trametes*), gilled hymenium (*Lenzites*), and maze-like or daedaloid hymenium (*Daedalea*). Ames (1913) attempted to describe the gross consistency of the context, using such terms as coriaceous, tough-fleshy, spongy, and woody.

Clamp connections and hyphal systems have been described above. The presence of clamps is thought to be the primitive condition and occurs in the majority of genera; the simple-septate condition is found in *Oxyporus, Laetiporus, Rigidoporus, Heterobasidion,* and all of the Hymenochaetaceae. Condition of the modified hyphae has been a widely used character, especially since the publication of Corner's papers on hyphal systems (1932a,b). The "trametoid" and "fomitoid" groups discussed below are all characterized by having a trimitic hyphal system, in which both binding and skeletal hyphae are present in the context. The major difficulties in using Corner's terminology are as follows: (1) use of only three terms to describe a wide variety of hyphal types in differing combinations is too simplistic; (2) the proper analysis of the hyphal system requires careful and tedious dissection, although recent developments with ultrasounds (O. Fidalgo, 1967) have helped considerably; (3) condition of the hyphae may vary with age and position in the fruiting body; and, (4) the development of supportive structures, such as skeletal or binding hyphae, is correlated with the evolution of larger fruiting bodies and may have occurred several times independently (Donk, 1971). The most extensive use of hyphal systems was made by Cunningham (1947, 1954, 1965) in his studies of New Zealand and Australian polypores.

The color of hyphal walls, and particularly the change in color produced by potassium hydroxide, has been used frequently in polypore classification. In the Hymenochaetaceae and in many of the "fomitoids" such as *Gloeophyllum* and some *Ganoderma,* the application of KOH solution will turn the tissue permanently black. This character appears to play an important role in host preference and is discussed further on pages 174 and 176.

Teixeira (1962) discusses surface characters in detail, emphasizing the micromorphological studies made by Lohwag (1940). Spore characters were used extensively by Murrill (1907, 1908) but have not been emphasized by recent workers, at least at the generic level. Spore color may be quite variable, but the complex spore covering found in *Ganoderma* is correlated with a number of other characters of the sporophore. Hymenial structures were used by Patouillard (1900) and especially by Donk (1933) to define genera, but authorities disagree as to their importance. The presence of setae (dark, thick-walled, lance-like projections) characterize most of the Hymenochaetaceae, while certain other groups, such as *Oxyporus* and *Hirschioporus* have cystidia (blunt and thin-walled, colorless projections), which are often covered with crystals of calcium oxalate.

The most recent set of characters to be used in polypore classification are the so-called cultural characters, that is, the structure and behavior of sterile hyphae grown in culture. The most important papers on this subject are those of Nobles (1958, 1965, 1971). In addition to several hyphal features, such as the presence of clamps, other characters, such as the production of extracellular oxidase and infertility phenomena are considered.

Annotated List of Host Species

The following list includes the complete citation for every host species and the more commonly encountered synonyms of each. In the majority of cases, the species names are the same as those used in my recent revision of the North American Ciidae (Lawrence, 1971); exceptions are as follows: *Oxyporus populinus* (= *Fomes connatus*), *Dichomitus squalens* (= *Polyporus anceps*), *Lenzites elegans* (= *Daedalea ambigua* and *D. elegans*), and *Inonotus rheades* (= *Polyporus vulpinus*). The generic concepts, on the other hand, are completely different and are discussed briefly below. An attempt was made to avoid new combinations, but some of those listed could not be found in the mycological literature available to me. The order in which the genera are placed will be followed throughout the text.

HETEROBASIDIAE
AURICULARIALES
AURICULARIACEAE

Auricularia. The fruiting bodies of these fungi are soft and gelatinous, but when they dry out they become rubbery or hard and may be relatively persistent.

Auricularia auricula (Linnaeus ex Hooker) Underwood

Auricularia polytricha (Montagne) Saccardo

HOMOBASIDIAE: HYMENOMYCETES
AGARICALES

Most of the records for the Agaricales are from members of the Tricholomataceae in the sense of Singer (1951). All those encountered are lignicolous and have relatively durable fruiting bodies, in contrast to most members of the order. Occurrences on the ground-dwelling *Boletus* and *Russula* appear to be incidental nonbreeding records.

TRICHOLOMATACEAE

Lentinus crinitus Linnaeus ex Fries
Panellus stipticus (Bulliard ex Fries) Karsten
Pleurotus ostreatus (Jacquin ex Fries) Quelet
Pleurotus sp.
Schizophyllum commune Fries

BOLETACEAE

Boletus sp.

RUSSULACEAE

Russula sp.

POLYPORALES (= *APHYLLOPHORALES*)

MERULIACEAE

Phlebia merismoides Fries. The fruiting body of this species is thin and sheet-like.

THELEPHORACEAE

Species of *Stereum* are common hosts for certain ciids. Their fruiting bodies are very thin and somewhat rubbery at first, but upon drying out they become rigid. *Lopharia papyrina*, placed in a distinct genus following Boidin (1959), has a very thin and almost paper-like, violet or brownish sporophore.

Stereum hirsutum (Willdenow) Persoon ex Fries
Stereum ostrea (Blume and Nees) Fries [= *Stereum fasciatum* (Schweinitz) Fries]
Stereum sp.
Lopharia papyrina (Montagne) Boidin

HYDNACEAE

Steccherinum ochraceum Persoon ex Gray

POLYPORACEAE

This includes the majority of woody fungi serving as hosts for Ciidae, but in the present treatment *Phellinus* and its allies are excluded (see below).

Poria. This genus, as it is here constituted, contains only a few species, none of which represent major hosts. The remainder of the resupinate polypores included in *Poria* by Lowe (1966) have been placed in other genera, such as *Oxyporus, Rigidoporus,* and *Phellinus* (see below).

Poria carbonica Overholts
Poria corticola (Fries) Cooke
Poria versipora (Persoon) Romell

Polyporus. In the more conservative system of Overholts (1953) and others, this genus would include the majority of polypore species, but here it is restricted to those stipitate species related to *P. squamosus.* The fruiting body is quite soft and fleshy at first, but later it becomes harder and more durable with felt-like context tissue. According to Corner (1953), this is caused by the late development of binding hyphae and thickening of hyphal walls. The same author comments on the similarity in micromorphological detail between this species and certain *Pleurotus* (Agaricales).

Polyporus mutabilis Berkeley and Curtis
Polyporus squamosus Micheli ex Fries
Gloeoporus dichrous (Fries) Bresadola
Hapalopilus alboluteus (Ellis and Everhart) Bondarzew and Singer
Hapalopilus fibrillosus (Karsten) Bondarzew and Singer
Laetiporus sulphureus (Bulliard ex Fries) Bondarzew and Singer. This is the common sulphur bracket, which is bright yellow, soft, and fleshy, and which usually grows at the bases of dead trees, both hardwoods and conifers. Older fruiting bodies become somewhat cheesy and crumble easily. Hyphal development of this species has been described by Corner (1953).

Tyromyces. This genus includes a few minor hosts, which may not all be related. The first three have relatively soft, annual fruiting bodies, with a monomitic hyphal system. *T. spraguei* is included for convenience on the basis of Murrill's placement.

Tyromyces albellus (Peck) Bondarzew and Singer

Tyromyces cinerascens (Bresadola) Bondarzew and Singer

Tyromyces galactinus (Berkeley) Bondarzew

Tyromyces spraguei (Berkeley and Curtis) Murrill

Bjerkandera. B. adusta and the related *B. fumosa* have been placed in several generic groups, including *Tyromyces, Gloeoporus,* and *Leptoporus.* The fruiting body is monomitic and remains relatively soft; the context tissue is light brown or cream, while the hymenium is dark brown. *B. adusta* is a fairly common species on dead hardwoods.

Bjerkandera adusta (Willdenow ex Fries) Karsten

Oxyporus. This genus is used here in the sense of Donk (1966), in that it includes the resupinate *O. latemarginata,* as well as the perennial *O. populinus.* In both, the context tissue is light in color and relatively soft.

Oxyporus latemarginatus (Durieu and Montagne) Donk [= *Poria ambigua* Bresadola]

Oxyporus populinus (Fries) Donk [= *Polyporus connatus* Weinmann]

Ischnoderma resinosum (Schrader ex Fries) Karsten. This has a dark brown, somewhat sappy sporophore, which becomes quite hard upon drying out; it produces white rot in conifers.

Nigroporus vinosus (Berkeley) Murrill

Fomitella supina (Swartz ex Fries) Murrill. This and the preceding are subtropical species placed in monotypic genera by Murrill (1905).

Piptoporus betulinus (Bulliard ex Fries) Karsten. This is the common birch bracket, which occurs on *Betula* throughout the Holarctic region. The fruiting body is somewhat kidney-shaped and substipitate, with a whitish context, which is fairly corky when dry, and an easily detachable hymenial region. The microstructure is complex and has been described by Corner (1953). The species is thought to be related to *P. portentosus* from Australia (Cunningham, 1965).

Cryptoporus volvatus (Peck) Hubbard. This species is unique among the polypores in that the dissepiments are almost completely enclosed by a mantle extending out from the margin of the pileus. The fungus causes a white rot in gymnosperms, and the small, globular, cream-colored sporophores are often seen on standing dead conifers which have been killed by bark beetles. The species is very common in western North America but also occurs in the Northeast and in China and Japan. Some aspects of its biology are discussed by Borden and McClaren (1970 and in press).

Laricifomes, Fomitopsis, Heterobasidion, Rigidoporus. This group of genera includes most of the species formerly placed in the genus *Fomes,* but differing from *F. fomentarius* in having hyaline hyphal walls and thus a lightly pigmented context (Sections IV and V of Lowe, 1957). The fruiting structures are usually large and perennial, with a corky or woody texture. *Laricifomes* was proposed by Kotlaba and Pouzar (1957) on the basis of the trimitic hyphal system with clamp connections. *Fomitopsis pinicola* and *F. cajanderi* are dimitic with clamps and produce a brown rot, usually in gymnosperms. *F. fraxinea* and *F. fraxinophila* are only provisionally placed here. *Heterobasidion* and *Rigidoporus* differ from the above two genera in lacking clamp connections and in other microstructural details. The species tend to have sporophores that become very hard and rigid when dry. *Heterobasidion annosum* produces a white rot of gymnosperms in Europe and North America, while *Rigidoporus* includes not only the Holarctic *R. ulmarius* but a complex of tropical forms related to *R. lignosus.*

Laricifomes officinalis (Villars ex Fries) Kotlaba and Pouzar

Fomitopsis cajanderi (Karsten) Kotlaba and Pouzar [= *Fomes subroseus* Karsten]

Fomitopsis fraxinea (Bulliard ex Fries)

Fomitopsis fraxinophila (Peck)

Fomitopsis pinicola (Swartz ex Fries) Karsten [= *Fomes marginatus* (Fries) Gillet]

Heterobasidion annosum (Fries) Brefeld

Rigidoporus lignosus (Klotzsch) Imazeki

Rigidoporus nigrescens (Bresadola) Donk

Rigidoporus rigidus (Leveille)

Rigidoporus ulmarius (Sowerby ex Fries) Imazeki [= *Fomes geotropus* Cooke, of authors]

Rigidoporus vitreus (Persoon ex Fries) Donk [= ? *Poria undata* (Persoon) Bresadola]

Rigidoporus zonalis (Berkeley) Imazeki

Antrodia and *Dichomitus. Antrodia* is used here in the sense of Donk (1966) and includes most of the species treated as *Coriolellus* by Bondarzew and Singer (1941). Fruiting bodies are dimitic with hyaline skeletal hyphae, and are discussed in detail by Sarkar (1959). *Dichomitus* was proposed by Reid (1965) for *D. squalens,* commonly known as *Polyporus anceps* in North America (David, 1967). It differs from *Antrodia* species in the presence of dendritically branched skeletal hyphae, and in cultural characters it resembles members of the genus *Coriolus* and their relatives (Nobles, 1958). The fungus causes white pocket rot in conifers.

Antrodia sepium (Berkeley) Donk [= ? *Coriolellus albida* (Fries) Bondarzew]

Antrodia serialis (Fries) Donk

Dichomitus squalens (Karsten) Reid [= *Polyporus anceps* Peck]

Irpex tulipiferae (Schweinitz) Fries. This species is characterized by having an irpiciform or tooth-like hymenium with encrusted cystidia, no clamp connections, and a soft-leathery, whitish context.

Hirschioporus. The species comprising this group have thin, leathery sporophores resembling those of *Coriolus,* but the hyphal system is dimitic, the context is usually duplex, the dissepiments (and sometimes the context) are violet or brownish in color, and the hymenium bears a number of crystal-encrusted cystidia. Kotlaba and Pouzar (1957) have excluded *H. pargamenus* because the context is homogeneous, but in other respects it is similar to *H. abietinus.* Other common species not yet recorded as hosts are *H. fusco-violaceus* and *H. laricinus.*

Hirschioporus abietinus (Dickson ex Fries) Donk

Hirschioporus pargamenus (Fries) Bondarzew and Singer

Hirschioporus sector (Ehrenberg ex Fries) Teng

Hirschioporus versatilis (Berkeley) Imazeki

Cerrena unicolor (Bulliard ex Fries) Murrill. This is characterized by having a violet or grayish, daedaloid pore surface, a whitish, trimitic context, and a distinct black layer beneath the surface hairs (duplex context). The species is common on hardwoods in the northeastern United States.

Trametes *and the Trametoid Genera.* The genus *Trametes* is one of the more confusing of the polypore genera and has been used in different ways by various authorities. It is sometimes treated as a form genus to include all those species in which the tubes extend to unequal depths in the context. More commonly it encompasses *Coriolus* and several related genera, such as *Pycnoporus* and *Earliella,* in which the context is whitish and homogeneous, the hyphal system trimitic with clamp connections, and the tubes unequal. O. Fidalgo (1958) has suggested that gilled and daedaloid species, such as *Lenzites betulina* and *Daedalea quercina* be included as well. In the present paper, the trametoid genera (*Trametes* to *Coriolopsis* below) are treated separately and *Coriolus,* rather than *Trametes,* is used for *C. versicolor* and its relatives. The type of *Trametes, T. suaveolens,* is not recorded as a host, and the three species listed under this genus are New World forms of uncertain affinities, which were placed here by Lloyd and Murrill.

Trametes cirrifer (Berkeley and Curtis) Lloyd

Trametes plebeja (Berkeley) Lloyd

Trametes robiniophila Murrill

Pycnoporus. The two species included here differ from those in *Coriolus* mainly in the bright red color of the fruiting body, which is caused, according to Cunningham (1965), by pigmented mucilage granules coating the hyphae and embedded between them.

Pycnoporus cinnabarinus (Jacquin ex Fries) Karsten

Pycnoporus sanguineus (Linnaeus ex Fries) Murrill

Coriolus. This includes the majority of poroid species belonging to the trametoid group. The context is usually whitish or cream in color and leathery in texture. *Coriolus versicolor, C. hirsutus,* and *C. pubescens* are common white rots of hardwoods in the Holarctic Region, while *C. maximus, C. pinisitus,* and *C. tenuis* are more tropical in distribution.

Coriolus biformis (Fries) Patouillard

Coriolus conchifer (Schweinitz) Patouillard

Coriolus hirsutus (Wulfen ex Fries) Quelet

Coriolus maximus (Montagne) Murrill

Coriolus pinisitus (Fries) Patouillard

Coriolus pubescens (Schumacher ex Fries) Quelet

Coriolus subectypus Murrill

Coriolus tenuis (Saccardo)

Coriolus versicolor (Linnaeus ex Fries) Quelet

Lenzites. This genus is used here for those trametoid forms in which the hymenium lines gills or daedaloid pores; in most other respects they are similar to species of *Coriolus.* In older systems, *Lenzites* was used for all gilled polypores (see *Gloeophyllum* below), while *Daedalea* was used for those with a daedaloid hymenium (see *Daedaleopsis* below). The type of the genus *Daedalea, D. quercina,* although common in North America and Europe, has never been recorded as a host for Ciidae.

Lenzites betulina (Linnaeus ex Fries) Fries

Lenzites elegans (Sprengel ex Fries) Patouillard [= *Daedalea ambigua* Berkeley]

Earliella corrugata (Persoon) Murrill [= ?*Trametes scabrosa* Persoon ex Fries]. This species is common throughout the tropics and is known under various names (Fidalgo and Fidalgo, 1966); the pore surface varies from poroid to daedaloid and the upper surface is usually encrusted and reddish at the base.

Funalia. The two species below were placed in a distinct group by Bondarzew and Singer (1941), and David (1967) has pointed out certain mycelial characters that distinguish them from related trametoids. *F. hispida* is particularly common on *Populus* and *Salix* in the more arid parts of the United States.

Funalia hispida (Baglietto) [= ?*Trametes gallica* Fries]; [= ?*Funalia extenuata* (Durieu and Montagne) Domansky]

Funalia trogii (Berkeley) Bondarzew and Singer

Coriolopsis. Included here are three primarily tropical species which have a darker context than those above. The differences between *Coriolopsis occidentalis* and *Coriolus hirsutus* are slight and the two are easily confused.

Coriolopsis crocata (Fries) Murrill

Coriolopsis fulvocinerea Murrill

Coriolopsis occidentalis (Klotzsch) Murrill

The Fomitoid Genera. The next six groups include the darkly pigmented counterparts of the trametoids, in which the hyphal system is trimitic with clamp connections, but the hyphal walls are distinctly colored (with some exceptions in the genus *Ganoderma*) and usually turn black when treated with KOH.

Gloeophyllum. The two species listed under this genus have a gilled hymenium and dark brown or reddish brown context. *Gloeophyllum saepiarium* is very common on coniferous slash in northern areas, while *G. striatum* is a tropical species usually associated with *Taxodium* and *Juniperus*: both fungi cause brown rots.

Gloeophyllum saepiarium (Wulfen ex Fries) Karsten

Gloeophyllum striatum (Swartz ex Fries) Murrill

Datronia mollis (Sommerfeldt) Donk. The name *Datronia* was proposed by Donk (1966) to replace *Antrodia,* which had been misapplied to the old *Trametes mollis. D. mollis* has a resupinate sporophore with a brownish context and large, shallow tubes. According to Cunningham (1965), the species is allied to *Osmoporus odoratus,* a species not encountered in this study.

Daedaleopsis confragosa (Bolton ex Fries) Schroeter. The fruiting body of this species is pileate and firm, with a dark brown context and a hymenium that may be poroid, gilled, or daedaloid. The sporophore of *Daedalea quercina* is usually larger, with a lighter context and very thick tube walls.

Pogonomyces hydnoides (Swartz ex Fries) Murrill. This subtropical species is characterized by having small pores, dark brown context, and coarsely hirsute upper surface. According to M. Fidalgo (1968), the species should be placed in the genus *Hexagona,* which is normally restricted to those tropical forms with large, hexagonal pores.

Fomes. As mentioned above, this name has been used for a variety of fungi with large, perennial sporophores. The type, *F. fomentarius,* and its tropical counterpart *F. sclerodermeus,* may be distinguished from other perennial species by the yellowish brown context, hard surface cuticle, trimitic hyphal system with clamp connections, and simple spores.

Fomes fomentarius (Linnaeus ex Fries) Kickx

Fomes sclerodermeus (Leveille) Cooke [= *Fomes marmoratus* (Berkeley and Curtis) Cooke]

Ganoderma. This genus contains a large number of species in which the spores have a spiny inner coat and a smooth, colorless outer coat. The species also share a number of micromorphological characters discussed in detail by Hansen (1958). As in the genus *Fomes,* the hyphal system (of the context) is trimitic, but the color of the hyphal walls varies from brown in *G. applanatum* or *G. zonatum* to yellowish or hyaline in *G. tsugae.* Some authors (Cunningham, 1965) include the darker forms in the genus *Elfvingia.* The general form of the fruiting body is also variable, being stipitate with a thin, varnished cuticle in *G. tsugae* and its relatives, and sessile with a thick, woody cuticle in *G. applanatum.*

Ganoderma applanatum (Persoon ex Wallroth) Patouillard [= *Ganoderma australe* (Fries) Patouillard]

Ganoderma brownii (Murrill) Gilbertson

Ganoderma curtisii (Berkeley) Murrill

Ganoderma fulvellum Bresadola

Ganoderma lobatum (Schweinitz) Atkinson

Ganoderma lucidum (Leysser ex Fries) Karsten

Ganoderma oregonense Murrill

Ganoderma tsugae Murrill

Ganoderma zonatum Murrill

Ganoderma sp.

HYMENOCHAETACEAE

This family includes those species with characteristic yellow-brown hyphae, permanently blackening in KOH, and a monomitic or dimitic hyphal system, always lacking clamp connections. Binding hyphae never occur in this group, and setae are usually present in the hymenium (secondarily lost in some). In addition to the "polypore" genera mentioned below, the family also includes *Hymenochaete,* formerly considered to be in the Thelephoraceae because of the flat hymenial surface.

Cyclomyces iodinus (Montagne) Patouillard. This has a small, dark brown fruiting body with a very thin layer of context tissue. The hyphal system is monomitic as in the next genus.

Inonotus. This genus, which was reviewed by Pegler (1964), contains the majority of brown, monomitic species which usually possess setae. The context may be soft and spongy when fresh, but older specimens are fibrous or woody and may be brittle. *I. corrosus* is placed here for convenience, although it was removed by Pegler. *I. munzii* is considered to be a distinct species following Gilbertson (1969).

Inonotus corrosus Murrill
Inonotus munzii (Lloyd) Gilbertson
Inonotus porrectus Murrill ?
Inonotus rheades (Persoon) Bondarzew and Singer [= *Polyporus vulpinus* Fries]
Inonotus sp.
Phaeolus schweinitzii (Fries) Patouillard. This species produces a brown rot in conifers. In microstructural details the fruiting body is similar to those of *Inonotus*.
Melanoporia nigra (Berkeley) Murrill. This is a resupinate form with deep purple coloration which soon turns black. It appears to be closely related to the perennial *Nigrofomes melanoporus* (Lowe, 1957); both species are tropical.

Phellinus. This is a large genus of perennial or persistent forms in which the hyphal system is dimitic. The texture of the context is much woodier than that in *Inonotus*, and the color is yellowish brown to reddish brown. *Phellinus gilvus* and its tropical counterpart *P. licnoides* are the commonest annual species, and both cause white rot in a variety of hardwoods. Of the perennial forms, *P. igniarius* is common on hardwoods in northern areas, *P. pini* produces a white rot in northern conifers, and *P. robiniae* is a parasite of locust trees in the eastern United States. In tropical areas, there are many closely related species.

Phellinus everhartii (Ellis and Galloway) Ames [= *Fomes praerimosus* (Murrill) Saccardo and D. Saccardo]
Phellinus ferruginosus (Schrader ex Fries) Bourdot and Galzin
Phellinus gilvus (Schweinitz) Patouillard
Phellinus igniarius (Linnaeus ex Fries) Quelet
Phellinus johnsonianus (Murrill)
Phellinus laevigatus (Fries) Bourdot and Galzin
Phellinus licnoides (Montagne) Patouillard
Phellinus pini (Broteri ex Fries) Ames
Phellinus pomaceus (Persoon) Maire
Phellinus ribis (Schumacher ex Fries) Bondarzew and Singer
Phellinus robiniae (Murrill) Ames [= *Fomes rimosus* (Berkeley) Cooke, of authors]
Phellinus robustus (Karsten) Bourdot and Galzin
Phellinus sp.

Other Fungus Species Mentioned in Text

Bjerkandera fumosa (Persoon ex Fries) Karsten
Coriolus velutinus (Fries) Quelet
Daedalea quercina Linnaeus ex Fries
Exidia glandulosa Fries [TREMELLACEAE]
"Fomes" pini-halepensis Patouillard
Hirschioporus fusco-violaceus (Ehrenberg) Donk
Hirschioporus laricinus (Karsten) Teramoto
Inonotus dryadeus (Persoon ex Fries) Murrill
Inonotus hispidus (Bulliard ex Fries) Karsten
Nigrofomes melanoporus (Montagne) Murrill
Osmoporus odoratus (Wulfen ex Fries) Singer
Piptoporus portentosus (Berkeley) Cunningham
Pseudotrametes gibbosa (Persoon) Bondarzew and Singer
Stereum rugosum Persoon
Trametes suaveolens (Linnaeus ex Fries) Fries
Tyromyces stipticus (Persoon ex Fries) Kotlaba and Pouzar

Nature of the Fungus Substrate

Since the fruiting body serves as habitat and food source for ciids and other mycetophagous arthropods, it might be well to examine a) those characteristics of the sporophore which are common to all or most of the host species and may be used in defining the general habitat, and b) those features that differ from group to group and may be involved in host selection by the beetles.

The following are some general features of the fruiting body which are shared by all or most of the fungi: 1) They grow on wood and may incorporate into their structures chemical substances derived from the wood (*see* below). 2) They are usually durable, often woody or corky, and persist long enough to be inhabited by relatively stationary insects (most boring larvae) with a life cycle exceeding several weeks. 3) They usually grow off the ground and are less likely to be subjected to rapid bacterial and fungal decay or water-logging; thus they tend to retain their chemical and structural characteristics longer than mushrooms and other ground fungi. 4) They contain a high percentage of plant chitin, which in most fungi assumes the role of cellulose in providing a skeletal framework for the cell wall. This is a linear molecule constituted entirely of β-1,4 linked N-acetylglucosamine residues (Aronson, 1965). 5) The hard texture of many sporophores may necessitate special boring adaptations in the insect inhabitants. 6) The fauna inhabiting these fruiting bodies is very diverse and contains more Coleoptera and fewer Diptera than that found in mushrooms and boletes. 7) The habitat is a very localized one, since each fungus species has a limited range of host plants, and the production of a fruiting structure is often seasonal and may involve a particular set of environmental prerequisites.

The second class of characteristics—those which differ from group to group and may be used by oligophagous insects in selecting preferred hosts—are either chemical or structural. The most obvious chemical character of the fruiting body is its color. The various pigments that produce the yellow-brown color of many hymenochaetaceous conks or the violet dissepiments in *Hirschioporus* may also produce the odors used by insects in differentiating among host species. A related feature is the color change produced by KOH. In many of the darker fruiting bodies the tissue will turn permanently black with the application of potassium hydroxide solution. The same reaction may be seen in the feces of Ciidae which have fed on sporophores of *Phellinus, Ganoderma,* and other dark forms; the fecal pellets are always black, whereas they are usually only slightly darker than the color of the context. Another less obvious feature is the presence of crystals on the cystidia or among the context hyphae; according to Overholts (1953) these are composed of calcium oxalate.

Unfortunately, there has been very little published on the biochemistry of fruiting bodies encountered in this study. Arpin and Fiasson (1971) discuss a number of fungus pigments, but few of these occur in polypores. One of the more well known is cinnabarin, which causes the bright red color in *Pycnoporus cinnabarinus.* An interesting pigment and one more relevant to the present study is hispidin, which is discussed by Bu'Lock (1967). This phenolic compound, which has been isolated from the sporophores of *Inonotus hispidus* and *Phaeolus schweinitzii,* contributes to the dark color of the conk but is also involved in the hardening of the fruiting body with age. In the unripe fruits of *I. hispidus,* there is an excess of alcohol-soluble phenolic material (from which hispidin can be extracted) and a powerful phenol oxidase system which causes polymerization of the hispidin. The resulting hispidin polymer contributes to the hardening of the tissue in the ripe conk. Hispidin is synthesized in part from breakdown products of lignin in the woody substrate; in a "white rot" fungus, such as *I. hispidus,* there is an excess of hispidin produced, which is then polymerized, but in a "brown rot" fungus, such as *P. schweinitzii,* polymerization is limited, since a lack of lignin breakdown products prevents the build up of excess hispidin. It is possible that this same system is operating in other "white rot" fungi with brownish sporophores, such as the species of *Phellinus.*

The structural features that are most likely to be involved in host preference are the thickness of hyphal walls and the branching and intertwining of context hyphae, since these are largely responsible for the consistency of the tissue on which the ciids must feed. The complexity of the hyphae may be expressed to some extent by using Corner's terms, but the limitations of this system have been discussed above (p. 168). Fruiting bodies with a monomitic hyphal system, such as those of *Bjerkandera adusta,* are usually fairly soft, since they are composed entirely of thin-walled generative hyphae; in species of *Inonotus,* however, the hyphal walls thicken with age, producing a fibrous or woody context. Dimitic species fall into two major groups, depending upon whether skeletal or binding hyphae are present. In species of *Phellinus, Rigidoporus,* and *Heterobasidion,* the context consists primarily of parallel, thick-walled, skeletal hyphae, and the result is a very hard and woody substrate. In certain other dimitic forms, such as *Polyporus squamosus* and *Piptoporus betulinus,* the major supportive structures are branched and intertwining binding hyphae, so that the tissue is more felt-like, resembling that of the next group. In trimitic species, including all of the "trametoids" and "fomitoids" discussed above, both skeletal and binding hyphae are present and the tissue is somewhat felty, leathery, or corky, but never hard and rigid.

BIOLOGY OF THE CIIDAE

Nearly all members of the family Ciidae feed in both larval and adult stages on fungal hyphae comprising the mycelia and especially the fruiting bodies of various wood-rotting Basidiomycetes. Several species have been recorded from under bark, in dead wood, in decaying branches and vines, or in the galleries of bark beetles (Donisthorpe, 1938; Reitter, 1878; Swezey, 1954), but it is likely that they were associated with fungi in these habitats.

Life Cycle

Little is known about the dispersal activities of ciids, but in spring they begin to congregate on newly formed fruiting bodies. Graves (1960) notes that individuals of *Cis levettei* often fly during daylight hours, and I have collected a female of *Cis fuscipes* flying at dusk in April. Linsley and Usinger (1944) reported on large dispersal flights of subcortical and wood-boring Hemiptera and Coleoptera encountered on spring afternoons in the Sierra Nevada; no ciids were taken in these flights, although several species are common in the area. Ciidae may fly at night, but they are almost never taken at lights.

The method of entry into the sporophore will vary with the species of beetle and the form, position, and physical condition of the fruiting body. In several California species, adults enter the sporophore from the upper surface near the base. Entry at this point will put the beetle into immediate contact with the largest mass of context tissue, which is usually the preferred food of the larvae. Occasionally individuals will enter the conk by moving through cracks in the bark and boring into the base; there may be no visible signs of entry, and yet a large colony of ciids may be present within. According to Matthewman and Pielou (1971), *Cis levettei* and *Dolichocis manitoba* will usually begin work in the upper part of the context (of *Fomes fomentarius*) and will spread through the context and "mycelial core." As the populations grow, however, the hymenium is also attacked. I have observed a similar pattern in various Ciidae attacking the larger conks of *Fomes, Fomitopsis,* and *Ganoderma,* but in thinner fruiting bodies, such as those of *Coriolus* or *Hirschioporus,* the beetles may bore into the tramal tissue just beneath the hymenium or even through the walls of the pores.

The female of *Cis vitulus* bores immediately into the fungus tissue and is usually out of sight in a short time, while the male is more active on the surface of the conk. According to Entwistle (1955), the male of *Cis bilamellatus* Wood wanders about the surface and does not take part in construction of an egg gallery. Males were observed to become excited when encountering the abdomen of a female protruding from a gallery, and this was postulated to be the stimulus for copulation, which lasted from five to ten minutes.

Oviposition behavior has been described by Chapman (1869) and Entwistle (1955). Chapman observed that the female of *Octotemnus glabriculus* (Gyllenhal) constructs a definite egg gallery with egg cavities placed irregularly along the walls. One egg is placed in each cavity, which is then closed with a tightly packed plug of frass (chewed but undigested fungus tissue). Entwistle observed similar behavior in *O. glabriculus, Sulcacis affinis* (Gyllenhal), and *Cis boleti* (Scopoli), but she noted that in *Cis bilamellatus* eggs were laid in pairs within each cavity. Graves (1960) recorded the oviposition by *Cis levettei* directly on the pore surface (probably of *Ganoderma applanatum*); the egg hatched after two days and the larva crawled into one of the tubes. I have observed the frass-plugged egg cavities of *Ceracis minutissimus* lining a gallery at the base of the hymenium of *Cerrena unicolor,* and similar cavities were constructed by *Malacocis brevicollis* in the hard context tissue of *Phellinus gilvus.* The egg-laying period appears to be several months long and there is considerable overlap in generations.

The ciid larvae, upon hatching, bore directly into the fungus tissue, and not through the frass plug. There are five larval instars in *Cis vitulus* and each stadium lasts about six or seven days. *Sulcacis curtulus* was reared through its cycle on a mash of *Coriolus versicolor* in less than 60 days, but the exact length of a generation was not determined. Entwistle (1955) found the life cycle to be about eight weeks long in *Cis bilamellatus.* She also noted that adults do not become fully pigmented for three or four weeks. According to Klopfenstein (1972), there are only three larval instars in *Hadraule blaisdelli* reared on various hosts in the laboratory; each stadium is 13 or 14 days long and the pupal stage lasts ten days, so that the total life cycle (egg to adult) is still about eight weeks in duration. Adults remain in their pupal chambers for a few days after eclosion and then bore out onto the surface of the conk. It is not known whether adults disperse immediately to other fruiting bodies or remain within the same one. It is possible that dispersal flights are stimulated by depletion of the medium or by an unfavorable change owing to fouling, dessication, or decay. Under laboratory conditions some ciids may be reared through several generations on the same piece of fungus, a record of thirteen years without added food or moisture being reported by Klopfenstein (1972) for *H. blaisdelli.*

Ecological Role, Competitors, Predators, Parasites

As mentioned above, the Ciidae are normally restricted to wood-rotting fungi and are most common in those with durable, leathery or woody sporophores. In addition, both larvae and adults feed internally within the sterile pileus, where they chew the fungal hyphae comprising the context tissue. Some species may feed on the dissepiments, but this is usually after much of the context has been exhausted (Matthewman and Pielou, 1971). Moreover, Ciidae usually concentrate on those fruiting bodies which have shed their spores and are beginning to decompose (stages III and IV of Graves, 1960) and are less common on very old conks (stage V). In perennial fruiting bodies, it is usually the upper, older portions that are attacked. In the terminology of Scheerpeltz and Höfler (1948), ciids are mycetobionts; that is, they spend most of their lives within the fungus sporophores and are entirely dependent upon them for food and shelter.

Ciidae may be contrasted with the facultative fungus-feeders or mycetophiles and with those mycetobionts which differ in their feeding habits and are thus not in direct competition with ciids. For example, certain flies and tetratomid beetles (*Tetratoma*) attack only living sporophores

(Paviour-Smith, 1960b, 1965a, 1965b); nitidulids such as *Aphenolia monogama* (Crotch) and ptiliid beetles in the Nanosellinae feed exclusively on spores (Dybas, 1956; Gillogly, 1965; Gillogly and Gillogly, 1954); aradid bugs suck the juices from fresh fruiting bodies (Korinek, 1935); many beetles in the Lathridiidae and Corylophidae are attracted to molds and other secondary fungi (Crowson, 1955); and insects such as the Psocoptera occur in very old conks where they feed on dead insect remains as well as fungus tissue (Graves, 1960).

The most important direct competitors of ciids are tenebrionid beetles presently included in the tribes Bolitophagini, Rhipidandrini, and Diaperini. In North America, the most common of these are *Bolitotherus cornutus* (Panzer), *Eleates* spp., *Diaperis maculata* Olivier, *Neomida bicornis* (Fabricius), and several species of *Platydema*. Further south and in the New World tropics, species of *Rhipidandrus, Neomida,* and *Platydema* are abundant in fungi.

Other important groups of competitors among the Coleoptera are the dorcatomine Anobiidae (*Dorcatoma, Priotoma*), bostrichids of the genus *Hendecatomus*, members of the family Peltidae (*Ostoma, Thymalus*), eustrophine Melandryidae (*Orchesia, Eustrophinus*), and the anthribid beetle *Euparius marmoreus* (Olivier) (Lawrence, unpublished data; Matthewman and Pielou, 1971; Weiss and West, 1920, 1921).

Among the Lepidoptera, tineid moths, especially the genus *Nemapogon*, are particularly common (Lawrence and Powell, 1969). In the Diptera, phorid flies of the genus *Megaselia* are generally common in this habitat, and the platypezid *Polyporivora polypori* (Willard) is a regular inhabitant of *Coriolus versicolor* (Borgmeier, 1966; Kessel, 1969). Finally, the Acarina include a number of fungus-feeding forms, particularly among the Cryptostigmata (*Carabodes*) (Matthewman and Pielou, 1971).

Predators of Ciidae include a variety of forms, many of which also work adjacent habitats, such as bark, wood, and foliage. Among these are Carabidae (*Tachys*), numerous Staphylinidae, Trogositidae (*Temnochila*), Cleridae (*Ababa, Zenodosus*), Cerylonidae, anthocorid bugs (*Lyctocoris, Xylocoris*), cecidomyid flies (*Lestodiplosis*), spiders, and mites. Parasitic Hymenoptera are probably more important in the regulation of ciid populations, and many of these appear to be restricted to fungi, if not to the ciid hosts. These include Braconidae (*Meteorus, Eubadizon*), Pteromalidae (*Janssoniella*), Eulophidae (*Astichus*), and Bethylidae (*Plastanoxus chittendenii* Ashmead and *Cephalonomia perpusilla* Evans).

PATTERNS OF HOST PREFERENCE

The following analysis is based on 2075 host records (995 breeding) presented in the next section (pp. 190–207) and summarized in Table 1. Although 74 North American Ciidae have been recorded from fungi, seven of these are known from a single occurrence, and only 51 have been collected five or more times. Five species have never been recorded as breeding in a particular host, while 11 are represented by a single breeding record and 45 are known from five or more. To some extent these figures reflect a geographic collecting bias, since many of the lower numbers represent poorly known Neotropical species extending into the southern United States. In analyzing the host data, an attempt will first be made to express the degree of host or habitat preference without reference to specific host species, and this will be followed by a discussion of particular groups of host fungi, their major features, and characteristic faunas.

Host Range and "Niche Breadth"

The host range (or the total number of fungus species with which an animal is known to be associated) gives the roughest measure of the degree of host preference, and this may be further refined by eliminating incidental or nonbreeding hosts. The North American ciid with the broadest

TABLE 1. SUMMARY OF HOST DATA FOR NORTH AMERICAN CIIDAE

Beetle Species	Geographical* Distribution	Fungi TOT(BR)	Records TOT(BR)	Niche Breadth** B_s	B_g	Preference Group or Preferred Host
1. Cis acritus	SW	1(1)	7(1)			Hirschioporus
2. Cis americanus	NW–SE	24(18)	69(35)	14.40		Ganoderma
3. Cis angustus	NW	3(1)	4(2)			Ganoderma
4. Cis biarmatus	NW	1(1)	10(6)	1.00		Ganoderma
5. Cis castlei	NE–SE	13(4)	27(7)	3.16		Ganoderma
6. Cis cayensis	SE	5(3)	16(7)	2.57		Phellinus
7. Cis congestus	SE	2(1)	4(2)			Coriolus
8. Cis cornelli	SE	1(1)	4(2)			Hirschioporus
9. Cis cornutus	NE–SE	2(2)	5(4)			Coriolus
10. Cis creberrimus	NE–SW	24(13)	47(18)	11.24		Ganoderma
11. Cis crinitus	SE	5(4)	10(5)	3.80		Ganoderma?
12. Cis discolor	SW	2(2)	4(2)			Ganoderma
13. Cis duplex	SW	4(4)	11(10)	3.39		Ganoderma?
14. Cis ephippiatus	NW–NE	8(3)	24(14)	2.57		Ganoderma
15. Cis floridae	SE	3(2)	5(2)			Phellinus
16. Cis fuscipes	NW–SE	13(8)	135(69)	2.82	1.48	Coriolus
17. Cis hirsutus	SE	17(9)	41(16)	7.95	4.68	Ganoderma
18. Cis horridulus	NW–NE	2(2)	22(10)	1.95	1.00	Hirschioporus
19. Cis hystriculus	NW	3(1)	29(16)	1.00		Hirschioporus
20. Cis laminatus	NE	1(0)	1(0)			
21. Cis levettei	NW–SE	19(10)	140(76)	4.79	3.55	Ganoderma
22. Cis maritimus	NW	2(2)	3(2)			Phellinus
23. Cis megastictus	NW	3(1)	3(1)			Ganoderma?
24. Cis miles	NE–SE	5(3)	13(4)			Coriolus
25. Cis niedhauki	SE	1(1)	4(2)			Phellinus
26. Cis pistoria	NW–NE	4(4)	11(8)	3.39	1.45	Coriolus
27. Cis robiniophilus	NE–SE	1(1)	3(2)			Tr. robiniophila
28. Cis rotundulus	SE	5(1)	7(1)			Ganoderma?
29. Cis stereophilus	NE–SE	2(2)	12(7)	1.82	1.00	Stereum spp.
30. Cis striolatus	NW–NE	4(4)	12(7)	3.55	2.24	Hirschioporus
31. Cis subfuscus	SE	3(2)	4(2)			Coriolus
32. Cis subtilis	NE–SE	7(3)	50(17)	2.14	1.00	Hirschioporus
33. Cis tetracentrum	SW	1(1)	6(5)	1.00		Coriolus
34. Cis tridentatus	NW	9(6)	19(12)	3.46		Ganoderma
35. Cis tristis	NE–SE	9(5)	14(7)	4.36	2.57	Coriolus
36. Cis ursulinus	SE	5(0)	5(0)			
37. Cis versicolor	NW–SW	7(4)	40(23)	2.78	2.18	Coriolus
38. Cis vitulus	NW–SW	4(3)	36(22)	1.78		Coriolus
39. Enn. aurisquamosum	NE–SE	1(0)	1(0)			
40. Enn. spenceri	NW	1(0)	1(0)			
41. Dol. indistinctus	NW–NE	3(1)	9(5)	1.95		Ganoderma
42. Dol. manitoba	NW–NE	12(7)	73(31)	2.95		Ganoderma
43. Orth. punctatus	NW–SE	1(1)	1(1)			Aur. auricula?
44. Str. bilimeki	SW	2(1)	2(1)			Coriolus?
45. Str. opacicollis	NE–SE	10(5)	48(18)	2.29	1.23	Coriolus
46. Str. opalescens	NE–SE	1(1)	3(1)			Coriolus
47. Hadr. blaisdelli	NW–SW	11(7)	19(8)	6.77		
48. Hadr. elongatula	NE	1(1)	1(1)			Ganoderma?
49. Ples. cribrum	NW–NE	3(2)	58(35)	1.51		Crypt. volvatus
50. Cer. californicus	NW–SW	20(15)	80(32)	11.20	5.89	Ganoderma?
51. Cer. curtus	SE	2(1)	4(2)			Ganoderma
52. Cer. dixiensis	SW	2(1)	12(9)	1.00		Coriolus
53. Cer. magister	SE	1(1)	4(4)			Phellinus
54. Cer. minutissimus	NE–SE	3(1)	11(9)	1.00		Cerr. unicolor

TABLE 1. (*Continued*)

	Beetle Species	Geographical* Distribution	Fungi TOT(BR)	Records TOT(BR)	Niche Breadth** B_s	B_g	Preference Group or Preferred Host
55.	Cer. minutus	SE	9(8)	34(24)	7.09		Coriolus?
56.	Cer. monocerus	SE	1(1)	2(1)			Coriolus?
57.	Cer. multipunctatus	SE	6(3)	17(13)	2.95	1.99	Ganoderma
58.	Cer. nigropunctatus	SE	4(2)	14(5)	1.66		Ganoderma
59.	Cer. obrieni	SW	1(1)	5(5)	1.00		Phellinus
60.	Cer. pecki	NE–SE	1(1)	1(1)			Phellinus?
61.	Cer. powelli	SW	2(1)	3(1)			Hirschioporus
62.	Cer. pullulus	SE	10(7)	43(23)	5.13	3.09	Phellinus
63.	Cer. punctulatus	NE–SE	19(9)	92(45)	4.26	2.88	Phellinus
64.	Cer. quadricornis	SE	7(5)	21(13)	4.26		Coriolus?
65.	Cer. sallei	NE–SE	10(6)	45(22)	2.45	1.31	Ganoderma
66.	Cer. schaefferi	SE	1(0)	1(0)			
67.	Cer. similis	SW	3(3)	6(6)	2.78	1.00	Ganoderma
68.	Cer. singularis	NE–SE	21(9)	59(17)	6.45	2.40	Phellinus
69.	Cer. thoracicornis	NE–SE	36(21)	187(73)	12.00	8.31	Hirschioporus?
70.	Sulc. curtulus	NW–NE	14(7)	119(55)	3.46	2.51	Coriolus
71.	Sulc. lengi	NE–SE	5(3)	20(7)	2.95		Coriolus
72.	Mal. brevicollis	NE–SE	16(9)	79(37)	5.50	1.12	Phellinus
73.	Rhop. americanus	NE	3(1)	3(1)			Ganoderma?
74.	Oct. laevis	NW–SE	14(6)	130(63)	2.24	1.26	Coriolus

* *See* explanatory notes on p. 165.

** B_s computed for species with 5 or more breeding records. B_g computed for selected species (*see* p. 182).

host range is *Ceracis thoracicornis*, which has been recorded from 36 different hosts and is capable of breeding in at least 21 of them. Other polyphagous species are *Cis americanus* and *Cis creberrimus*, each of which is known from 24 different fungus species. As many as 26 Ciidae are recorded from more than five fungi and 15 from more than ten, but when nonbreeding hosts are excluded, these figures are reduced to 18 and four, respectively. Almost one-fourth of the species appear to be monophagous, but this is partly due to sampling error.

A more precise measure of degree of preference may be obtained by using one of the indices of ecological diversity, based on the equation $H = -\Sigma p_i \log p_i$, where p_i is the proportion of individuals of a particular species inhabiting segment i of the environment, or the proportion of individuals in a particular environment belonging to species i, depending upon whether habitat diversity or species diversity is desired (MacArthur, 1965; E. Pielou, 1969). The measure used here is a modified form of B or niche breadth, discussed by Levins (1968: 43), and defined by the equation $\log B = -\Sigma p_i \log p_i$. In the strict sense, this is a measure of the "niche" of a species in a particular community, and p_i is the proportion of individuals of that species occupying a specific habitat (or host) i. In the present treatment, B_s refers to "niche breadth" over the entire geographic range of the species, and p_i is the proportion of breeding records for a specific host. The measure B_g is similar, except that p_i is the proportion of breeding records for hosts within a certain genus of fungi. In Table 1, B_s is given for all ciids with five or more breeding records, while B_g is given for selected species only. The value of B varies from 1.00 for monophagous species to almost 15 for certain polyphagous forms.

The distribution of B_s values is shown in Figure 1, with sample size (number of breeding records) indicated by shading. The mode lies between 2.5 and 3.0, while

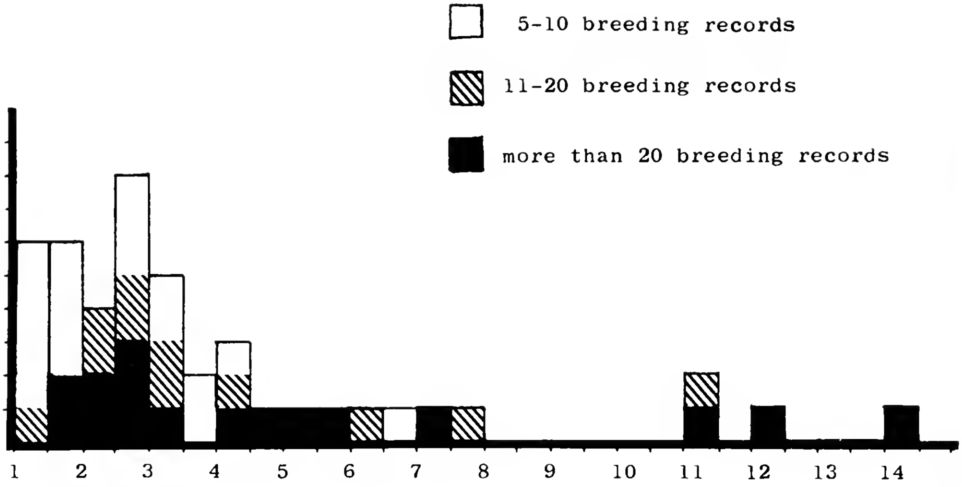

Figure 1. "Niche Breadth" Distribution and Sample Size

the median is 2.91. Although species with less than five breeding records were excluded, the B values are still correlated with sample size, and further sampling would probably eliminate several species from the first class (1.00–1.49). The majority of ciids appear to breed in several hosts, with a preference for one or two. In interpreting these values, it must be remembered that the calculations are based on all breeding records throughout the geographic range (which may be several thousand miles in diameter), and that no consideration has been given to the abundance of certain fungus species or the number of potential hosts to which a ciid has access.

The second value, B_g, based on the genera of fungi discussed on pages 169–175, gives a better idea of which species prefer a group of phylogenetically related fungi, which possess one or several sporophore characters in common and thus may be considered as one type of habitat or food source. It has been calculated for selected species, in order to illustrate how it compares with B_s in group-specific ciids and with those which are apparently less discriminate. The best example of a group-specific species with a high B_s is *Malacocis brevicollis*; although B_s is 5.5 and the number of breeding hosts is nine, almost all of the fungi are in the genus *Phellinus*, so that B_g is only 1.12. In other species, such as *Cis hirsutus*, B_g is not much lower than B_s.

Headquarters and Host Preference Groups

Paviour-Smith (1960a), in her study of host utilization by Ciidae inhabiting Wytham Woods, near Oxford, England, found that the beetles could be divided into two breeding groups and the fungi into two corresponding habitat groups, so that ciids in one group would only rarely breed in fungi of the other. She used the term "headquarters" for the one fungus species in whose fruiting bodies a particular beetle most commonly breeds and successfully completes its life cycle. Within each habitat group, a specific host might serve as headquarters for one species and be inhabited less frequently by others. These assemblages of Ciidae and their hosts are referred to here and in my earlier papers (Lawrence, 1967a, 1971, in press) as host preference groups.

The first group in the Wytham study included the common *Piptoporus betulinus* and *Ganoderma applanatum*, along with several rarer forms, such as *Polyporus squa-*

mosus, Bjerkandera adusta, Inonotus dryadeus, Phellinus pomaceus, and *Phellinus igniarius.* The Ciidae inhabiting these fungi included *Cis nitidus* (Fabricius), *Cis bidentatus* (Olivier), *Cis fagi* Waltl, *Cis bilamellatus* Wood, and *Ennearthron cornutum* (Gyllenhal). The headquarters of *Cis bilamellatus* was *P. betulinus,* while *Cis nitidus* bred most often in *G. applanatum* and *E. cornutum* preferred species of *Phellinus* (Paviour-Smith, 1969 and personal communication). *Cis bilamellatus* was usually the first species to colonize the fruiting bodies of *P. betulinus,* while *Cis bidentatus* and others were found in older conks. Paviour-Smith's second group included *Coriolus versicolor, Coriolus hirsutus, Pseudotrametes gibbosa, Lenzites betulina,* and an unidentified "*Daedalea*" among the hosts, while the Ciidae inhabiting them were *Cis boleti* (Scopoli), *Cis hispidus* (Paykull), *Strigocis bicornis* (Mellié), *Sulcacis affinis* (Gyllenhal), and *Octotemnus glabriculus* (Gyllenhal). No definite headquarters could be determined, but succession apparently took place in the conks of *C. versicolor,* with *O. glabriculus* being the first colonizer and *Cis boleti* occurring on older sporophores.

Paviour-Smith found that the main difference between fungi of the two groups, which might account for the selective utilization by ciids, was in the microstructure of the fruiting body. In the *Coriolus versicolor* group, sporophores of all species are trimitic, with both skeletal and binding hyphae, while fungi in the *Piptoporus betulinus* group are usually monomitic or dimitic. One of the more common hosts in the latter group, however, is *Ganoderma applanatum,* which is trimitic. The possibility of chemical attractants was dismissed on the grounds that old fruiting bodies are colonized after long periods of wetting and drying. The division into two host or habitat groups has been confirmed in later studies of southern European ciids (Paviour-Smith, 1969; Roman, 1970), and the same scheme, with some modifications, may be applied to the North American species as well.

The majority of North American Ciidae for which breeding hosts have been identified tends to fall into four host preference groups, as shown in Table 2. Beetles in each group are listed according to their occurrence in a particular geographic sector, as defined on page 165, and an asterisk is placed after those species common in that sector. Species that are questionably included within a group may be represented by too few breeding records or may have a broad host range including fungi in more than one group. Species placed in parentheses are common in fungi of a particular group, but still show a preference for those of another group. *Ceracis californicus,* for example, in the Northwest and Southwest sectors, appears to prefer the fruiting bodies of *Ganoderma* and yet is a fairly common member of the *Coriolus* fauna in those areas. The major characteristics of the four groups are given below, followed by a discussion of those Ciidae and host fungi which are not readily placed in any group.

The *Coriolus* Group. This is a large and well-defined assemblage corresponding to the "*Polystictus versicolor* group" of Paviour-Smith and including all of the trametoid fungi with thin, lightly pigmented, leathery fruiting bodies containing both skeletal and binding hyphae (trimitic). On the Pacific Coast, there are five common ciids, three of which extend across the northern part of the continent. *Cis fuscipes* and *Octotemnus laevis* are equally common on both coasts, while *Sulcacis curtulus* is mainly western. *Cis pistoria* is primarily a northeastern species, and in the southern part of New England, it is replaced by two species with Neotropical affinities, *Strigocis opacicollis* and *Sulcacis lengi.* In the Southeast, several other Neotropical species enter into the fauna, and *C. fuscipes* and *O. laevis* begin to drop out. The southwestern fauna includes *Cis versicolor,* which extends into Oregon, *Cis tetracentrum,* a southern mon-

TABLE 2. HOST PREFERENCE GROUPS IN NORTH AMERICAN CIIDAE

Northwest	Northeast	Southeast	Southwest
CORIOLUS GROUP: Hyphae pale; hyphal system trimitic. Fruiting body thin, leathery, whitish or cream. *Pycnoporus, Coriolus, Lenzites, Earliella?, Funalia, Coriolopsis.*			
		Cis congestus	
	Cis cornutus	Cis cornutus*	
Cis fuscipes*	Cis fuscipes*	Cis fuscipes*	
	Cis miles	Cis miles*	
Cis pistoria	Cis pistoria*		
		Cis subfuscus	
			Cis tetracentrum*
	Cis tristis	Cis tristis	
Cis versicolor*			Cis versicolor*
Cis vitulus*			Cis vitulus
			?Str. bilimeki
	Str. opacicollis*	Str. opacicollis*	
	Str. opalescens	Str. opalescens	
(Cer. californicus)*			(Cer. californicus)*
			Cer. dixiensis*
		?Cer. minutus	
		?Cer. monocerus	
		?Cer. quadricornis	
	(Cer. thoracicornis)*	(Cer. thoracicornis)*	
Sulc. curtulus*	Sulc. curtulus		
	Sulc. lengi*	Sulc. lengi*	
Oct. laevis*	Oct. laevis*	Oct. laevis*	
HIRSCHIOPORUS GROUP: Hyphae pale; hyphal system dimitic. Fruiting body thin, leathery or rigid, whitish to gray or violet; hymenium violet or brown with encrusted cystidia. *Hirschioporus.*			
			Cis acritus*
		Cis cornelli	
Cis horridulus	Cis horridulus*		Cis horridulus
Cis hystriculus*			
Cis striolatus	Cis striolatus		
	Cis subtilis*	Cis subtilis*	
			Cer. powelli
	?Cer. thoracicornis*	?Cer. thoracicornis*	
PHELLINUS GROUP: Hyphae brown, black in KOH; hyphal system monomitic or dimitic. Fruiting body usually woody, perennial or persistent, sometimes fibrous, annual; usually brownish in color. *Cyclomyces, Inonotus, Phaeolus, Melanoporia, Phellinus.*			
		Cis cayensis	
		Cis floridae	
Cis maritimus			
		Cis niedhauki	
		Cer. magister	
			Cer. obrieni
	Cer. pecki	Cer. pecki	
		Cer. pullulus*	
	Cer. punculatus*	Cer. punctulatus*	
	Cer. singularis*	Cer. singularis*	
	Mal. brevicollis*	Mal. brevicollis*	

TABLE 2. (*Continued*)

Northwest	Northeast	Southeast	Southwest
GANODERMA GROUP: Hyphae pale to brown; hyphal system monomitic, dimitic, or usually trimitic. Fruiting body variable, usually corky to woody, perennial, and tan to brown in color. *Laetiporus, Bjerkandera, Oxyporus, Ischnoderma, Piptoporus, Laricifomes, Fomitopsis, Heterobasidion, Rigidoporus, Antrodia, Gloeophyllum, Datronia, Daedaleopsis, Pogonomyces, Fomes, Ganoderma.*			
Cis americanus*	Cis americanus*	Cis americanus	
Cis angustus			
Cis biarmatus*			
	Cis castlei	Cis castlei*	
	Cis creberrimus	Cis creberrimus*	Cis creberrimus*
		?Cis crinitus	
			Cis discolor
			?Cis duplex*
Cis ephippiatus*	Cis ephippiatus		
		Cis hirsutus*	
Cis levettei	Cis levettei*	Cis levettei	
?Cis megastictus			
		?Cis rotundulus	
Cis tridentatus			
Dol. indistinctus	Dol. indistinctus		Dol. indistinctus
Dol. manitoba*	Dol. manitoba*		
	?Hadr. elongatula		
?Cer. californicus*			?Cer. californicus*
		Cer. curtus	
		Cer. multipunctatus*	
		Cer. nigropunctatus	
		(Cer. punctulatus)*	
	Cer. sallei*	Cer. sallei*	
			Cer. similis
	(Cer. thoracicornis)	(Cer. thoracicornis)	
	?Rhop. americanus		

tane form, and *Ceracis dixiensis,* which is usually associated with *Populus* at lower elevations. Two polyphagous species, *Ceracis californicus* and *Ceracis thoracicornis,* may be common inhabitants in the west and east, respectively, but each prefers a different group of fungi. It is difficult to determine any definite headquarters for most species with sufficient host records, but *Ceracis dixiensis* in the Southwest appears to be restricted to *Funalia hispida.* Like its Palaearctic counterpart, *Octotemnus laevis* prefers fresh fruiting bodies and is usually the first colonizer. Other common insects inhabiting the *Coriolus* group in eastern North America are *Neomida bicornis* (Fabricius) [Coleoptera: Tenebrionidae] and *Orchesia castanea* Melsheimer [Col.: Melandryidae].

The *Hirschioporus* Group. Although the fruiting bodies of *Hirschioporus* species resemble those of *Coriolus* and related genera, they harbor a distinct fauna in most areas studied. *Cis hystriculus* is the only common species on the west coast, while *Cis horridulus* and *Cis striolatus* are northern and montane. The main inhabitants in eastern North America are *Cis subtilis* and the eurytrophic *Ceracis thoracicornis.* Although no members of this group were found in Paviour-Smith's study area, the Palaearctic *Cis punctulatus* is known from various *Hirschioporus.*

The *Phellinus* Group. Fungi in this group are all included in the family Hymenochaetaceae and have darkly pigmented, woody or fibrous fruiting bodies without binding hyphae. The fauna is largest and most diverse in tropical regions. In the Pacific Northwest, only *Cis maritimus* is known to breed in fungi of this group, although several host species (*Phellinus gilvus, P. igniarius, P. pini, Phaeolus schweinitzii,* and certain *Inonotus*) are common in the area. The Southwest is similarly devoid of species in this group, and *Ceracis obrieni* is a Neotropical form occurring in a small area of high rainfall in southern Arizona. In both of these areas, the most common inhabitants of *Phellinus* and their relatives are moths of the genus *Nemapogon* (Lawrence and Powell, 1969). In the Northeast, *Ceracis punctulatus, Ceracis singularis,* and *Malacocis brevicollis* are all fairly common, but only the last extends into the Boreal parts of the continent. In the southeastern United States, several other Neotropical species are added to the fauna. *Malacocis brevicollis* and *Ceracis singularis* show some preference for the larger, perennial conks of *Phellinus igniarius* and *P. robiniae,* while *Ceracis punctulatus* and *Ceracis pullulus* are usually found on the smaller sporophores of *P. gilvus* and *P. licnoides.* Several ciids in this group may also occur on the more darkly pigmented fomitoids in the *Ganoderma* group. Among the Palaearctic Ciidae, *Ennearthron cornutum* (Gyllenhal) and *Cis quadridentulus* Perris occur on hymenochaetaceous hosts (Paviour-Smith, 1969; Roman, 1970). Other beetles inhabiting these fungi in eastern North America are *Platydema ellipticum* (Fabricius) [Tenebrionidae], *Orchesia gracilis* Melsheimer [Melandryidae], and *Microsternus ulkei* (Crotch) [Erotylidae] (Lawrence, unpublished data).

The *Ganoderma* Group. This is the largest and most poorly defined section, which corresponds roughly with the "*Polyporus betulinus* group" of Paviour-Smith. The fungi included form a heterogeneous assemblage with very different sporophore characteristics. *Bjerkandera adusta,* for instance, has small, pale brown fruiting bodies with a soft, monomitic context; *Fomitopsis pinicola* has large, pale, corky or woody conks with a trimitic context; and the fomitoid groups, such as *Fomes* and *Pogonomyces,* are characterized by having darkly pigmented, trimitic context tissue. In the western coniferous forests a common host is *Fomitopsis pinicola,* which may be inhabited by as many as five sympatric ciids in certain areas (although no more than three have been recorded from a single conk). In a typical situation, the fauna of *F. pinicola* will include *Dolichocis manitoba,* one member each of the *Cis americanus-tridentatus* and *Cis ephippiatus-biarmatus* species pairs (*see* p. 189), *Ostoma pippingskoeldi* (Mannerheim) [Col.: Peltidae], and a species of *Eleates* [Col.: Tenebrionidae]. In the summergreen forests of eastern North America, *Bjerkandera adusta, Fomes fomentarius, Ganoderma applanatum,* and *G. lucidum* are all abundant, and the commonest ciid species is *Cis levettei,* which coexists with *Ceracis sallei* in species of *Ganoderma.* In the northern birch forests, *Piptoporus betulinus* is also common and serves as an alternate host for *Dolichocis manitoba* and *Cis americanus,* but the more characteristic inhabitants of this fungus are *Thymalus marginicollis* Chevrolat [Col.: Peltidae], *Diaperis maculata* Olivier [Col.: Tenebrionidae], tineid moths of the genus *Nemapogon,* and various chloropid flies (Pielou and Verma, 1968). *Bjerkandera adusta* is a major host of *Cis castlei* and *Cis creberrimus* south of New England, while *Fomes sclerodermeus, Ganoderma zonatum,* and *Pogonomyces hydnoides* occur in Florida and the Gulf states, where several West Indian ciids, such as *Cis hirsutus* and *Ceracis multipunctatus* are added to the fauna. *Cis levettei* drops out in the Southeast, but *Ceracis sallei* extends into Florida, where it may coexist with *Ceracis punctulatus,* a species restricted to fungi of the *Phellinus* group in the northern parts of its range (*see* p. 189). Associated Coleoptera in the eastern United States include species of *Dorcatoma* and *Priotoma* [Anobiidae]; *Bolitotherus cornutus* (Panzer) [Tenebrionidae]; *Platydema americanum*

Laporte and Brulle [Tenebrionidae] in the Northeast; and *Neomida ferruginea* (LeConte), *Platydema ruficorne* (Sturm), and species of *Rhipidandrus* [Tenebrionidae] in the Southeast. The anthribid weevil, *Euparius marmoreus* (Olivier), is also a common inhabitant, but it has a broad host range, including fungi in other groups. In the Southwest, *Ceracis californicus* occurs on *Ganoderma* at lower elevations, while *Cis creberrimus* and *Cis duplex* inhabit *Fomitopsis* and *Ganoderma* in montane situations. Palaearctic Ciidae associated with this group include *Rhopalodontus perforatus* (Gyllenhal), *Cis bidentatus* (Olivier), and several members of the *Cis nitidus* group (Lawrence, unpublished data; Matthewman and Pielou, 1971; Paviour-Smith, 1969; Saalas, 1923).

Cryptoporus volvatus. The fauna inhabiting the sporophores of this species is a unique one, which is shared with few other fungi (*see* below). Hubbard (1892) listed 14 species from conks collected in British Columbia, Hisamatsu (1962) compared inhabitants from Japan and North America, while Borden and McClaren (1970 and in press) have treated various aspects of its biology, including arthropod infestation. The only North American ciid known to breed in *C. volvatus* is *Plesiocis cribrum*, but other common inhabitants in western North America include *Aradus debilis* Uhler [Hemiptera: Aradidae], *Morophaga cryptophori* Clarke [Lepidoptera: Tineidae]; *Megaselia polyporicola* Borgmeier [Diptera: Phoridae]; *Aphenolia monogama* (Crotch) [Coleoptera: Nitidulidae]; *Cryptophagus maximus* Blake [Col.: Cryptophagidae], *Corticaria* sp. [Col.: Lathridiidae]; and *Platydema neglectum* Triplehorn [Col.: Tenebrionidae] (Borden and McClaren, in press; Gillogly, 1965; Gillogly and Gillogly, 1954; Lawrence and Powell, 1969; Lawrence, unpublished data).

Dichomitus squalens. This species is particularly interesting because it serves as an alternate host for *Plesiocis cribrum* and certain other inhabitants of *C. volvatus*. This may be due to the fact that the two fungi often occur on the same conifer logs and are somewhat similar in the color and texture of the context. Another ciid breeding in *D. squalens* is *Cis duplex*, which also occurs on fungi in the *Ganoderma* group. According to Nobles (1971), both of these fungi resemble *Coriolus* with respect to cultural characters.

Cerrena unicolor. Fruiting bodies of this species are trametoid-like with a trimitic hyphal system and pale context, but the hymenium is grayish in color. It serves as headquarters for *Ceracis minutissimus*, which is not known to breed elsewhere, while the few other ciid inhabitants are from the *Hirschioporus* and *Ganoderma* groups. In Europe, it is a host for three ciids which also breed in *Coriolus*-group fungi.

Stereum ostrea. This fungus, which is common throughout southeastern United States, serves as headquarters for *Cis stereophilus* and the aradid bug *Mezira granulata* Say; the only other record for *C. stereophilus* is from an unidentified *Stereum*.

Auricularia auricula. This species and certain other primitive Basidiomycetes appear to harbor a distinct beetle fauna, although the data presented here are insufficient to show this. The Palaearctic literature (Benick, 1952; Falcoz, 1922) and a number of unpublished records from various parts of the world indicate that certain species of *Orthocis* and *Cis* breed in these soft and rubbery fruiting bodies and in the mycelial mats from which they arise. Further collecting in these habitats may reveal the headquarters of some of the rarer North American Ciidae.

The data presented here indicate that few, if any, Ciidae are monophagous, and probably none are totally indiscriminate in the type of fungus substrate utilized by the larvae. The great majority of species prefer a few to several hosts, most of which may be placed in one of four host preference groups, whose members share the same ciid inhabitants in any one area. These groups of host fungi and associated Ciidae are not mutually exclusive, but, with the exception of a few relatively eurytrophic species, ciids are rarely encountered breeding in hosts of the "wrong" group. These groups established on the basis of North American Ciidae are, on the whole, similar to those of Paviour-Smith for the European species, and unpublished data from the Canal Zone indicate that similar groupings occur there. Finally, there is some indication that certain other fungus inhabitants, such as tenebrionid and anobiid beetles, may show the same patterns of host preference.

Discussion

According to Dethier (1954), the problem of food plant selection may be stated in the form of two questions: "(1) how is the preference implemented? and (2) what is the genetic basis and evolutionary history of specific plant preferences?" In the following paragraphs, I will first discuss the possible mechanisms of host selection in the Ciidae and the features of various hosts which are most likely to be used in discrimination by the beetles, and then take up various evolutionary and zoogeographic factors which may have played a role in the formation of host preference patterns.

The actual mechanism by which a dispersing ciid locates a suitable fungus substrate on which to feed, mate, and/or oviposit can only be guessed at, since there have been almost no experimental studies conducted with mycetophagous insects. The initial cue may well be humidity or some other factor associated with the rotting of wood and production of fungus sporophores. The possibility that humidity is involved is supported by the fact that Ciidae have on the antennal club very large and multi-pronged basiconic sensillae (sensillifers of Lawrence, 1971), which appear to be homologous with the hygroreceptor organs of *Tribolium*, studied experimentally by Roth and Willis (1951).

At close range, a beetle may be responding to either structural (substrate consistency) or chemical stimuli, and the latter may be either gustatory or olfactory, as discussed by Thorsteinson (1960) for phytophagous insects. Since a response to taste or consistency requires physical contact, a mechanism involving either would necessitate chance colonization of individual fruiting bodies, which are often small and widely scattered. It is more likely that olfactory stimuli play a major role in locating the host, and this is supported by the fact that large numbers of ciids are commonly observed on the same conk (when they have not developed *in situ*). This leaves us with Paviour-Smith's objection that old and dead conks, which have undergone repeated wetting and drying, are still able to attract ciids, although it is unlikely that they can still produce a volatile attractant. The answer to this may lie in the work of Wood and his associates (Wood, 1932; Wood and Bushing, 1963; Wood and Vite, 1961) on host selection in bark beetles. If the first colonizing ciid reaches a fruiting body more or less by chance, and, upon receiving the proper feeding stimulus, bores into the tissue, then the beetle itself may produce a pheromone (perhaps in the feces) which would attract other members of the species in the vicinity. The initial stimulus could be variable, but the secondary mechanism would always involve olfaction. Experiments with a multiple-choice olfactometer, such as those carried out by Wood and his group, are needed to verify this.

Some of the more obvious structural and chemical features of the fruiting body which may be involved in host selection have been mentioned on pages 175–177. The leathery consistency and presence of binding hyphae characteristic of the *Coriolus* group and the woody texture and thick-walled skeletal hyphae of *Phellinus* may both represent feeding deterrents, which the beetles in each group have been able to overcome. The melanic substances found in the hyphal walls of the Hymenochaetaceae and certain "fomitoids" may be involved in the synthesis of attractants or repellents, and

Bu'Lock (1967) has shown that at least one of these (hispidin) contributes to the hardening of the tissue. Little else can be said about the chemical basis of host selection without the aid of biochemical analyses of fungal sporophores and bioassay experiments with ciids and other mycetophagous organisms.

One fact that has not been emphasized in the presentation of host data is the change in preference from one part of the geographic range to another. In general, the preferences of a species remain the same throughout the range, and most of the changes which do occur involve differences in the fungus flora. Ciidae that inhabit the fruiting bodies of *Phellinus gilvus* in the Northeast, for instance, will occupy those of its tropical counterpart *P. licnoides* in the southern part of the range. The same is true for inhabitants of *Fomes fomentarius* and *F. sclerodermeus.* Certain other floral changes occur from west to east, where gymnosperms and angiosperms, respectively, form the dominant woody substrate on which the fungi develop.

Change in host preference appears to be associated with competitive displacement in two pairs of sibling species, *Cis biarmatus-Cis ephippiatus* and *Cis tridentatus-Cis americanus.* In each case, the two species occur sympatrically along the Pacific coast, while the latter member of each pair extends across the entire northern part of the continent. In the area of sympatry, *Cis biarmatus* and *Cis tridentatus* both show a strong preference for *Fomitopsis pinicola,* while their respective siblings, *Cis ephippiatus* and *Cis americanus,* avoid this host completely, the former preferring *Ganoderma applanatum* and the latter occurring on several species, including *Bjerkandera adusta.* Where *Cis ephippiatus* and *Cis americanus* occur alone, however, both are commonly found on *F. pinicola,* as well as on other hosts. In the eastern United States, another pair of sympatric species, *Ceracis sallei* and *Ceracis punctulatus,* exhibit strong preferences for *Ganoderma applanatum* and *Phellinus gilvus,* respectively; in this case the preferences break down in Floridian populations, where the two may occur on the same fungi (*see* Lawrence, 1967b).

Certain cases of change in host preference occur in areas which are at the periphery of the geographic range and which apparently have been recently colonized. In western North America, *Dolichocis manitoba* shows a strong preference for *Fomitopsis pinicola* and occurs occasionally in other fungi of the *Ganoderma* group. The species extends across the northern part of the continent and is fairly common in New England, where it has a broader host range, including *Cerrena unicolor* and *Hirschioporus pargamenus.* One possible explanation is that the species evolved in the coniferous forests of the Northwest and has only recently invaded the Northeast, where a peripheral population is competing with a different set of species which have evolved in the eastern deciduous forest community. Similar situations occur in the Florida peninsula, which has undergone considerable change during Pleistocene flooding and is continually being colonized by wind-dispersed organisms from the West Indies. *Ceracis punctulatus,* as mentioned above, has a much broader host range in Florida than it does further north. Two West Indian species, *Cis hirsutus* and *Ceracis minutus,* occur on a variety of hosts in Florida, but both species have evolved in the Greater Antilles, where each exhibits a more definite preference for one group.

Few generalizations can be made on the possible coevolution of the Ciidae and their host fungi until more data are available on the phylogeny of the two groups. The type of close host-parasite interaction exhibited by certain plant-feeding insects probably has not occurred in the Ciidae, since the beetles are primarily saprophagous organisms, usually feeding on dead context tissue and not attacking the hymenium until after the spores are shed. Since the beetles do not interfere with the production or dissemination of spores, it is unlikely that the fungus would respond by producing toxins or repellents. This possibility should not be dismissed, however, until the biology of these organisms is more thoroughly worked out.

Several genera and species groups of Ciidae have evolved on a single type of substrate and are rarely found elsewhere. Species of *Strigocis, Sulcacis,* and *Octotemnus* are almost always associated with *Coriolus* and its relatives, as are the *boleti, fuscipes, pallidus,* and *tricornis* groups of *Cis.* Species of *Malacocis* are restricted to *Phellinus*-group fungi, as are certain sections of *Ceracis.* The Neotropical *Cis taurus* group and the Holarctic *Cis nitidus* group are usually found in fungi of the *Ganoderma* group, while exceptions in both involve a switch to the *Phellinus* group.

Although the present treatment is based primarily on data from temperate and subtropical regions, unpublished records indicate that in tropical forests the degree of host specificity may be greater than shown here. On Barro Colorado Island in the Canal Zone, the conks of *Ganoderma applanatum, Fomes sclerodermeus,* and *Pogonomyces hydnoides* have certain shared faunal elements, but in addition each is inhabited by one or more species of Ciidae and/or Tenebrionidae that are not found in the other two. An analysis of this tropical host data is now in progress.

CIIDAE AND THEIR HOST FUNGI

1. *Cis acritus* Lawrence

Geographical range. Montane regions of southern California, Arizona, and New Mexico.

Host range. Fungi: 1(1). Records: 7(1). Known from *Hirschioporus abietinus* only.

Discussion. This species is the western counterpart of *Cis subtilis.* In the mountains of the Southwest, it may be taken along with *Cis horridulus* and *Ceracis powelli* in the fruiting bodies of *Hirschioporus* on conifers.

2. *Cis americanus* Mannerheim

Geographical range. Northern part of North America, from southern Alaska to Nova Scotia, south in California to Monterey County (coastal) and Fresno County (Sierra Nevada), in the Rocky Mountain region south to northern Utah and Colorado, and in the Appalachians as far south as western North Carolina.

Host range. Fungi: 24(18). Records: 69(35). $B_s = 14.40$. Group: *Ganoderma.*

Records.	NB	BR	TOT	%BR
Pleurotus ostreatus	2	1	3	2.8
Phlebia merismoides	1	0	1	0.0
Stereum hirsutum	2	4	6	11.4
Steccherinum ochraceum	1	2	3	5.7
Poria versipora	1	2	3	5.7
Polyporus squamosus	0	2	2	5.7
Laetiporus sulphureus	2	1	3	2.8
Bjerkandera adusta	2	6	8	17.1
Ischnoderma resinosum	0	1	1	2.8
Piptoporus betulinus	3	4	7	11.4
Fomitopsis pinicola	3	2	5	5.7
Heterobasidion annosum	3	1	4	2.8
Rigidoporus nigrescens	1	0	1	0.0
Irpex tulipiferae	1	0	1	0.0
Hirschioporus abietinus	3	0	3	0.0
Hirschioporus pargamenus	0	1	1	2.8
Coriolus biformis	1	0	1	0.0
Coriolus hirsutus	0	1	1	2.8
Coriolus versicolor	4	1	5	2.8
Datronia mollis	0	2	2	5.7
Daedaleopsis confragosa	0	1	1	2.8
Fomes fomentarius	1	0	1	0.0
Ganoderma applanatum	1	1	2	2.8
Ganoderma tsugae	2	2	4	5.7
Totals	34	35	69	100.0

Discussion. This is probably the most eurytrophic of the North American Ciidae, breeding in at least 18 different fungi belonging to various groups. As mentioned in an earlier paper (Lawrence, 1971) the species is quite variable and may represent a complex of sibling species (along with *Cis tridentatus*). There is some indication that two distinct forms with slightly different host preferences occur in California, but more field data will be necessary to determine this.

3. *Cis angustus* Hatch

Geographical range. Mountains of the

Pacific Coast from south-central British Columbia to the southern Sierra Nevada.

Host range. Fungi: 3(1). Records: 4(2). Group: *Ganoderma.*

Records.	NB	BR	TOT	%BR
Laricifomes officinalis	1	0	1	0.0
Fomitopsis pinicola	0	2	2	100.0
Heterobasidion annosum	1	0	1	0.0
Totals	2	2	4	100.0

Discussion. This beetle is relatively uncommon in large and woody, pale-colored conks growing on conifers in the Northwest. It is related to the Palaearctic *Cis fagi* Waltl and *C. castaneus* Mellié, the former of which has been recorded from *Piptoporus betulinus, Laetiporus sulphureus, Inonotus dryadeus,* and *Ganoderma applanatum* (Donisthorpe, 1935; Paviour-Smith, 1960a, 1969).

4. *Cis biarmatus* Mannerheim

Geographical range. Pacific Coast of North America from southern Alaska to Marin County, California.

Host range. Fungi: 1(1). Records: 10(6). $B_s = 1.00$. Known from *Fomitopsis pinicola* only.

Discussion. *Cis biarmatus* is known only from the narrow Pacific coastal belt where it is associated with *Fomitopsis pinicola;* the closely related beetle *Cis ephippiatus* in the same area prefers the sporophores of *Ganoderma applanatum.*

5. *Cis castlei* (Dury)

Geographical range. Eastern North America, from extreme southern Ontario south to central Florida, west to Iowa, and south through eastern Mexico to Costa Rica.

Host range. Fungi: 13(4). Records: 27(7). $B_s = 3.16$. Group: *Ganoderma.*

Records.	NB	BR	TOT	%BR
Lentinus crinitus	1	0	1	0.0
Stereum ostrea	2	0	2	0.0
Polyporus mutabilis	0	1	1	14.3
Bjerkandera adusta	5	4	9	57.1
Oxyporus latemarginata	1	0	1	0.0
Nigroporus vinosus	0	1	1	14.3
Rigidoporus lignosus	1	0	1	0.0
Rigidoporus zonalis	1	0	1	0.0
Hirschioporus pargamenus	5	0	5	0.0
Trametes plebeja	1	0	1	0.0
Earliella corrugata	0	1	1	14.3
Pogonomyces hydnoides	2	0	2	0.0
Ganoderma applanatum	1	0	1	0.0
Totals	20	7	27	100.0

Discussion. This species is known from scattered localities throughout the eastern half of the continent and is not particularly common. It is usually encountered on *Bjerkandera adusta* where it may be associated with *Cis creberrimus.*

6. *Cis cayensis* Lawrence

Geographical range. Florida Keys and Cuba.

Host range. Fungi: 5(3). Records: 16 (7). $B_s = 2.57$. Group: *Phellinus.*

Records.	NB	BR	TOT	%BR
Lopharia papyrina	1	0	1	0.0
Pogonomyces hydnoides	1	2	3	28.6
Inonotus corrosus	0	1	1	14.3
Inonotus porrectus	2	4	6	57.1
Phellinus robiniae	5	0	5	0.0
Totals	9	7	16	100.0

7. *Cis congestus* Casey

Geographical range. Southeastern United States, from Maryland south to northern Florida and west to southern Illinois and eastern Texas.

Host range. Fungi: 2(1). Records: 4 (2). Group: *Coriolus.*

Records.	NB	BR	TOT	%BR
Coriolus hirsutus	1	2	3	100.0
Coriolus pinisitus	1	0	1	0.0
Totals	2	2	4	100.0

Discussion. This is the southeastern counterpart of *Cis vitulus* and both species have an obvious preference for members of the *Coriolus* group.

8. *Cis cornelli* Lawrence

Geographical range. The Carolinas and Florida.

Host fungi. Fungi: 1(1). Records: 4 (2). Known from *Hirschioporus sector* only.

Discussion. *Cis cornelli* belongs to a large Neotropical species-group, which includes *Cis setifer* (Gorham) and *Cis taurus* (Reitter). It appears to prefer the fruiting bodies of *Hirschioporus* but its tropical relatives occur on a wide variety of other fungi. On Barro Colorado Island, Canal Zone, about ten species in this group have been collected, each preferring different host fungi.

9. *Cis cornutus* Blatchley

Geographical range. Eastern United States, from New York south to northern Florida and west to Illinois and Arkansas.

Host range. Fungi: 2(2). Records: 5 (4). Group: *Coriolus.*

Records.	NB	BR	TOT	%BR
Coriolus subectypus	0	1	1	25.0
Coriolus versicolor	1	3	4	75.0
Totals	1	4	5	100.0

10. *Cis creberrimus* Mellié

Geographical range. Eastern North America, from Vermont south to Florida and west to eastern Nebraska, Kansas, and Texas; montane regions of the Southwest; throughout the West Indies; scattered localities in Mexico, Central and South America.

Host range. Fungi: 24(13). Records: 47(18). $B_s = 11.24$. Group: *Ganoderma.*

Records.	NB	BR	TOT	%BR
Pleurotus sp.	1	0	1	0.0
Schizophyllum commune	1	0	1	0.0
Poria corticola	0	1	1	5.6
Laetiporus sulphureus	1	0	1	0.0
Bjerkandera adusta	1	4	5	22.2
Oxyporus latemarginatus	1	1	2	5.6
Fomitella supina	1	0	1	0.0
Laricifomes officinalis	0	2	2	11.1
Fomitopsis pinicola	1	1	2	5.6
Heterobasidion annosum	0	1	1	5.6
Dichomitus squalens	1	0	1	0.0
Hirschioporus pargamenus	1	1	2	5.6
Pycnoporus sanguineus	0	1	1	5.6
Coriolus hirsutus	1	0	1	0.0
Lenzites elegans	1	0	1	0.0
Earliella corrugata	1	1	2	5.6
Funalia hispida	1	0	1	0.0
Gloeophyllum striatum	1	0	1	0.0
Pogonomyces hydnoides	2	1	3	5.6
Fomes sclerodermeus	5	1	6	5.6
Ganoderma applanatum	4	0	4	0.0
Ganoderma fulvellum	0	1	1	5.6
Ganoderma lucidum	2	2	4	11.1
Phellinus gilvus	2	0	2	0.0
Totals	29	18	47	100.0

Discussion. This is another widely distributed and eurytrophic species which breeds in at least 13 host fungi. As mentioned in an earlier paper (Lawrence, 1971) there are at least four geographical races (or perhaps species) that occur in North America. The populations are largely allopatric, and the host preferences do not differ much among the different populations. In the eastern United States, the beetle is usually encountered in small numbers under bark or in various hosts. It is usually not the dominant species in a fruiting body. Part of the reason for the wide host range may be the inclusion of several Neotropical records which may represent distinct species. The entire complex is in need of further revision.

11. *Cis crinitus* Lawrence

Geographical range. Southeastern United States, from North Carolina to Florida and west to eastern Texas; the Bahamas, and the Greater Antilles.

Host range. Fungi: 5(4). Records: 10 (5). $B_s = 3.80$. Group: *Ganoderma*?

Records.	NB	BR	TOT	%BR
Lopharia papyrina	0	2	2	40.0
Coriolopsis fulvocinerea	2	1	3	20.0
Gloeophyllum striatum	0	1	1	20.0
Pogonomyces hydnoides	2	1	3	20.0
Ganoderma zonatum	1	0	1	0.0
Totals	5	5	10	100.0

12. *Cis discolor* Lawrence

Geographical range. Montane regions of southern Arizona.

Host range. Fungi: 2(2). Records: 4 (4). Group: *Ganoderma.*

Records.	NB	BR	TOT	%BR
Fomitopsis cajanderi	0	3	3	75.0
Antrodia sepium	0	1	1	25.0
Totals	0	4	4	100.0

13. *Cis duplex* Casey

Geographical range. Mountains of the southwestern United States and Mexico, from southern California east to north-central New Mexico, and south as far as Morelos and the southern tip of Baja California.

Host range. Fungi: 4(4). Records: 11 (10). $B_s = 3.39$. Group: *Ganoderma*?

Records.	NB	BR	TOT	%BR
Laricifomes officinalis	0	2	2	20.0
Fomitopsis pinicola	0	2	2	20.0
Dichomitus squalens	1	5	6	50.0
Ganoderma oregonense	0	1	1	10.0
Totals	1	10	11	100.0

Discussion. This is a relatively common species in the mountains of the Southwest where it is associated with conifers. The beetle is commonly found in the fruiting bodies of *Dichomitus squalens,* where it may coexist with *Plesiocis cribrum.*

14. *Cis ephippiatus* Mannerheim

Geographical range. Western North America, from southern Alaska south in California to Alameda County and the southern Sierra Nevada, and in the Rocky Mountain Region to northern Nevada and Colorado. Also known from Vermont, New Hampshire, and the Gaspé Peninsula of Quebec.

Host range. Fungi: 8(3). Records: 24 (14). $B_s = 2.57$. Group: *Ganoderma.*

Records.	NB	BR	TOT	%BR
Poria versipora	1	0	1	0.0
Laetiporus sulphureus	1	0	1	0.0
Ischnoderma resinosum	1	0	1	0.0
Piptoporus betulinus	1	0	1	0.0
Fomitopsis pinicola	3	4	7	28.6
Heterobasidion annosum	1	0	1	0.0
Ganoderma applanatum	2	8	10	57.1
Ganoderma brownii	0	2	2	14.3
Totals	10	14	24	100.0

Discussion. This species occurs throughout the northern part of the continent, but most of the records are from the Pacific Coast. Where it is sympatric with the closely related *C. biarmatus,* it is usually found on *Ganoderma applanatum* or *G. brownii,* but in areas outside the range of *C. biarmatus,* it is commonly associated with *Fomitopsis pinicola.* This appears to be a case of competitive exclusion.

15. *Cis floridae* Dury

Geographical range. Southern Georgia, Florida, and Cuba.

Host range. Fungi: 3(2). Records: 5 (2). Group: *Phellinus.*

Records.	NB	BR	TOT	%BR
Lopharia papyrina	2	0	2	0.0
Phellinus gilvus	1	1	2	50.0
Phellinus sp.	0	1	1	50.0
Totals	3	2	5	100.0

16. *Cis fuscipes* Mellié

Geographical range. Widespread throughout most of northern and eastern North America, from northern British Columbia south to Los Angeles County in California, east across Canada to Nova Scotia, and south throughout eastern and midwestern United States (east of the 100th meridian) to southern Texas and Florida. Also known from Cuba, Madeira, and Hawaii.

Host range. Fungi: 13(8). Records: 135(69). $B_s = 2.82$. $B_g = 1.48$. Group: *Coriolus.*

Records.	NB	BR	TOT	%BR
Polyporus squamosus	0	1	1	1.4
Bjerkandera adusta	0	1	1	1.4
Fomitopsis fraxinea	1	0	1	0.0
Fomitopsis pinicola	1	0	1	0.0
Coriolus conchifer	1	2	3	2.9
Coriolus hirsutus	4	10	14	14.5
Coriolus pubescens	4	2	6	2.9
Coriolus subectypus	1	0	1	0.0
Coriolus versicolor	43	49	92	71.0
Lenzites betulina	9	3	12	4.3
Lenzites elegans	1	0	1	0.0
Ganoderma applanatum	1	0	1	0.0
Ganoderma brownii	0	1	1	1.4
Totals	66	69	135	100.0

Discussion. Cis fuscipes is the widespread and parthenogenetic beetle which has been discussed at length elsewhere (Lawrence, 1967a, 1971). Because of the large number of collections made for this species, its preference for members of the *Coriolus* group is well established. Its relatives in eastern Asia appear to have similar preferences (Chujo, 1939; Fukuda, 1940; Lawrence, 1967a).

17. *Cis hirsutus* Casey

Geographical range. Florida, the Bahamas, and the Greater Antilles.

Host range. Fungi: 17(9). Records: 41 (16). $B_s = 7.95$. $B_g = 4.68$. Group: *Ganoderma.*

Records.	NB	BR	TOT	%BR
Auricularia polytricha	1	0	1	0.0
Fomitella supina	1	0	1	0.0
Rigidoporus rigidus	1	0	1	0.0
Hirschioporus pargamenus	0	1	1	6.2
Hirschioporus sector	0	1	1	6.2
Coriolus maximus	2	0	2	0.0
Coriolus pinisitus	2	0	2	0.0
Lenzites elegans	1	0	1	0.0
Earliella corrugata	1	2	3	12.5
Coriolopsis fulvocinerea	1	1	2	6.2
Pogonomyces hydnoides	8	3	11	18.7
Fomes sclerodermeus	4	1	5	6.2
Ganoderma applanatum	1	0	1	0.0
Ganoderma lucidum	0	1	1	6.2
Ganoderma zonatum	1	3	4	18.7
Ganoderma sp.	0	3	3	18.7
Cyclomyces iodinus	1	0	1	0.0
Totals	25	16	41	100.0

Discussion. Although this is primarily an Antillean species, most of the host records are from southern Florida. The Floridian records indicate that the species breeds on a wide variety of fungi, but it is quite possible that the host range is narrower in more stable areas (the larger islands) closer to the center of distribution (*see* p. 189). There appears to be a preference for *Pogonomyces hydnoides* and species of *Ganoderma.*

18. *Cis horridulus* Casey

Geographical range. Northern and montane regions of North America, except Pacific Coast, ranging from south-central British Columbia to the Atlantic Coast, south in the Rocky Mountain Region as far as the Chiricahua Mountains of Arizona, and along the Appalachian Chain as far as western North Carolina.

Host range. Fungi: 2(2). Records: 22 (10). $B_s = 1.95$. $B_g = 1.00$. Group: *Hirschioporus.*

Records.	NB	BR	TOT	%BR
Hirschioporus abietinus	5	4	9	40.0
Hirschioporus pargamenus	7	6	13	60.0
Totals	12	10	22	100.0

Discussion. This species and *C. hystriculus* are part of a northern complex which includes the Palaearctic *Cis punctulatus* Gyllenhal and *C. tomentosus* Mellié. All of these forms breed in the fruiting bodies of various *Hirschioporus,* primarily in the northern coniferous forests. In eastern North America, *C. horridulus* appears to be equally common in *H. abietinus* and *H. pargamenus,* which occur on conifers and hardwoods, respectively. In the Old World, *C. punctulatus* has been recorded from *H. abietinus* and *H. fuscoviolaceus* (Benick, 1952; Lohse, 1967; Saalas, 1923; Scheerpeltz and Höfler, 1948).

19. *Cis hystriculus* Casey

Geographical range. Western British Columbia, Washington, and Oregon, south through the Sierra Nevada and coastal California to the Transverse Ranges in the southern part of the state.

Host range. Fungi: 3(1). Records: 29 (16). $B_s = 1.00$. Group: *Hirschioporus.*

Records.	NB	BR	TOT	%BR
Poria versipora	1	0	1	0.0
Tyromyces cinerascens	1	0	1	0.0
Hirschioporus abietinus	11	16	27	100.0
Totals	13	16	29	100.0

Discussion. This is the western counterpart of *Cis horridulus,* and it may not be a distinct species. It is the most common insect inhabiting *Hirschioporus abietinus* on the Pacific Coast.

20. *Cis laminatus* Mellié

Geographical range. In North America, known from Albany, New York. In Europe, recorded from France, Italy, Germany, Poland, Czechoslovakia, and Hungary.

Host range. In North America, known from *Cryptoporus volvatus* only. In Europe, recorded from *"Fomes" pini-halepensis, Pseudotrametes gibbosa,* and *Tyromyces stipticus* (Peyerimhoff, 1919; Scheerpeltz and Höfler, 1948; Roman, 1970).

Records. A single unverified record from *C. volvatus.*

Discussion. This species has not been collected since 1920 and may not be established in North America.

21. *Cis levettei* (Casey)

Geographical range. Widespread in North America east of the 100th meridian, from Newfoundland south to Alabama and west to Manitoba, Kansas, and Texas. In the western part of the continent, recorded from Alberta, northwestern Colorado, eastern British Columbia, Washington, and California.

Host range. Fungi: 19(10). Records: 140(76). $B_s = 4.79$. $B_g = 3.55$. Group: *Ganoderma.*

Records.	NB	BR	TOT	% BR
Stereum ostrea	2	0	2	0.0
Polyporus squamosus	2	0	2	0.0
Bjerkandera adusta	1	0	1	0.0
Oxyporus populinus	1	3	4	3.9
Ischnoderma resinosum	0	1	1	1.3
Piptoporus betulinus	1	1	2	1.3
Fomitopsis pinicola	3	13	16	17.1
Rigidoporus nigrescens	0	1	1	1.3
Rigidoporus vitreus	1	0	1	0.0
Hirschioporus pargamenus	2	0	2	0.0
Coriolus pubescens	2	0	2	0.0
Coriolus versicolor	3	0	3	0.0
Lenzites betulina	1	0	1	0.0
Daedaleopsis confragosa	0	2	2	2.6
Fomes fomentarius	6	12	18	15.8
Ganoderma applanatum	32	37	69	48.7
Ganoderma lucidum	1	1	2	1.3
Ganoderma tsugae	5	5	10	6.6
Phellinus robiniae	1	0	1	0.0
Totals	64	76	140	100.0

Discussion. Cis levettei occurs throughout central and eastern North America, but it is most common in the Northeast. It is usually found breeding in *Ganoderma applanatum,* but it is also relatively common in the conks of *Fomes fomentarius, Fomitopsis pinicola,* and *Ganoderma tsugae.* According to Matthewman and Pielou (1971), this species is the second most common beetle infesting the sporophores of *F. fomentarius* in Quebec, where it is most often associated with the anobiid *Dorcatoma dresdensis* (Herbst) and the tenebrionid *Bolitotherus cornutus* (Panzer). In the fruiting bodies of *G. applanatum,* it is often found along with *Ceracis sallei. Cis levettei* belongs to a group of species which includes the Palaearctic *Cis nitidus* (Fabricius), *C. jacquemarti* Mellié, *C. glabratus* Mellié, *C. hanseni* Strand, and *C. lineatocribratus* Mellié. Most of the members of this group have similar host preferences, being most commonly encountered in *G. applanatum, F. fomentarius,* and *F. pinicola,* but it is not clear from the literature whether or not they further subdivide the habitat in areas of overlap (Benick, 1952; Paviour-Smith, 1960a, 1969; Peyerimhoff, 1915; Roman, 1970; Scheerpeltz and Höfler, 1948).

22. *Cis maritimus* (Hatch)

Geographical range. Pacific Coast from southwestern British Columbia to extreme northwestern California. Also known from south-central Manitoba.

Host range. Fungi: 2(2). Records: 3 (2). Group: *Phellinus.*

Records.	NB	BR	TOT	% BR
Phaeolus schweinitzii	1	1	2	50.0
Phellinus pini	0	1	1	50.0
Totals	1	2	3	100.0

Discussion. According to the few records available, this species appears to prefer the xanthochroic fruiting bodies of *Phaeolus* and *Phellinus,* which is unusual both for the species-group (*Cis nitidus* group) and the geographic area. Although both *Phaeolus schweinitzii* and *Phellinus pini* are common in the Pacific Northwest, *C. maritimus* is the only ciid to utilize them.

23. *Cis megastictus* Lawrence

Geographical range. Montane regions of northern California.

Host range. Fungi: 3(1). Records: 3 (1). Group: *Ganoderma*?

Records.	NB	BR	TOT	%BR
Laetiporus sulphureus	1	0	1	0.0
Fomitopsis pinicola	1	0	1	0.0
Heterobasidion annosum	0	1	1	100.0
Totals	2	1	3	100.0

24. *Cis miles* (Casey)

Geographical range. Eastern North America, from New York south to central Florida and west to Arkansas and Louisiana.

Host range. Fungi: 5(3). Records: 13 (4). Group: *Coriolus.*

Records.	NB	BR	TOT	%BR
Stereum ostrea	1	0	1	0.0
Fomitella supina	1	0	1	0.0
Coriolus subectypus	0	1	1	25.0
Coriolus versicolor	6	1	7	25.0
Lenzites betulina	1	2	3	50.0
Totals	9	4	13	100.0

Discussion. This is the only Nearctic member of a large Neotropical species-group which includes *Cis tricornis* Gorham and *C. delicatulus* (Jacquelin DuVal). Like most of its relatives, *Cis miles* breeds in the pale, coriaceous sporophores characteristic of the *Coriolus* group.

25. *Cis niedhauki* Lawrence

Geographical range. Known from Lignum Vitae Key, Florida.

Host range. Fungi: 1(1). Records: 4 (2). Known from *Phellinus robiniae* only.

26. *Cis pistoria* Casey

Geographical range. Northeastern North America from central Alberta to southern Minnesota and southern New England.

Host range. Fungi: 4(4). Records: 11 (8). $B_s = 3.39$. $B_g = 1.45$. Group: *Coriolus.*

Records.	NB	BR	TOT	%BR
Bjerkandera adusta	0	1	1	12.5
Coriolus hirsutus	0	1	1	12.5
Coriolus pubescens	0	2	2	25.0
Coriolus versicolor	3	4	7	50.0
Totals	3	8	11	100.0

Discussion. Cis pistoria is primarily a northeastern species, inhabiting *Coriolus versicolor* and its allies, and often found in association with *Cis fuscipes* and *Octotemnus laevis.* Its Palaearctic relatives, such as *Cis micans* (Fabricius), *C. villosulus* (Marsham), and *C. boleti* (Scopoli), have similar preferences, occurring on various *Coriolus,* as well as *Lenzites betulina* and *Pseudotrametes gibbosa* (Benick, 1952; Donisthorpe, 1935; Falcoz, 1921; Paviour-Smith, 1960a; Peyerimhoff, 1915; Roman, 1970; Scheerpeltz and Höfler, 1948).

27. *Cis robiniophilus* Lawrence

Geographical range. Maryland, Kentucky, and Ohio.

Host range. Fungi: 1(1). Records: 3 (2). Known from *Trametes robiniophila* only.

28. *Cis rotundulus* Lawrence

Geographical range. Southeastern United States, from North Carolina to Florida and west to eastern Texas.

Host range. Fungi: 5(1). Records: 7 (1). Group: *Ganoderma*?

Records.	NB	BR	TOT	%BR
Stereum ostrea	1	0	1	0.0
Ganoderma curtisii	2	0	2	0.0
Ganoderma lucidum	1	1	2	100.0
Cyclomyces iodinus	1	0	1	0.0
Phellinus gilvus	1	0	1	0.0
Totals	6	1	7	100.0

29. *Cis stereophilus* Lawrence

Geographical range. Eastern coast of the United States, from southern Massachusetts to northern Florida, and northeastern Mexico.

Host range. Fungi: 2(2). Records: 12 (7). $B_s = 1.82$. $B_g = 1.00$.

Records.	NB	BR	TOT	%BR
Stereum ostrea	5	5	10	71.4
Stereum sp.	0	2	2	28.6
Totals	5	7	12	100.0

Discussion. This is the only known North American ciid that breeds only in the fruiting bodies of the thelephoraceous *Stereum.* In western North America, *Cis* *americanus* may breed in *Stereum hirsutum,* but that is one of many hosts. In the European fauna, *Cis festivus* (Panzer) and *Orthocis alni* (Gyllenhal) have both been recorded from *Stereum rugosum* (Benick, 1952), while several undescribed Neotropical Ciidae have been found in association with various thelephores.

30. *Cis striolatus* Casey

Geographical range. Widespread across the northern part of North America, from northern Mackenzie District, Northwest Territory, to Nova Scotia, south into the Sierra Nevada and Rocky Mountains, in the Midwest as far as Kansas, and on the Atlantic Coast as far as northern Florida.

Host range. Fungi: 4(4). Records: 12 (7). $B_s = 3.55$. $B_g = 2.24$. Group: *Hirschioporus.*

Records.	NB	BR	TOT	% BR
Hirshchioporus abietinus	4	2	6	28.6
Hirschioporus pargamenus	1	3	4	42.8
Cerrena unicolor	0	1	1	14.3
Coriolus hirsutus	0	1	1	14.3
Totals	5	7	12	100.0

Discussion. This is another northern species that inhabits the fruiting bodies of *Hirschioporus,* but it is far less common than either *C. horridulus* or *C. subtilis.* Similar and probably related species in North America include *Cis versicolor* and *C. tristis,* both of which prefer fungi in the *Coriolus* group. Allied species in the Old World, *Cis comptus* Gyllenhal and *C. striatulus* Mellié, have been taken on *Hirschioporus abietinus, Cerrena unicolor,* and various *Coriolus* (Lawrence, unpublished data; Peyerimhoff, 1915; Roman, 1970; Saalas, 1923; Scheerpeltz and Höfler, 1948) but it is unclear just how specific each is.

31. *Cis subfuscus* Gorham

Geographical range. Central Texas south along the eastern coast of Mexico to Veracruz.

Host range. Fungi: 3(2). Records: 4 (2). Group: *Coriolus.*

Records.	NB	BR	TOT	% BR
Panellus stipticus	0	1	1	50.0
Coriolus hirsutus	1	1	2	50.0
Lenzites elegans	1	0	1	0.0
Totals	2	2	4	100.0

32. *Cis subtilis* Mellié

Geographical range. Eastern North America, from New Hampshire south to Florida and west to Illinois, Arkansas, and eastern Texas.

Host range. Fungi: 7(3). Records: 50 (17). $B_s = 2.14$. $B_g = 1.00$. Group: *Hirschioporus.*

Records.	NB	BR	TOT	% BR
Stereum ostrea	1	0	1	0.0
Bjerkandera adusta	1	0	1	0.0
Hirschioporus abietinus	6	1	7	5.9
Hirschioporus pargamenus	22	12	34	70.6
Hirschioporus sector	1	4	5	23.5
Ganoderma applanatum	1	0	1	0.0
Phellinus gilvus	1	0	1	0.0
Totals	33	17	50	100.0

Discussion. This species is the most common inhabitant of *Hirschioporus* throughout the eastern United States. It is usually found in association with *Ceracis thoracicornis,* but the latter has a much broader host range.

33. *Cis tetracentrum* Gorham

Geographical range. Mountains of southern California and Arizona, south through the Mexican highlands as far as central Veracruz.

Host range. Fungi: 1(1). Records: 6 (5). $B_s = 1.00$. Known from *Coriolus versicolor* only.

Discussion. This species and the closely related *C. corticinus* Gorham from the Mexican highlands both prefer the fruiting bodies of *Coriolus versicolor* and its relatives.

34. *Cis tridentatus* Mannerheim

Geographical range. Pacific Coast from southern Alaska to Monterey County, California.

Host range. Fungi: 9(6). Records: 19 (12). $B_s = 3.46$. Group: *Ganoderma.*

Records.	NB	BR	TOT	%BR
Pleurotus ostreatus	1	0	1	0.0
Poria carbonica	0	1	1	8.3
Laetiporus sulphureus	0	1	1	8.3
Tyromyces cinerascens	1	1	2	8.3
Fomitopsis pinicola	3	7	10	58.3
Antrodia sepium	0	1	1	8.3
Ganoderma applanatum	1	0	1	0.0
Ganoderma oregonense	0	1	1	8.3
Phellinus gilvus	1	0	1	0.0
Totals	7	12	19	100.0

Discussion. This is a member of the *Cis americanus* complex and is restricted to the Pacific Coast (*see* p. 189). It is usually found in *Fomitopsis pinicola* where it may coexist with *Cis biarmatus* and *Dolichocis indistinctus.*

35. *Cis tristis* Mellié

Geographical range. Eastern North America, from New York and Massachusetts south to Florida and west as far as southeastern Colorado and northeastern Mexico.

Host range. Fungi: 9(5). Records: 14 (7). $B_s = 4.36$. $B_g = 2.57$. Group: *Coriolus.*

Records.	NB	BR	TOT	%BR
Pleurotus sp.	1	0	1	0.0
Fomitella supina	2	0	2	0.0
Pycnoporus cinnabarinus	1	0	1	0.0
Coriolus hirsutus	2	0	2	0.0
Coriolus maximus	0	1	1	14.3
Coriolus versicolor	0	3	3	42.9
Lenzites betulina	1	1	2	14.3
Lenzites elegans	0	1	1	14.3
Funalia hispida	0	1	1	14.3
Totals	7	7	14	100.0

36. *Cis ursulinus* Casey

Geographical range. Southeastern United States, from North Carolina south to Florida and west to Arkansas and Louisiana.

Host range. Fungi: 5(0). Records: 5 (0).

Records.	NB	BR	TOT	%BR
Laetiporus sulphureus	1	0	1	0.0
Bjerkandera adusta	1	0	1	0.0
Hirschioporus versatilis	1	0	1	0.0
Ganoderma tsugae	1	0	1	0.0
Phellinus gilvus	1	0	1	0.0
Totals	5	0	5	0.0

37. *Cis versicolor* Casey

Geographical range. Extreme southern Oregon, south throughout most of California west of the Sierran crest, into Baja California Norte and east through Arizona into New Mexico and western Texas.

Host range. Fungi: 7(4). Records: 40 (23). $B_s = 2.78$. $B_g = 2.18$. Group: *Coriolus.*

Records.	NB	BR	TOT	%BR
Schizophyllum commune	1	0	1	0.0
Pycnoporus cinnabarinus	1	0	1	0.0
Coriolus hirsutus	3	2	5	8.7
Coriolus versicolor	8	15	23	65.2
Lenzites betulina	0	2	2	8.7
Funalia hispida	3	4	7	17.4
Ganoderma brownii	1	0	1	0.0
Totals	17	23	40	100.0

Discussion. Cis versicolor is a relatively common species throughout the Southwest in both mesic (central California coast) and xeric (California and Arizona deserts) environments.

38. *Cis vitulus* Mannerheim

Geographical range. California, from Del Norte County to San Diego County, and north-central Arizona.

Host range. Fungi: 4(3). Records: 36 (22). $B_s = 1.78$. Group: *Coriolus.*

Records.	NB	BR	TOT	%BR
Schizophyllum commune	1	0	1	0.0
Bjerkandera adusta	1	1	2	4.6
Coriolus versicolor	11	18	29	81.8
Lenzites betulina	1	3	4	13.6
Totals	14	22	36	100.0

Discussion. This species belongs to a Neotropical group including the southeastern *C. congestus*, the Mexican *C. bubalus* Reitter, and the Central American *C. fasciatus* Gorham. In California, it breeds primarily on *Coriolus versicolor* in mesic situations, where it may be associated with *Cis fuscipes, C. versicolor, Sulcacis curtulus,* and *Octotemnus laevis.* Other tropical members of the group have been collected in *C. versicolor* and *C. pinisitus* (Lawrence, unpublished data).

39. *Ennearthron aurisquamosum* Lawrence

Geographical range. Kentucky and North Carolina.

Host range. Fungi: 1(0). Records: 1 (0). Known from *Bjerkandera adusta* only.

Discussion. This is an isolated species whose closest relatives occur in eastern Asia; it is apparently rare. An undescribed relative from western China was collected in a herbarium specimen of *Cryptoporus volvatus* (Lawrence, unpublished data).

40. *Ennearthron spenceri* (Hatch)

Geographical range. Known only from Vancouver, British Columbia. Probably introduced from Japan.

Host range. Known from *Cryptoporus volvatus* only.

Records. A single unverified record from *C. volvatus*.

Discussion. It is not known that this species occurs naturally in British Columbia. The records do not make it clear whether the infested specimens of *Cryptoporus volvatus* were sent from Japan or taken locally. The species most closely related to *E. spenceri* are all Japanese.

41. *Dolichocis indistinctus* Hatch

Geographical range. Known from scattered localities throughout the northern and montane parts of North America, from the northern coast of British Columbia to the Gaspé Peninsula of Quebec and south into the Sierra Nevada, Chiricahua Mountains of southern Arizona, and Green Mountains of Vermont.

Host range. Fungi: 3(1). Records: 9 (5). $B_s = 1.95$. Group: *Ganoderma.*

Records.	NB	BR	TOT	% BR
Laricifomes officinalis	1	0	1	0.0
Fomitopsis pinicola	3	3	6	60.0
Antrodia serialis	0	2	2	40.0
Totals	4	5	9	100.0

Discussion. This is the North American counterpart of the European *D. laricinum* (Mellié) and the two are doubtfully distinct. It is most commonly taken in *Fomitopsis pinicola* along the Pacific Coast, while its Palaearctic sibling has been recorded from the same fungus in Scandinavia (Saalas, 1923).

42. *Dolichocis manitoba* Dury

Geographical range. Northern and montane regions of North America, from the northern coast of British Columbia to New Brunswick and south to the central California coast, southern Sierra Nevada, southeastern Utah, and northern Pennsylvania.

Host range. Fungi: 12(7). Records: 73 (31). $B_s = 2.95$. Group: *Ganoderma.*

Records.	NB	BR	TOT	%BR
Laetiporus sulphureus	0	1	1	3.2
Bjerkandera adusta	2	0	2	0.0
Piptoporus betulinus	2	3	5	9.7
Cryptoporus volvatus	1	0	1	0.0
Laricifomes officinalis	0	1	1	3.2
Fomitopsis pinicola	29	22	51	71.0
Heterobasidion annosum	1	2	3	6.5
Irpex tulipiferae	1	0	1	0.0
Hirschioporus pargamenus	4	0	4	0.0
Cerrena unicolor	1	1	2	3.2
Fomes fomentarius	1	0	1	0.0
Ganoderma applanatum	0	1	1	3.2
Totals	42	31	73	100.0

Discussion. In western North America, this is a common and characteristic inhabitant of *Fomitopsis pinicola,* while in the Northeast it occurs in association with several other fungi, including *Piptoporus betulinus, Fomes fomentarius,* and *Cerrena unicolor.* Matthewman and Pielou (1971), in their study of arthropods associated with *F. fomentarius* in Quebec (data not included above), found that *D. manitoba* was less common than *Cis levettei* but still capable of causing considerable damage to sporophores. This is one of the few ciids in which there is an apparent change in host preference with geographic area (*see* p. 189). This may be connected with floristic change, since *F. fomentarius* and *P. betulinus* are much less common in the western coniferous forests, but it may also be an indication that *D. manitoba* has more recently colonized the eastern part of the continent.

43. *Orthocis punctatus* (Mellié)

Geographical range. Widespread across North America from the edge of the Beaufort Sea (Mackenzie District, Northwest Territory) to the island of Newfoundland, south on the Pacific Coast to Santa Barbara, California, through the Rocky Mountains to northeastern New Mexico, into the Black Hills of South Dakota, and through the eastern and midwestern states from New England to Florida and west to Kansas and Texas.

Host range. Fungi: 1(1). Records: 1 (1). Known from *Auricularia auricula* only.

Discussion. As mentioned in an earlier paper (Lawrence, 1971), this species may represent a complex of two or more related forms. The single record from *Auricularia auricula* is from coastal North Carolina (Atlantic Beach) and represents the southern form rather than the typical *O. punctatus.* Among the Palaearctic species of *Orthocis, O. coluber* (Abeille) has been collected in *Auricularia auricula* (Falcoz, 1922), while *O. alni* (Gyllenhal) is known from *A. auricula, Stereum rugosum,* and the tremellaceous *Exidia glandulosa* (Benick, 1952). In Panama, an undescribed *Orthocis* appears to be common in *Auricularia polytricha* (Lawrence, unpublished data).

44. *Strigocis bilimeki* (Reitter)

Geographical range. Mountains of northern Mexico; probably extending into southern Arizona.

Host range. Fungi: 2(1). Records: 2 (1). Group: *Coriolus*?

Records.	NB	BR	TOT	% BR
Coriolus versicolor	1	0	1	0.0
Lenzites betulina	0	1	1	100.0
Totals	1	1	2	100.0

45. *Strigocis opacicollis* Dury

Geographical range. Eastern North America, from southern Vermont and New Hampshire to the Florida Keys, west as far as eastern Kansas, and south into Mexico.

Host range. Fungi: 10(5). Records: 48 (18). $B_s = 2.29$. $B_g = 1.23$. Group: *Coriolus.*

Records.	NB	BR	TOT	% BR
Bjerkandera adusta	1	0	1	0.0
Pycnoporus sanguineus	1	0	1	0.0
Coriolus hirsutus	5	0	5	0.0
Coriolus maximus	0	1	1	5.6
Coriolus pinisitus	0	1	1	5.6
Coriolus subectypus	0	1	1	5.6
Coriolus tenuis	1	0	1	0.0
Coriolus versicolor	15	14	29	77.8
Lenzites betulina	6	1	7	5.6
Phellinus gilvus	1	0	1	0.0
Totals	30	18	48	100.0

Discussion. Strigocis opacicollis is a fairly common inhabitant of *Coriolus versicolor* and its relatives in eastern North America. The European member of this genus, *S. bicornis* (Mellié), is known to breed in the same fungus, as well as *Pseudotrametes gibbosa* (Paviour-Smith, 1960a, 1969; Peyerimhoff, 1915; Roman, 1970). Other New World species, such as *S. opalescens* and *S. bilimeki,* have a similar preference for members of the *Coriolus* group.

46. *Strigocis opalescens* (Casey)

Geographical range. Eastern North America, from southern Michigan and New York south and west as far as northeastern Mexico.

Host range. Fungi: 1(1). Records: 3 (1). Known from *Coriolus versicolor* only.

47. *Hadraule blaisdelli* (Casey)

Geographical range. Western North America, from southern British Columbia to southern California, east through Utah, Arizona, and New Mexico into Texas, and south into Mexico. Also known from Michigan, Iowa, Ohio, Connecticut, Massachusetts, and Florida, but all but the first represent herbarium infestations.

Host range. Fungi: 11(7). Records: 19 (8). $B_s = 6.77$.

Records.	NB	BR	TOT	% BR
Bjerkandera adusta	2	1	3	12.5
Heterobasidion annosum	0	1	1	12.5
Antrodia sepium	3	0	3	0.0

Dichomitus squalens	0	1	1	12.5
Coriolus biformis	0	1	1	12.5
Coriolus versicolor	2	0	2	0.0
Funalia hispida	0	1	1	12.5
Gloeophyllum saepiarium	1	2	3	25.0
Daedaleopsis confragosa	0	1	1	12.5
Inonotus munzii	2	0	2	0.0
Phellinus robiniae	1	0	1	0.0
Totals	11	8	19	100.0

Discussion. This species has a relatively broad host range and it is difficult to determine from existing records if it does prefer one group of fungi. This is the only ciid known to infest herbarium fungus collections (Lawrence, 1971).

48. *Hadraule elongatula* (Gyllenhal)

Geographical range. In North America, known only from New Brunswick. In the Old World, widespread throughout Europe, North Africa, and Siberia.

Host range. Fungi: 1(1). Records: 1 (1). Known from *Piptoporus betulinus* only.

Discussion. It is not known whether the New Brunswick population represents a single introduction from Europe or whether this species is more widespread in northern North America. Palm (1946) has reported *H. elongatula* from a birch fungus in Scandinavia, while all other records for the species are from under bark, in rotten wood, or in the galleries of other beetles (*see* Lawrence, 1971).

49. *Plesiocis cribrum* Casey

Geographical range. Northern and montane regions of North America (particularly the western part), from British Columbia to the Gaspé Peninsula of Quebec, south to the Laguna Mountains in California, the edge of the Colorado Plateau in Arizona and New Mexico, the Great Lakes region, and the Shenandoah Mountains of Virginia.

Host range. Fungi: 3(2). Records: 58 (35). $B_s = 1.51$.

Records.	NB	BR	TOT	% BR
Hapalopilus alboluteus	2	0	2	0.0
Cryptoporus volvatus	18	30	48	85.7
Dichomitus squalens	3	5	8	14.3
Totals	23	35	58	100.0

Discussion. This species is extremely common in *Cryptoporus volvatus* and is also known to breed in *Dichomitus squalens.* If the somewhat doubtful records for *Cis laminatus* and *Ennearthron spenceri* are disregarded, *Plesiocis cribrum* is the only North American ciid known to breed in the fruiting bodies of *C. volvatus* (*see* p. 187).

50. *Ceracis californicus* (Casey)

Geographical range. Western North America, from Seattle, Washington, east to western Nebraska, south along the Pacific Coast to southern California, through the Great Basin and Rocky Mountains to southern Arizona and New Mexico, and south in Mexico as far as Baja California Sur and southern Sinaloa.

Host range. Fungi: 20(15). Records: 80(32). $B_s = 11.20$. $B_g = 5.89$. Group: *Ganoderma*?

Records.	NB	BR	TOT	% BR
Pleurotus ostreatus	2	1	3	3.1
Steccherinum ochraceum	2	1	3	3.1
Poria versipora	1	1	2	3.1
Bjerkandera adusta	9	2	11	6.3
Fomitopsis cajanderi	1	0	1	0.0
Fomitopsis fraxinophilus	0	1	1	3.1
Heterobasidion annosum	0	1	1	3.1
Hirschioporus pargamenus	0	1	1	3.1
Cerrena unicolor	0	1	1	3.1
Coriolus versicolor	19	5	24	15.6
Lenzites betulina	5	0	5	0.0
Funalia hispida	2	2	4	6.3
Datronia mollis	1	0	1	0.0
Ganoderma applanatum	0	2	2	6.3
Ganoderma brownii	2	8	10	25.0
Ganoderma lobatum	0	3	3	9.4
Ganoderma lucidum	0	1	1	3.1
Ganoderma oregonense	1	0	1	0.0
Ganoderma sp.	1	2	3	6.3
Phellinus gilvus	2	0	2	0.0
Totals	48	32	80	100.0

Discussion. Ceracis californicus has a relatively broad host range, including breeding records for at least 15 fungi. There is some indication that it prefers the conks of various *Ganoderma*, especially towards the center of its geographical range (Arizona and northern Mexico), while its apparent preference for *Coriolus versicolor* in northern California is partly due to the abundance of that particular host.

51. *Ceracis curtus* (Mellié)

Geographical range. Southeastern United States, from Florida to south-central Texas, the Bahamas, and the Greater Antilles.

Host range. Fungi: 2(1). Records: 4 (2). Group: *Ganoderma.*

Records.	NB	BR	TOT	%BR
Pogonomyces hydnoides	1	2	3	100.0
Fomes sclerodermeus	1	0	1	0.0
Totals	2	2	4	100.0

52. *Ceracis dixiensis* (Tanner)

Geographical range. Southwestern North America, from southern Utah to Guadalajara, Mexico, and from the Colorado River in California to the Big Bend Region in Texas.

Host range. Fungi: 2(1). Records: 12 (9). $B_s = 1.00$. Group: *Coriolus.*

Records.	NB	BR	TOT	%BR
Funalia hispida	2	9	11	100.0
Ganoderma sp.	1	0	1	0.0
Totals	3	9	12	100.0

Discussion. In southwestern North America, this species is commonly found in the sporophores of *Funalia hispida* on cottonwoods (*Populus* sp.) growing along river beds. It is often associated with *Cis versicolor.*

53. *Ceracis magister* Lawrence

Geographical range. Known only from Lignum Vitae Key, Florida.

Host range. Fungi: 1(1). Records: 4 (4). Known from *Phellinus robiniae* only.

54. *Ceracis minutissimus* (Mellié)

Geographical range. Eastern United States, from New Hampshire and Michigan to Alabama.

Host range. Fungi: 3(1). Records: 11 (9). $B_s = 1.00$.

Records.	NB	BR	TOT	%BR
Bjerkandera adusta	1	0	1	0.0
Cerrena unicolor	0	9	9	100.0
Coriolus versicolor	1	0	1	0.0
Totals	2	9	11	100.0

Discussion. This species is most common in the Northeast where it breeds exclusively on *Cerrena unicolor.*

55. *Ceracis minutus* Dury

Geographical range. Southern Texas, Florida, the Bahamas, and the Greater Antilles.

Host range. Fungi: 9(8). Records: 34 (24). $B_s = 7.09$. Group: *Coriolus*?

Records.	NB	BR	TOT	%BR
Lopharia papyrina	2	3	5	12.5
Pycnoporus sanguineus	0	3	3	12.5
Coriolus maximus	0	3	3	12.5
Coriolus pinisitus	4	6	10	25.0
Lenzites elegans	0	1	1	4.2
Earliella corrugata	0	1	1	4.2
Coriolopsis occidentalis	0	3	3	12.5
Pogonomyces hydnoides	3	4	7	16.7
Fomes sclerodermeus	1	0	1	0.0
Totals	10	24	34	100.0

Discussion. Ceracis minutus is another species with a broad host range and no apparent preference for one group of fungi. Most of the records, however, are from the Florida Keys, and several ciids appear to be more polyphagous in this area (*see* p. 189).

56. *Ceracis monocerus* Lawrence

Geographical range. Florida, Louisiana, and Cuba.

Host range. Fungi: 1(1). Records: 2 (1). Known from *Pycnoporus sanguineus* only.

Discussion. This southeastern species is known only from *Pycnoporus sanguineus,* but its Neotropical relatives, such as *Ceracis furcifer* Mellié and *C. ruficornis* (Pic), are known from various *Coriolus* and *Lenzites* as well.

57. *Ceracis multipunctatus* (Mellié)

Geographical range. Alabama, Florida, Cuba, Jamaica, and Montserrat.

Host range. Fungi: 6(3). Records: 17 (13). $B_s = 2.95$. $B_g = 1.99$. Group: *Ganoderma.*

Records.	NB	BR	TOT	%BR
Fomitella supina	1	0	1	0.0
Pogonomyces hydnoides	1	0	1	0.0
Fomes sclerodermeus	0	4	4	30.8
Ganoderma applanatum	0	4	4	30.8
Ganoderma lucidum	1	0	1	0.0
Ganoderma zonatum	1	5	6	38.5
Totals	4	13	17	100.0

Discussion. This is one of several southeastern and Neotropical *Ceracis* with a preference for *Fomes* and *Ganoderma.* In Florida, it is commonly associated with *Cis hirsutus* and *Ceracis punctulatus.*

58. *Ceracis nigropunctatus* Lawrence

Geographical range. Louisiana and Texas south, through Mexico and Central America, to Panama.

Host range. Fungi: 4(2). Records: 14 (5). $B_s = 1.66$. Group: *Ganoderma.*

Records.	NB	BR	TOT	%BR
Coriolus hirsutus	2	0	2	0.0
Pogonomyces hydnoides	5	4	9	80.0
Fomes sclerodermeus	0	1	1	20.0
Ganoderma sp.	2	0	2	0.0
Totals	9	5	14	100.0

59. *Ceracis obrieni* Lawrence

Geographical range. Southeastern Arizona and southern Sinaloa, Mexico.

Host range. Fungi: 1(1). Records: 5 (5). $B_s = 1.00$. Known from *Phellinus gilvus* only.

Discussion. This is the only member of the southwestern fauna to breed in *Phellinus gilvus,* which harbors many species in the Southeast and tropical America.

60. *Ceracis pecki* Lawrence

Geographical range. Eastern United States, from Illinois and Maryland south to Florida.

Host range. Fungi: 1(1). Records: 1 (1). Known from *Melanoporia nigra* only.

61. *Ceracis powelli* Lawrence

Geographical range. Southeastern Arizona and southern Durango, Mexico.

Host range. Fungi: 2(1). Records: 3 (1). Group: *Hirschioporus.*

Records.	NB	BR	TOT	%BR
Hirschioporus abietinus	1	1	2	100.0
Hirschioporus pargamenus	1	0	1	0.0
Totals	2	1	3	100.0

Discussion. Ceracis powelli is the only species of *Ceracis* known to breed exclusively in *Hirschioporus,* although *C. thoracicornis* is commonly found in these fruiting bodies.

62. *Ceracis pullulus* (Casey)

Geographical range. Southeastern United States, from North Carolina to Florida and west to Louisiana, the Greater Antilles, and the Virgin Islands.

Host range. Fungi: 10(7). Records: 43 (23). $B_s = 5.13$. $B_g = 3.09$. Group: *Phellinus.*

Records.	NB	BR	TOT	%BR
Nigroporus vinosus	1	0	1	0.0
Pogonomyces hydnoides	2	0	2	0.0
Ganoderma zonatum	2	2	4	8.7
Cyclomyces iodinus	1	1	2	4.3
Inonotus corrosus	0	1	1	4.3
Inonotus porrectus	0	4	4	17.4
Inonotus sp.	1	0	1	0.0
Melanoporia nigra	0	1	1	4.3
Phellinus gilvus	12	8	20	34.8
Phellinus licnoides	1	6	7	26.1
Totals	20	23	43	100.0

Discussion. This species and the related *C. singularis* have an obvious preference for xanthochroic fruiting bodies, especially those of *Phellinus.*

63. *Ceracis punctulatus* Casey

Geographical range. Eastern United States (east of the 100th meridian), from Michigan and southern Vermont to southern Texas and the Florida Keys, Cuba, and Jamaica.

Host range. Fungi: 19(9). Records: 92

(45). $B_s = 4.26$. $B_g = 2.88$. Group: *Phellinus.*

Records.	NB	BR	TOT	%BR
Stereum ostrea	1	0	1	0.0
Lopharia papyrina	0	2	2	4.4
Bjerkandera adusta	1	0	1	0.0
Hirschioporus pargamenus	1	0	1	0.0
Pycnoporus sanguineus	2	0	2	0.0
Coriolus pinisitus	1	0	1	0.0
Earliella corrugata	1	0	1	0.0
Coriolopsis fulvocinerea	1	2	3	4.4
Pogonomyces hydnoides	9	9	18	20.0
Fomes fomentarius	1	0	1	0.0
Ganoderma curtisii	1	0	1	0.0
Ganoderma lucidum	1	0	1	0.0
Ganoderma zonatum	2	1	3	2.2
Ganoderma sp.	1	0	1	0.0
Inonotus porrectus	0	1	1	2.2
Inonotus sp.	0	1	1	2.2
Phellinus gilvus	21	25	46	55.6
Phellinus licnoides	0	2	2	4.4
Phellinus robiniae	3	2	5	4.4
Totals	47	45	92	100.0

Discussion. Throughout most of its range, *Ceracis punctulatus* breeds in the sporophores of *Phellinus gilvus.* In Florida, however, the species is more variable in color (*see* Lawrence, 1967b) and has a broader host range, including *Pogonomyces hydnoides, Coriolopsis fulvocinerea,* and *Lopharia papyrina.* This may be tied in with the relatively recent disruption of the Floridian fauna, owing to Pleistocene flooding, and also to the constant immigration of Caribbean forms through the action of hurricanes (*see* p. 189). In the middle and northern parts of the range, the species is a characteristic inhabitant of *P. gilvus,* while the closely related *C. sallei* occurs in *Ganoderma applanatum.*

64. *Ceracis quadricornis* Gorham

Geographical range. Southern Texas through eastern and southern Mexico and as far south as Costa Rica.

Host range. Fungi: 7(5). Records: 21 (13). $B_s = 4.26$. Group: *Coriolus*?

Records.	NB	BR	TOT	%BR
Trametes cirrifer	1	0	1	0.0
Coriolus hirsutus	1	1	2	7.7
Coriolus maximus	1	3	4	23.1
Earliella corrugata	0	1	1	7.7
Coriolopsis crocata	1	0	1	0.0
Coriolopsis occidentalis	3	4	7	30.8
Pogonomyces hydnoides	1	4	5	30.8
Totals	8	13	21	100.0

65. *Ceracis sallei* Mellié

Geographical range. Eastern North America, from southern Ontario and Quebec to southern Texas and Florida, east of the 100th meridian.

Host range. Fungi: 10(6). Records: 45 (22). $B_s = 2.45$. Group: *Ganoderma.*

Records.	NB	BR	TOT	%BR
Oxyporus populinus	0	1	1	4.5
Fomitopsis pinicola	1	0	1	0.0
Pycnoporus cinnabarinus	1	0	1	0.0
Pogonomyces hydnoides	1	1	2	4.5
Fomes sclerodermeus	1	0	1	0.0
Ganoderma applanatum	15	17	32	77.3
Ganoderma curtisii	2	1	3	4.5
Ganoderma lobatum	0	1	1	4.5
Ganoderma zonatum	1	1	2	4.5
Ganoderma sp.	1	0	1	0.0
Totals	23	22	45	100.0

Discussion. This species is almost entirely restricted to the fruiting bodies of *Ganoderma applanatum* and its relatives and usually occurs in association with *Cis levettei* in the Northeast.

66. *Ceracis schaefferi* Dury

Geographical range. Southern Texas and eastern Mexico.

Host range. Known from *Ganoderma* sp. only.

Records. A single unverified record from "*Ganoderma pseudoboletus.*"

67. *Ceracis similis* Horn

Geographical range. Baja California Sur and Nayarit, Mexico, south to El Salvador.

Host range. Fungi: 3(3). Records: 6 (6). $B_s = 2.78$. $B_g = 1.00$. Group: *Ganoderma.*

Records.	NB	BR	TOT	%BR
Ganoderma applanatum	0	1	1	16.7
Ganoderma zonatum	0	3	3	50.0
Ganoderma sp.	0	2	2	33.3
Totals	0	6	6	100.0

68. *Ceracis singularis* (Dury)

Geographical range. Eastern North America, from northern Minnesota and Massachusetts to southern Texas and Louisiana; a single record from Mt. Irazu in Costa Rica.

Host range. Fungi: 21(9). Records: 59 (17). $B_s = 6.45$. $B_g = 2.40$. Group: *Phellinus.*

Records.	NB	BR	TOT	%BR
Fomitella supina	1	0	1	0.0
Heterobasidion annosum	1	0	1	0.0
Hirschioporus pargamenus	2	0	2	0.0
Trametes plebeja	1	0	1	0.0
Coriolus versicolor	1	0	1	0.0
Funalia hispida	1	0	1	0.0
Gloeophyllum saepiarium	0	1	1	5.9
Daedaleopsis confragosa	1	0	1	0.0
Fomes sclerodermeus	2	0	2	0.0
Ganoderma applanatum	6	2	8	11.8
Ganoderma curtisii	1	1	2	5.9
Ganoderma tsugae	1	0	1	0.0
Ganoderma sp.	1	0	1	0.0
Inonotus sp.	2	0	2	0.0
Melanoporia nigra	1	1	2	5.9
Phellinus gilvus	14	7	21	41.2
Phellinus igniarius	1	1	2	5.9
Phellinus licnoides	1	0	1	0.0
Phellinus ribis	0	1	1	5.9
Phellinus robiniae	4	2	6	11.8
Phellinus sp.	0	1	1	5.9
Totals	42	17	59	100.0

Discussion. Ceracis singularis is found throughout eastern North America but is particularly common in the Midwest. It is one of the few Nearctic ciids which breeds in the woody conks of *Phellinus robiniae* and *P. igniarius.*

69. *Ceracis thoracicornis* (Ziegler)

Geographical range. Eastern North America, from southeastern Manitoba and southern Quebec to southern Texas and Florida.

Host range. Fungi: 36(21). Records: 187(73). $B_s = 12.00$. $B_g = 8.31$. Group: *Hirschioporus*?

Records.	NB	BR	TOT	%BR
Boletus sp.	1	0	1	0.0
Stereum ostrea	2	0	2	0.0
Polyporus squamosus	1	2	3	2.7
Gloeoporus dichrous	1	0	1	0.0
Laetiporus sulphureus	1	0	1	0.0
Tyromyces spraguei	0	1	1	1.4
Bjerkandera adusta	9	7	16	9.6
Nigroporus vinosus	1	0	1	0.0
Fomitella supina	10	15	25	20.5
Fomitopsis fraxineus	1	0	1	0.0
Fomitopsis pinicola	1	0	1	0.0
Rigidoporus ulmarius	5	1	6	1.4
Rigidoporus vitreus	0	1	1	1.4
Irpex tulipiferae	0	1	1	1.4
Hirschioporus abietinus	2	1	3	1.4
Hirschioporus pargamenus	26	16	42	21.9
Hirschioporus sector	4	2	6	2.7
Cerrena unicolor	4	2	6	2.7
Trametes plebeja	2	0	2	0.0
Pycnoporus cinnabarinus	1	0	1	0.0
Coriolus hirsutus	3	1	4	1.4
Coriolus versicolor	8	3	11	4.1
Lenzites betulina	4	6	10	8.2
Lenzites elegans	3	7	10	9.6
Earliella corrugata	1	1	2	1.4
Funalia hispida	0	1	1	1.4
Funalia trogii	0	1	1	1.4
Pogonomyces hydnoides	1	0	1	0.0
Fomes fomentarius	2	0	2	0.0
Fomes sclerodermeus	1	1	2	1.4
Ganoderma applanatum	7	0	7	0.0
Ganoderma curtisii	1	0	1	0.0
Ganoderma lucidum	3	2	5	2.7
Ganoderma tsugae	4	1	5	1.4
Ganoderma sp.	1	0	1	0.0
Phellinus gilvus	3	0	3	0.0
Totals	114	73	187	100.0

Discussion. This is another eurytrophic species whose host range is almost as broad as that of *Cis americanus.* There is some indication of a preference for *Hirschioporus,* but there are also numerous records for *Coriolus, Lenzites,* and *Fomitella supina.* The number of records for the last may represent an artifact resulting from the abundance of that particular fungus in Florida and Louisiana. In spite of the large number of host fungi for this species, there is a notable absence of breeding records for members of the Hymenochaetaceae.

70. *Sulcacis curtulus* (Casey)

Geographical range. Northern and montane regions of North America, from British Columbia to southern Quebec and New England, south to San Diego County, California, the mountains of southern Arizona and northern Mexico, and the states of Nebraska, Illinois, and North Carolina.

Host range. Fungi: 14(7). Records: 119(55). $B_s = 3.46$. $B_g = 2.51$. Group: *Coriolus.*

Records.	NB	BR	TOT	%BR
Pleurotus ostreatus	3	0	3	0.0
Schizophyllum commune	0	1	1	1.8
Stereum hirsutum	1	0	1	0.0
Steccherinum ochraceum	1	0	1	0.0
Bjerkandera adusta	8	3	11	5.5
Pycnoporus cinnabarinus	1	1	2	1.8
Coriolus hirsutus	6	6	12	10.9
Coriolus versicolor	34	35	69	63.6
Lenzites betulina	3	5	8	9.1
Funalia hispida	2	4	6	7.3
Ganoderma applanatum	1	0	1	0.0
Inonotus rheades	1	0	1	0.0
Phellinus gilvus	1	0	1	0.0
Phellinus igniarius	2	0	2	0.0
Totals	64	55	119	100.0

Discussion. This is primarily a western species, although it does occur in the Northeast as well. It is a fairly common inhabitant of *Coriolus versicolor* and its relatives on the Pacific Coast. It appears to be closely related to the Palaearctic *Sulcacis bidentulus* (Rosenhauer), which has been recorded from *Funalia extenuata* (probably the same as *F. hispida*) and from *F. trogii* (Peyerimhoff, 1915; Roman, 1970). Other members of the genus, such as *S. affinis* (Gyllenhal) and *S. fronticornis* (Panzer), usually prefer members of the *Coriolus* group (Benick, 1952; Falcoz, 1921; Roman, 1970; Saalas, 1923; Scheerpletz and Höfler, 1948).

71. *Sulcacis lengi* Dury

Geographical range. Eastern North America, from Maine to the Carolinas and west to eastern Kansas and Texas.

Host range. Fungi: 5(3). Records: 20 (7). $B_s = 2.95$. Group: *Coriolus.*

Records.	NB	BR	TOT	%BR
Boletus sp.	1	0	1	0.0
Coriolus hirsutus	1	0	1	0.0
Coriolus pubescens	0	2	2	28.6
Coriolus versicolor	8	3	11	42.8
Lenzites betulina	3	2	5	28.6
Totals	13	7	20	100.0

72. *Malacocis brevicollis* (Casey)

Geographical range. Eastern North America, from northern Maine to the Florida Keys and west to southern Manitoba, eastern Kansas, and Texas.

Host range. Fungi: 16(9). Records: 79 (37). $B_s = 5.50$. $B_g = 1.12$. Group: *Phellinus.*

Records.	NB	BR	TOT	%BR
Nigroporus vinosus	1	0	1	0.0
Pogonomyces hydnoides	1	0	1	0.0
Fomes fomentarius	1	0	1	0.0
Inonotus corrosus	0	1	1	2.7
Phellinus everhartii	1	1	2	2.7
Phellinus ferruginosus	1	0	1	0.0
Phellinus gilvus	20	16	36	43.2
Phellinus igniarius	5	8	13	21.6
Phellinus johnsonianus	1	0	1	0.0
Phellinus laevigatus	1	3	4	8.1
Phellinus licnoides	3	0	3	0.0
Phellinus pini	0	1	1	2.7
Phellinus pomaceus	1	0	1	0.0
Phellinus robiniae	4	3	7	8.1
Phellinus robustus	2	2	4	5.4
Phellinus sp.	0	2	2	5.4
Totals	42	37	79	100.0

Discussion. Malacocis brevicollis breeds only in the darker hymenochaetoid fungi and is the most common inhabitant of *Phellinus robiniae* and *P. igniarius* throughout eastern North America. Several undescribed *Malacocis* in Central America have similar preferences.

73. *Rhopalodontus americanus* Lawrence

Geographical range. Known only from northern Wisconsin.

Host range. Fungi: 3(1). Records: 3 (1). Group: *Ganoderma*?

Records.	NB	BR	TOT	%BR
Russula sp.	1	0	1	0.0
Hapalopilus fibrillosus	1	0	1	0.0
Piptoporus betulinus	0	1	1	100.0
Totals	2	1	3	100.0

Discussion. This is the only New World representative of the Eurasian genus *Rhopalodontus.* Its European relative *R. perforatus* (Gyllenhal) has been recorded as breeding in *Fomes fomentarius* and *Piptoporus betulinus* (Benick, 1952; Paviour-Smith, 1969; Saalas, 1923).

74. *Octotemnus laevis* Casey

Geographical range. Northern part of North America, from southern Alaska to Quebec and Nova Scotia, south along the Pacific Coast to Monterey County, California, in the Sierra Nevada to Tulare County, in the Midwest to southern Iowa and Kansas, and on the East Coast to Alabama.

Host range. Fungi: 14(6). Records: 130(63). $B_s = 2.24$. $B_g = 1.26$. Group: *Coriolus.*

Records.	NB	BR	TOT	% BR
Stereum sp.	1	0	1	0.0
Polyporus squamosus	1	0	1	0.0
Laetiporus sulphureus	1	0	1	0.0
Tyromyces albellus	1	0	1	0.0
Tyromyces galactinus	1	0	1	0.0
Bjerkandera adusta	1	0	1	0.0
Hirschioporus abietinus	1	0	1	0.0
Hirschioporus pargamenus	1	0	1	0.0
Coriolus conchifer	1	4	5	6.3
Coriolus hirsutus	10	1	11	1.6
Coriolus pubescens	3	5	8	7.9
Coriolus versicolor	37	50	87	79.4
Lenzites betulina	4	2	6	3.2
Ganoderma applanatum	4	1	5	1.6
Totals	67	63	130	100.0

Discussion. This is an extremely common species throughout the northern part of North America, where it breeds almost exclusively on *Coriolus versicolor* and its relatives. It is only doubtfully distinct from the Palaearctic *O. glabriculus* (Gyllenhal), which is known to have similar host preferences, being most commonly recorded as breeding in *C. versicolor, C. hirsutus, Lenzites betulina,* and *Pseudotrametes gibbosa* (Benick, 1952; Donisthorpe, 1935; Falcoz, 1921; Paviour-Smith, 1960a; Roman, 1970; Scheerpeltz and Höfler, 1948).

HOST FUNGI AND ASSOCIATED CIIDAE

For each fungus species below, the total number of records and number of breeding records (in parentheses) are given, and these are followed by a list of ciid species known to breed in the sporophores (BR) and those known from nonbreeding records only (NB). To conserve space, each ciid species is represented by its corresponding number in Table 1.

Auricularia auricula. 1(1). BR: 43.
Auricularia polytricha. 1(0). NB: 17.
Lentinus crinitus. 1(0). NB: 5.
Panellus stipticus. 1(1). BR: 31.
Pleurotus ostreatus. 10(2). BR: 2, 50. NB: 34, 70.
Pleurotus sp. 2(0). NB: 10, 35.
Schizophyllum commune. 4(1). BR: 70. NB: 10, 37, 38.
Boletus sp. 2(0). NB: 69, 71.
Russula sp. 1(0). NB: 73.
Phlebia merismoides. 1(0). NB: 2.
Stereum hirsutum. 7(4). BR: 2. NB: 70.
Stereum ostrea. 20(5). BR: 29. NB: 5, 21, 24, 28, 32, 63, 69.
Stereum sp. 3(2). BR: 29. NB: 74.
Lopharia papyrina. 12(7). BR: 11, 55, 63.
Steccherinum ochraceum. 7(3). BR: 2, 50. NB: 70
Poria carbonica. 1(1). BR: 34.
Poria corticola. 1(1). BR: 10.
Poria versipora. 7(3). BR: 2, 50. NB: 14, 19.
Polyporus mutabilis. 1(1). BR: 5.
Polyporus squamosus. 9(5). BR: 2, 16, 69. NB: 21, 74.
Gloeoporus dichrous. 1(0). NB: 69.
Hapalopilus alboluteus. 2(0). NB: 49.
Hapalopilus fibrillosus. 1(0). NB: 73.
Laetiporus sulphureus. 11(3). BR: 2, 34, 42. NB: 10, 14, 23, 36, 69, 74.
Tyromyces albellus. 1(0). NB: 74.
Tyromyces cinerascens. 3(1). BR: 34. NB: 19.
Tyromyces galactinus. 1(0). NB: 74.
Tyromyces spraguei. 1(1). BR: 69.
Bjerkandera adusta. 77(27). BR: 2, 5, 10, 16, 26, 38, 47, 50, 69, 70. NB: 21, 32, 36, 39, 42, 45, 54, 63, 74.
Oxyporus latemarginatus. 3(1). BR: 10. NB: 5.
Oxyporus populinus. 5(4). BR: 21, 65.

Ischnoderma resinosum. 3(2). BR: 2, 21. NB: 14.

Nigroporus vinosus. 4(1). BR: 5. NB: 62, 69, 72.

Fomitella supina. 32(15). BR: 69. NB: 10, 17, 24, 35, 57, 68.

Piptoporus betulinus. 17(10). BR: 2, 21, 42, 48, 73. NB: 14.

Cryptoporus volvatus. 49(30) + 2 unverified. BR: 49. NB: 42. Unverified: 20, 40.

Laricifomes officinalis. 7(5). BR: 10, 13, 42. NB: 3, 41.

Fomitopsis cajanderi. 4(3). BR: 12. NB: 50.

Fomitopsis fraxinea. 2(0). NB: 16, 69.

Fomitopsis fraxinophila. 1(1). BR: 50.

Fomitopsis pinicola. 115(62). BR: 2, 3, 4, 10, 13, 14, 21, 34, 41, 42. NB: 16, 23, 65, 69.

Heterobasidion annosum. 14(7). BR: 2, 10, 23, 42, 47, 50. NB: 3, 14, 68.

Rigidoporus lignosus. 1(0). NB: 5.

Rigidoporus nigrescens. 2(1). BR: 21. NB: 2.

Rigidoporus rigidus. 1(0). NB: 17.

Rigidoporus ulmarius. 6(1). BR: 69.

Rigidoporus vitreus. 2(1). BR: 69. NB: 21.

Rigidoporus zonalis. 1(0). NB: 5.

Antrodia sepium. 5(2). BR: 12, 34. NB: 47.

Antrodia serialis. 2(2). BR: 41.

Dichomitus squalens. 16(11). BR: 13, 47, 49. NB: 10.

Irpex tulipiferae. 3(1). BR: 69. NB: 2, 42.

Hirschioporus abietinus. 65(26). BR: 1, 18, 19, 30, 32, 61, 69. NB: 2, 74.

Hirschioporus pargamenus. 124(41). BR: 2, 10, 17, 18, 30, 32, 50, 69. NB: 10, 21, 42, 61, 63, 68, 74.

Hirschioporus sector. 16(9). BR: 8, 17, 32, 69.

Hirschioporus versatilis. 1(10). NB: 36.

Cerrena unicolor. 20(14). BR: 30, 42, 50, 54, 69.

Trametes cirrifer. 1(0). NB: 64.

Trametes plebeja. 4(0). NB: 5, 68, 69.

Trametes robiniophila. 3(1). BR: 27.

Pycnoporus cinnabarinus. 6(1). BR: 70. NB: 35, 37, 65, 69.

Pycnoporus sanguineus. 8(5). BR: 10, 55, 56. NB: 45, 63.

Coriolus biformis. 2(1). BR: 47. NB: 2.

Coriolus conchifer. 8(6). BR: 16, 74.

Coriolus hirsutus. 68(27). BR: 2, 7, 16, 26, 30, 31, 37, 64, 69, 70, 74. NB: 10, 35, 45, 58, 71.

Coriolus maximus. 11(8). BR: 35, 45, 55, 64. NB: 17.

Coriolus pinisitus. 15(7). BR: 45, 55. NB: 7, 17, 63.

Coriolus pubescens. 20(11). BR: 16, 26, 71, 74. NB: 21.

Coriolus subectypus. 4(3). BR: 9, 24, 45. NB: 16.

Coriolus tenuis. 1(0). NB: 45.

Coriolus versicolor. 417(211). BR: 2, 9, 16, 24, 26, 33, 35, 37, 38, 45, 46, 50, 69, 70, 71, 74. NB: 21, 44, 47, 54, 68.

Lenzites betulina. 66(28). BR: 16, 24, 35, 37, 38, 44, 45, 69, 70, 71, 74. NB: 21, 50.

Lenzites elegans. 16(9). BR: 35, 55, 69. NB: 10, 16, 17, 31.

Earliella corrugata. 12(7). BR: 5, 10, 17, 55, 64, 69. NB: 63.

Funalia hispida. 33(21). BR: 35, 37, 47, 50, 52, 69, 70. NB: 10, 68.

Funalia trogii. 1(1). BR: 69.

Coriolopsis crocata. 1(0). NB: 64.

Coriolopsis fulvocinerea. 8(4). BR: 11, 17, 63.

Coriolopsis occidentalis. 10(7). BR: 55, 64.

Gloeophyllum saepiarium. 4(3). BR: 47, 68.

Gloeophyllum striatum. 2(1). BR: 11. NB: 10.

Datronia mollis. 3(2). BR: 2. NB: 50.

Daedaleopsis confragosa. 5(4). BR: 2, 21, 47. NB: 68.

Pogonomyces hydnoides. 71(31). BR: 5, 6, 10, 11, 17, 51, 55, 58, 63, 64, 65. NB: 57, 62, 69, 72.

Fomes fomentarius. 24(12). BR: 21. NB: 2, 42, 63, 69, 72.

Fomes sclerodermeus. 23(8). BR: 10, 17, 57, 58, 69. NB: 51, 55, 65, 68.

Ganoderma applanatum. 152(75). BR: 2, 14, 21, 42, 50, 57, 65, 67, 68, 74. NB: 5, 10, 16, 17, 32, 34, 69, 70.

Ganoderma brownii. 14(11). BR: 14, 16, 50. NB: 37.

Ganoderma curtisii. 9(2). BR: 65, 68. NB: 28, 63, 69.

Ganoderma fulvellum. 1(1). BR: 10.

Ganoderma lobatum. 4(4). BR: 50, 65.

Ganoderma lucidum. 17(8). BR: 10, 17, 21, 28, 50, 69. NB: 57, 63.

Ganoderma oregonense. 3(2). BR: 13, 34. NB: 50.

Ganoderma tsugae. 21(8). BR: 2, 21, 69. NB: 36, 68.

Ganoderma zonatum. 23(15). BR: 17, 57, 62, 63, 65, 67. NB: 11.

Ganoderma spp. 15(7). BR: 17, 50, 67. NB: 52, 58, 63, 65, 68, 69.

Cyclomyces iodinus. 4(1). BR: 62. NB: 17, 28.

Inonotus corrosus. 3(3). BR: 6, 62, 72.

Inonotus munzii. 2(0). NB: 47.

Inonotus porrectus. 11(9). BR: 6, 62, 63.

Inonotus spp. 4(1). BR: 63. NB: 62, 68.

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Phellinus gilvus. 144(62). BR: 15, 59, 62, 63, 68, 72. NB: 10, 28, 32, 34, 36, 45, 50, 69, 70.

Phellinus igniarius. 17(9). BR: 68, 72. NB: 70.

Phellinus johnsonianus. 1(0). NB: 72.

Phellinus laevigatus. 4(3). BR: 72.

Phellinus licnoides. 13(8). BR: 62, 63. NB: 68, 72.

Phellinus pini. 2(2). BR: 22, 72.

Phellinus pomaceus. 1(0). NB: 72.

Phellinus ribis. 1(1). BR: 68.

Phellinus robiniae. 33(13). BR: 25, 53, 63, 68, 72. NB: 6, 21, 47.

Phellinus robustus. 4(2). BR: 72.

Phellinus spp. 4(4). BR: 15, 68, 72.

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Osteology and Relationships of the Prochilodontidae, A South American Family of Characoid Fishes

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OSTEOLOGY AND RELATIONSHIPS OF THE PROCHILODONTIDAE, A SOUTH AMERICAN FAMILY OF CHARACOID FISHES

TYSON R. ROBERTS[1]

ABSTRACT. Little studied and poorly known, Prochilodontidae are among the most important of the inland food fishes in South America. A brief review of their biology is presented in the Introduction, followed by an account of their osteology. Observations are also given on the soft anatomy of the trophic structures. Prochilodontidae usually have been regarded as close relatives of the Curimatidae, but there are no shared specializations in support of such relationship (with the possible exception of paired epibranchial pouches). Rather, highly specialized features of the jaw suspension indicate they are closely related to Anostomidae and Chilodontidae. They have a number of unique specializations, especially of the trophic structures, which distinguish them from other characoids and support their taxonomic rank as a separate family.

INTRODUCTION

The thirty or so species of Prochilodontidae, all medium or large sized, comprise some of the most important fishes consumed in Ecuador, Colombia, Venezuela, the Guianas, Brazil, Perú, Bolivia and Argentina. Members of the family can be recognized at a glance by their characteristic appearance (Fig. 1). Superficially resembling some of the larger African and Asian fishes of the cyprinoid genus *Labeo*, they are iliophytophagous, ingesting mud, diatoms, periphyton and organic detritus. The enlarged, fleshy lips bear exceedingly numerous minute teeth and can be everted into a broad rasping (and suctorial?) disc.

There are only three genera of Prochilodontidae: *Ichthyoelephas, Semaprochilodus,* and *Prochilodus* (Mago Leccia, 1972). *Ichthyoelephas,* with only two species, has a very restricted range: one species in the Guayas basin on the Pacific coast of Ecuador, the other species in Pacific and Atlantic coastal river systems of Colombia, including the Río Magdalena. *Semaprochilodus,* with four species, has its range centered in the Amazon and Orinoco basins. It probably does not occur south of the Amazon. It should be noted that the type species of *Semaprochilodus, S. squamilentus* Fowler (1941: 170–174, fig. 83) is based on specimens purportedly collected from the Rio Parnaíba at Therezina in northeastern Brazil. This report, like that of *Boulengerella cuvieri* from the same locality (*ibid.*, p. 194, fig. 103), is almost certainly based on specimens having erroneous locality labels. Long-term collecting efforts in the Rio Parnaíba subsequently conducted by Sr. R. Adhemar Braga (Serviço de Piscicultura, Departamento Nacional das Obras Contra as Sêcas) at Therezina and other localities have failed to produce a specimen of either genus. Sr. Braga and I suspect that the *Semaprochilodus* (and *Boulengerella*) in question originated from the market in Belem-do-Pará and were inadvertently included with lots collected at Therezina. In all probability *S. squamilentus* is a junior syno-

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nym of one of the well-known Amazonian species. *Prochilodus,* with some 24 species, is very widely distributed. It occurs in the Magdalena basin, in the Guianas, throughout the Amazon, Orinoco, and Plate basins, and in most of the larger separate river systems of Brazil, including the Rio São Francisco.

It is well known that *Prochilodus* and *Semaprochilodus* undertake extensive upstream spawning migrations, after the onset or at the height of the rainy season (Ihering and Azevedo, 1934); Godoy, 1959, 1967; Schaller, 1968; Mago Leccia, 1972). The tremendous schools of *Prochilodus platensis* in the Río de la Plata (Ringuelet *et al.,* 1967: 206–7) are perhaps larger than the schools of any other species of freshwater fish in South America. Several species are noted as accumulating considerable fat deposits before the reproductive season, presumably as reserves for the spawning migration. Prochilodontidae are also known for the extremely large number of eggs they produce. The two ovaries of a *Prochilodus argenteus* of 640 mm in total length contained over 600,000 eggs (Fontenele, 1953).

Fishermen on the Amazon say they can distinguish different species of spawning Prochilodontidae by the sounds they make (personal communication from Prof. George S. Myers). During the spawning migration, males of *Prochilodus argenteus* emit a very loud and characteristic sound ("ronco") audible above the water surface. The sounds increase in intensity as spawning occurs (Fontenele, 1953). Schaller (1968) published a spectrogram of the sound made by a school of *Semaprochilodus.* They made a noise like that of a motorcycle. Actual spawning may occur in shallow water almost anywhere along the course of large rivers, sometimes below obstacles such as waterfalls. There are several reports that Prochilodontidae spawn at night: Ihering and Azevedo (1934) for *P. argenteus;* Godoy (1959) for *P. scrofa;* and Schaller (1968) for *S. insignis.* After spawning, the fishes form large schools that move downstream back to the feeding grounds.

The mechanism of sound production in the spawning males is not well understood. Fontenele (1953) reported vibratory movements of the opercular covers as the sounds were emitted, but such movements are possibly a secondary effect. Schaller (1968) suggested that sound is produced by vibration of the circular opening between the anterior and posterior chambers of the swim bladder, when air is forced from the anterior chamber into the posterior chamber by contractions of the epaxial muscles. Whether males of *Ichthyoelephas* produce sounds comparable to those of *Prochilodus* and *Semaprochilodus* is unrecorded. Comparable sounds have not been reported in any other family of characoids.

Techniques inducing *Prochilodus* to spawn in captivity, by means of injecting pituitary extracts, and for rearing the eggs and young until they are old enough for stocking, were developed by Brazilian fishery biologists (Fontenele *et al.,* 1946; Fontenele, 1953). Hatchery-produced *Prochilodus* have been stocked in açudes or reservoirs in northeastern and southeastern Brazil for more than 20 years. *Ichthyoelephas humeralis* and *I. longirostris* are among the most promising indigenous species in Ecuador and Colombia for stocking and fish culture.

A key to the genera of Prochilodontidae is given by Mago Leccia (1972) in his revision of the species in Venezuela. The family should be revised on a continent-wide basis. Citations of virtually all important systematic references can be found by consulting Eigenmann, 1912, 1922; Fowler, 1948-1954; Ringuelet *et al.,* 1967; and Mago Leccia, 1972.

The purpose of the present paper is to provide morphological and osteological information on Prochilodontidae as a basis for studies of their trophic habits, functional anatomy, and phyletic relationships to other characoids. Previous osteological

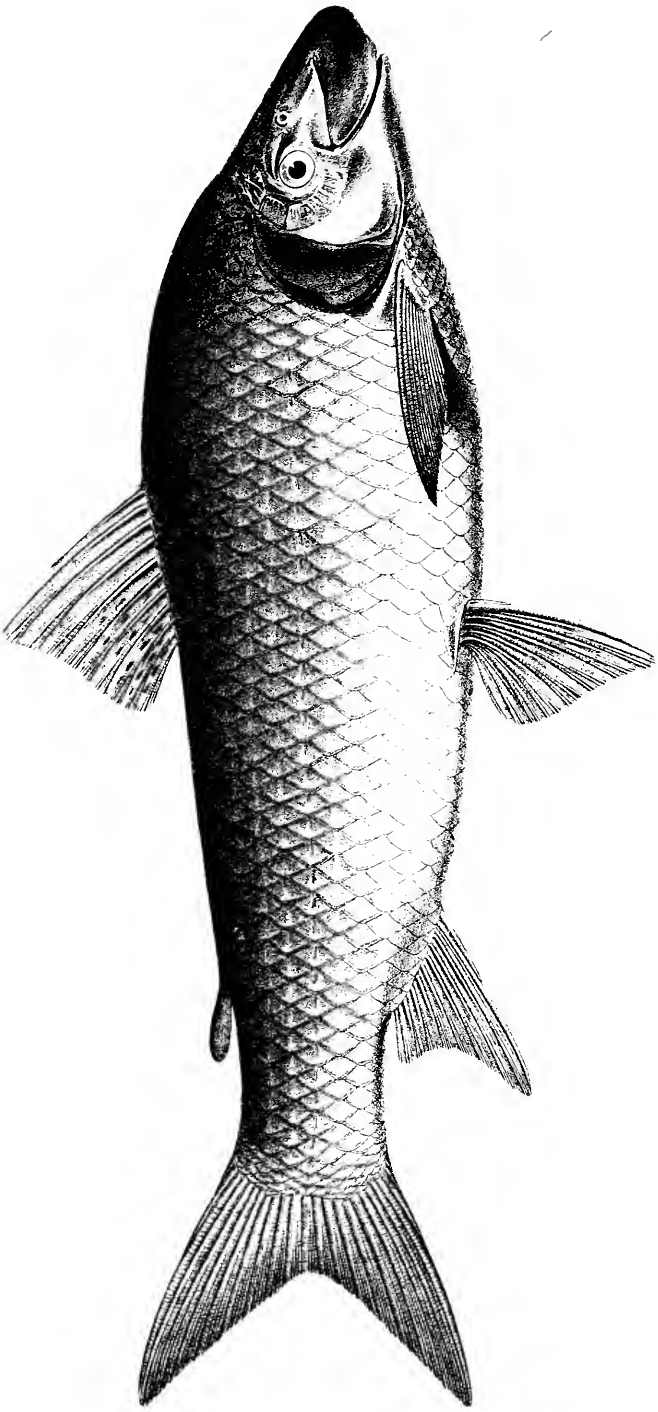

Figure 1. *Ichthyoelephas longirostris*, from the Río Cauca, Colombia (from Steindachner, 1880).

work on Prochilodontidae is limited to brief observations by Regan (1911) and to figures illustrating superficial differences in the crania of *Ichthyoelephas* and *Prochilodus* (Miles, 1943: 46). Schaller (1968) gave a brief description and figures of the swim bladder of *S. insignis.* I am unable to provide any further information concerning the mechanism of sound production. The most important conclusions reached herein concern the relationships and systematic status of Prochilodontidae. There is little in the way of shared specializations to indicate relationship with Curimatidae. The structure of the suspensorium of the jaws shows highly specialized conditions found elsewhere only in Anostomidae and Chilodontidae, and other osteological evidence tends to support the idea of relationship between Prochilodontidae and Anostomidae. The highly specialized dentition and soft anatomical features of both jaws and gill arches provide diagnostic features for the Prochilodontidae and justify its familial rank.

ACKNOWLEDGMENT

Dr. Stanley H. Weitzman, Division of Fishes, Smithsonian Institution, kindly read the manuscript and offered suggestions for its improvement.

OBSERVATIONS

Study material. The osteological observations described below are based on alizarin preparations of the following specimens: *Ichthyoelephas humeralis* (Gunther), MCZ 48723, two specimens, 97.2 and 102.4 mm in standard length; Río Vinces at Vinces, Guayas basin, Ecuador; T. Roberts, R. Gilbert, F. Silva M., 5 November, 1971. *Prochilodus vimboides* Kner, MCZ 20169, two specimens, 94.8 and 103.0 mm in standard length; Rio Paraíba, southeastern Brazil; Hassler Expedition, 1872. *Semaprochilodus insignis* (Schomburgk), MCZ 20129, three specimens, 95.3, 96.7, and 106.7 mm in standard length; lower Amazon River at Villa Bella, Brazil; Thayer Expedition, 1866.

The figures of prochilodontid osteology are based on *Ichthyoelephas humeralis* (hereafter referred to as *Ichthyoelephas*). *Prochilodus vimboides* and *Semaprochilodus insignis* (hereafter referred to as *Prochilodus* and *Semaprochilodus*) were thoroughly dissected and directly compared with *Ichthyoelephas.* In most respects the osteology of the three genera is extremely similar, but there are some noteworthy differences in the suspensorium of the jaws. The soft anatomy of the trophic structures is also closely similar in the three genera.

Cranium (Figures 2–5). Ethmoid bone relatively large and broad, especially in *Ichthyoelephas,* with a thin, ventrally directed median lamina. Ethmoid spine broadly rounded. Shape of ethmoid somewhat similar to that in anostomids such as *Leporinus* and *Schizodon.* Ethmoid with a short posterolateral process contacting a process from lateral ethmoid.

Vomer expanded anteriorly into a rounded plate, from which a dorsally directed median lamina projects. Head of vomer with a prominent pair of synchondral joint surfaces for ethmoid. Unlike Curimatidae, no substantial block of cartilage between vomer and ethmoid.

Lateral ethmoids large, with slender anterior processes contacting ethmoid (an unusual condition in characoids) and posterior processes contacting orbitosphenoid. In some specimens orbital blade or lamina of lateral ethmoids highly fenestrated (*cf.* Fig. 4).

Frontals broad, deeply notched posteriorly for dilator fossae. Dilator fossae not extending onto dorsal surface of frontals. Notch in frontals covered by closely adherent sixth infraorbital or dermosphenotic. Frontoparietal fontanel narrow, open for its entire length in juvenile *Prochilodus* and *Semaprochilodus.* In juvenile *Ichthyoelephas* only frontal portion of fontanel open, a relatively rare condition in characoids (occurs in some specimens of *Leporinus*). In large adults of Prochilodontidae frontoparietal fontanel sometimes entirely closed. Frontals bear extremely branched laterosensory canals.

Rhinosphenoid absent. Orbitosphenoid receiving well-developed processes from lateral ethmoids. Orbitosphenoid with ventrally directed process joined to parasphenoid in *Semaprochilodus* and *Prochilodus.* Similar process absent in *Ichthyoelephas.* Parasphenoid anteriorly and posteriorly with a well-developed ventromedian lamina. Parasphenoid terminating in a slight notch posteriorly, not deeply cleft.

Posttemporal fossae each with two well-developed openings, as in most (all?) Characidae and in Anostomidae. Parodontidae, Hemiodontidae, and (all?) Curimatidae have three openings into each posttemporal fossa. Subtemporal fossae well developed. Intercalar bone bridging a sizeable recess in posteromedial corner of subtemporal fossa. Prootic, pterotic and sphenotic with well-developed facets for hyomandibular joint. Lagenar capsules moderately large. Curimatidae with exceptionally large lagenar capsules. Pterotic with a well-developed posteriorly directed spine. Epiotic spineless. Supraoccipital spine enlarged, relatively deep and moderately elongate but narrow based.

Otoliths (Figure 6). Otoliths superficially similar to those of many other characoids, including *Brycon* (*cf.* Weitzman, 1962, fig. 7 of *Brycon meeki* otoliths).

Jaws; dentition (Figures 7–11). Greatly enlarged lips and gums of Prochilodontidae form a large, round, suckerlike disc when mouth fully opened. Entire rim of disc provided with minute labial papillae (not figured) and minute spatulate or ciliate teeth. In a 97.2-mm *Ichthyoelephas* there are around 600 functional teeth on periphery of oral disc. Teeth comparably numerous in *Prochilodus* and *Semaprochilodus.* Number of teeth on rim of oral disc increases (linearly?) with size of individual. In addition to functional teeth on rim of oral disc, there are two inner V-shaped rows of morphologically similar but slightly enlarged teeth, one row in upper lip and one row in lower lip. Within fleshy mouthparts lie row upon row of preformed replacement teeth. *Semaprochilodus* of 95.3 to 106.7 mm with only three to five rows of replacement teeth for functional row on rim of oral disc; *Prochilodus* of 94.8 to 103.0 mm with six to eight rows of replacement teeth; and *Ichthyoelephas* (*I. humeralis*) of 97.2 to 102.4 mm with ten to twelve rows of replacement teeth. Number of rows of replacement teeth presumably increases with increasing size of individual. *Ichthyoelephas longirostris,* with largest soft mouthparts of any Prochilodontidae, presumably also with largest number of replacement tooth rows. Perhaps closely packed rows of replacement teeth stiffen oral disc or perform some other mechanical function. To judge from the number of functional teeth and the number of rows of replacement teeth, more tooth replacement occurs in Prochilodontidae than in any other characoids.

Functional teeth movable, because they attach only to soft tissues of lips and gums. All teeth closely adjacent to each other, with crown of each tooth curved so that it overlaps tooth posterior to it (Fig. 7), thus transferring pressure on any one tooth to several more teeth anteriorly. Mago Leccia (1972) pointed out morphological differences between the teeth of *Ichthyoelephas, Semaprochilodus* and *Prochilodus* (Fig. 8). Range of tooth shapes greater in *Prochilodus* than in other two genera (personal observation).

Premaxillary movably articulated with ethmoid but not truly protractile. Curvature of premaxillary and maxillary provides greater area for attachment of lips and gums. Maxillary with well-developed anterior process for attachment of tendon from adductor mandibulae, and posterior process for maxillomandibular ligament. Maxillary (but not premaxillary) with several large foramina.

Lower jaw (Fig. 9) extremely modified,

its morphology distinct from that of other characoids. Jaw heavy and compact in construction, and foreshortened. Replacement tooth trench (typically present in lower jaw of characoids but absent in upper jaw) very deep and broadly open, with a single large foramen in its posterior wall. No fenestra at point where upper limb of articular passes externally to dentary. Such a fenestra usually (always?) present and well developed in Curimatidae and in characoids with normally elongate jaws. Dentary with a medial shelf bearing a stubby, dorsally directed flange partially overlying coronomeckelian bone and entirely overlying anteromedial process of articular bone. Proximal part of angular bone snugly tucked into a pocket in ventral margin of articular bone. In this feature and in their compaction and general morphology, prochilodontid lower jaws resemble those of Anostomidae more than any other characoids (*cf.* Figs. 12–13 of *Schizodon*). In contrast, jaws of hemiodontids and curimatids relatively elongate and of generalized characoid morphology, with angular bone exposed, a fenestra between articular and dentary, and anteromedial process of articular lying exposed on a medial surface of dentary (*cf.* Fig. 14 of *Acuticurimata macrops*).

Suspensorium and opercle (Figures 10–11). Suspensory apparatus of jaws composed of quadrate, symplectic, preopercular, palatine, ectopterygoid, mesopterygoid, metapterygoid, and hyomandibular. In addition three autogenous canal bones associated with preopercle—a suprapreopercle and two subpreopercles. Relationships of quadrate, preopercular, subpreopercles and interopercle highly specialized in prochilodontids, providing information of phyletic significance: similar specializations otherwise occur only in Anostomidae and Chilodontidae. In Prochilodontids quadrate with a broad, elongate, lateral flange or trough forming a shelf underlying the massive adductor mandibulae muscles. Quadrate also with a posteriorly directed process extending medially alongside anterior end of preopercle. Anterior end of preopercle extends only for a short distance in between this medial quadrate process and lateral flange or trough of quadrate and is thus unusually distant from quadratomandibular joint. Interopercle, which in characoids usually extends anteriorly to near quadratomandibular joint, extends only as far forward as preopercle. In consequence, preopercular segment of preoperculomandibular sensory canal passes anteriorly through two separate subpreopercular canal bones before reaching mandible. All of these highly specialized features also occur in Anostomidae such as *Leporinus* and *Schizodon* (*cf.* Figs. 12–13 of *Schizodon*), in which quadrate bone and its lateral trough or flange are even more elongate than in Prochilodontidae. In contrast, relationships of quadrate, interopercle and preopercle in Curimatidae are relatively generalized (*cf.* Fig. 14 of *Acuticurimata macrops*).

As in Parodontidae, Hemiodontidae, and Anostomidae (but not in Curimatidae), ectopterygoid movably articulated to quadrate. Mesopterygoid and metapterygoid, however, firmly united. Union between meso- and metapterygoids in Parodontidae, Hemiodontidae, and Anostomidae loose. Metapterygoid-quadrate foramen distinctive in that its dorsal border (formed by metapterygoid) is straight or slightly convex, rather than deeply indented as in typical Characidae, Hemiodontidae, Curimatidae (Figs. 14–15), and Anostomidae (Figs. 12–13). In *Ichthyoelephas* mesopterygoid relatively small, falling far short of palatine; in *Prochilodus* mesopterygoid larger; and in *Semaprochilodus* much larger, almost reaching palatine. At its movable articulation with quadrate, ectopterygoid forked or notched ventrally, much more so in *Prochilodus* and *Semaprochilodus* than in *Ichthyoelephas.* Symplectic more elongate and more loosely attached to quadrate in *Prochilodus* and *Semaprochilodus* than in *Ichthyoelephas.* Metapterygoid loosely bound to hyomandibular in *Prochilodus* and *Semaprochilodus*, less so in *Ichthyoelephas.*

All prochilodontids with a preopercle, interopercle, subopercle and opercle. Lateral surface of opercle smooth, without strong flange just above hyomandibulo-opercular joint, characteristic of Curimatidae (*cf.* Fig. 16 of *Acuticurimata macrops*). This flange readily detectable in specimens preserved in alcohol, and occurs in many (all?) curimatids, including *"Pseudocurimata" ocellata* (Eigenmann and Eigenmann, 1889), which superficially resembles *Hemiodus* very strongly. (Opercular flange absent in *Anodus;* my researches, as yet unpublished, strongly indicate that *Anodus,* despite its toothless jaws, belongs in the family Hemiodontidae rather than in Curimatidae.)

Nasal, antorbital, and circumorbital bones (Figure 17). Circumorbital series complete with a supraorbital, antorbital, and six infraorbitals. Infraorbitals and nasal with both laminar and tubular components. Shape of antorbital and of first infraorbital (lacrimal), and relation of first and second infraorbitals to each other rather similar in prochilodontids and anostomids (*cf.* Fig. 18 of *Schizodon*), although anostomid second infraorbital lacks anteroventrally directed flange characteristic of Prochilodontidae. First infraorbital greatly enlarged. Supraorbital lacking slender ventrally directed process contacting antorbital characteristic of many Curimatidae (*cf.* Fig. 15 of *Acuticurimata macrops*).

Hyoid bar and branchial arches (Figures 19–23). Hyoid bar (Fig. 19) with four greatly expanded branchiostegal rays, three on ceratohyal and one on epihyal. Basihyal moderately expanded anteriorly inside tongue. Interhyal large, its lower end forming a V-shaped joint saddling dorsal surface of epihyal (apparently a unique specialization). Dorsal and ventral hyopohyals fused or partially fused and difficult to distinguish.

Soft anatomy of prochilodontid branchial arches (Fig. 20) distinctive and highly specialized. Gill rakers of first four arches stubby and embedded in thick, tough epithelium. First arch bears about four rakers on its upper limb and ten to twelve rakers on its lower limb. Ceratobranchial bones of fifth arch covered by a highly papillose epithelium, with fine papillae arranged in numerous rows perpendicular to main axis of body. This papillose epithelium continues uninterrupted into dorsally situated pair of epibranchial sacs or pouches lying immediately posterior to fourth (last) pair of epibranchial bones. Fourth epibranchial (Figs. 21–22) with a large, dorsally directed lamina. Ventrally it has a well-developed tooth plate bearing two or three dozen minute conical teeth with greatly swollen round bases. No other teeth on prochilodontid branchial arches. Tooth plate articulated to fourth epibranchial bone by a moveable (synovial?) joint (Fig. 22).

Anostomidae bear opposable tricuspid teeth on third and fourth epibranchial and fifth ceratobranchial toothplates, as do Chilodontidae. Prochilodontid epibranchial teeth greatly reduced, apart from their swollen bases, no direct evidence found to indicate derivation of these teeth from tricuspid teeth. In Curimatidae third and fourth epibranchial and fifth ceratobranchial toothplates bear numerous conical teeth (without swollen bases).

Ichthyoelephas with first pair of suspensory pharyngeal bones or infrapharyngobranchials apparently absent. These bones definitely present in *Semaprochilodus* and *Prochilodus.* These first elements easily lost or overlooked, being smaller and more dorsal in position than second through fourth infrapharyngobranchials.

Pectoral and pelvic girdles (Figures 24–25). Prochilodontid pectoral and pelvic girdles of generalized characoid morphology apparently lacking in features of phyletic significance at generic or family levels. Position of forked posttemporal bone in relation to occiput as shown in Figure 5. Pectoral girdle complete, with posttemporal, supracleithrum, cleithrum, scapular, mesocoracoid, coracoid, four proximal radials and three postcleithra.

Third postcleithrum with proximal part expanded, distal part slender.

Pelvic bone with well-developed, elongate ischiac process. Innermost pelvic radial greatly enlarged, comma-shaped, as in many other characoids (*cf.* Roberts, 1971, fig. 14 of hemiodontid *Micromischodus sugillatus*). Pelvic fin usually with nine rays, although several specimens examined with pelvic fin of one side nine-rayed and pelvic fin of other side ten-rayed.

Weberian apparatus (Figure 26). Weberian apparatus of generalized characoid construction, apparently without phyletically significant features at generic or family levels. Comparisons closer than are now possible of Weberian apparatus among more characoid groups may prove informative.

Vertebral counts. Total vertebral counts in two specimens of *Ichthyoelephas,* 34 and 35; in two *Prochilodus,* 37 and 38; and in three *Semaprochilodus,* 40 and 41 (in two specimens). Abdominal plus candal vertebral counts in the same specimens are: *Ichthyoelephas,* 23 + 11 and 24 + 11; *Prochilodus,* 26 + 11 and 25 + 13; and *Semaprochilodus,* 26 + 14 and 27 + 14 (in two specimens).

Supraneurals (Figure 27). Supraneurals greatly expanded, four in *Prochilodus* and *Ichthyoelephas,* five in *Semaprochilodus.*

Caudal skeleton (Figure 28). Nomenclature of caudal skeleton followed here is that presented by Monod (1969). Prochilodontid caudal skeleton identical to the generalized or typical caudal skeleton pattern shared by diverse and unrelated characoids, including Curimatidae, Anostomidae, Parodontidae, and characids such as *Chalceus, Alestes,* and *Brycon* (*cf.* Weitzman, 1962), fig. 15 of *B. meeki*). Parhypural and six separate hypurals present. Parhypural without a distinct hypurapophysis. No secondary hypurapophysis on first hypural. Parhypural bears a moderately to strongly developed ridge for much or all of its length; this ridge is a continuation of side of hemal arch onto laminar portion of parhypural. Second hypural fused to complex hypural centrum. Two pairs of uroneurals and three epurals present. In common with all characoids, Prochilodontidae have 10 + 9 principal caudal rays.

Caudal skeleton of Hemiodontidae (including *Anodus*) differs significantly from above pattern in having first and second hypurals fused to each other and in having second hypural entirely separated from complex hypural centrum (*cf.* Roberts, 1971, fig. 15 of *Micromischodus sugillatus*), as verified in all genera of Hemiodontidae, except *Atomaster* (unavailable for study).

DIAGNOSTIC FEATURES OF THE FAMILY PROCHILODONTIDAE

The most distinctive features of Prochilodontidae described above are those having to do with the dentition, both oral and branchial, and with the anatomy of the trophic structures. The dentition is highly specialized and quite unlike that of other characoids. While Curimatidae have highly papillose branchial epithelium and paired epibranchial pouches, the distribution and form of the papillae are quite different in Prochilodontidae. It seems likely that the epibranchial pouches of Curimatidae are of independent origin. In at least one curimatid—"*Pseudocurimata*" *ocellata*—minute conical teeth are evenly distributed in the epithelial lining of the epibranchial pouches. The morphology of both the upper and lower jaws is highly distinctive, as is also the soft anatomy of the mouth and the exceptionally numerous rows of preformed replacement teeth. The interhyal bone is uniquely specialized. Although adequate comparative studies have yet to be made, it seems likely that the viscera (Fig. 29) may offer diagnostic features, for example, the minute and exceedingly numerous pyloric caeca. The intestine is only moderately coiled, in sharp contrast to the exceptionally coiled condition found in Curimatidae at comparable sizes. The sound-producing mechanism of the males, when it is properly understood and adequate comparative studies have been made, may also prove diagnostic. In my opinion the unique specializations exhibited by these fishes certainly justify their taxonomic rank as a separate family.

RELATIONSHIPS OF PROCHILODONTIDAE

Owing to superficial resemblances in appearance and feeding habits, it has generally been assumed that Prochilodontidae are closely related to Curimatidae, a family in which adults have thin-lipped edentulous jaws. Regan (1911) placed the Prochilodontidae (as the subfamily Prochilodontinae) in his family Anostomidae (consisting also of the subfamilies Anostominae and Curimatinae). Apart from the paired epibranchial pouches, discussed above, there are no shared specializations in support of a close relationship between Prochilodontidae and Curimatidae. The lateral opercular flange characteristic of Curimatidae is absent in Prochilodontidae, and the many striking specializations of the Prochilodontidae are notably absent in Curimatidae (*vide supra*). The evidence favoring relationship between Prochilodontidae and Anostomidae is relatively strong: the extremely specialized conditions in the suspensorium of the jaws characteristic of the two groups, and general similarities in the morphology of the jaws and cranium, including the shape of the ethmoids, frontoparietal fontanel, and presence of only two openings into the posttemporal fossae (versus three openings in Curimatidae).

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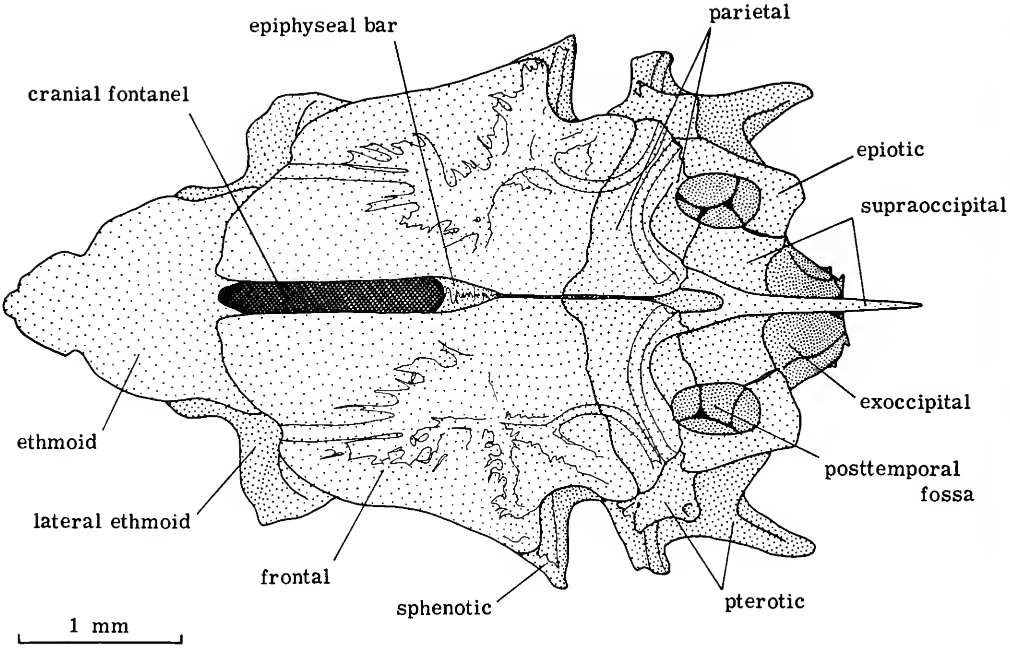

Figure 2. *Ichthyoelephas humeralis,* 97.2 mm, dorsal view of cranium.

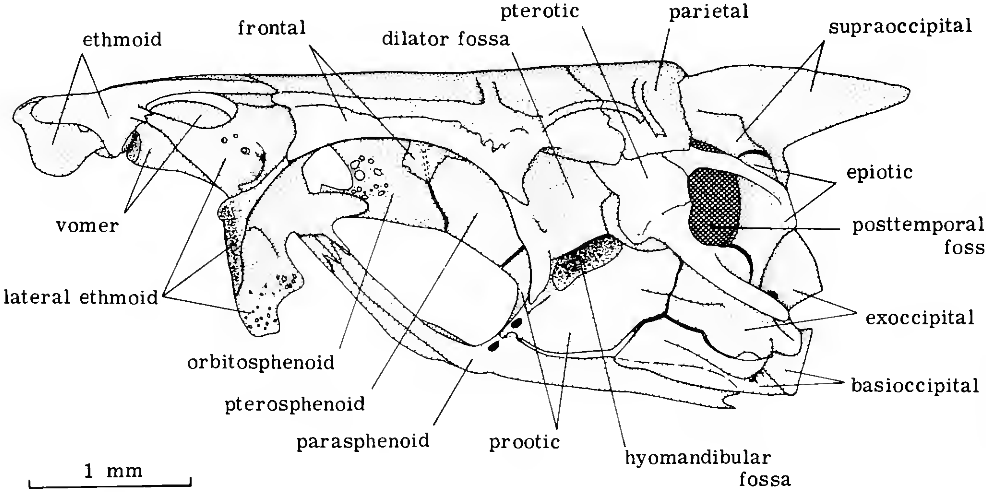

Figure 3. *Ichthyoelephas humeralis,* 102.4 mm, lateral view of cranium.

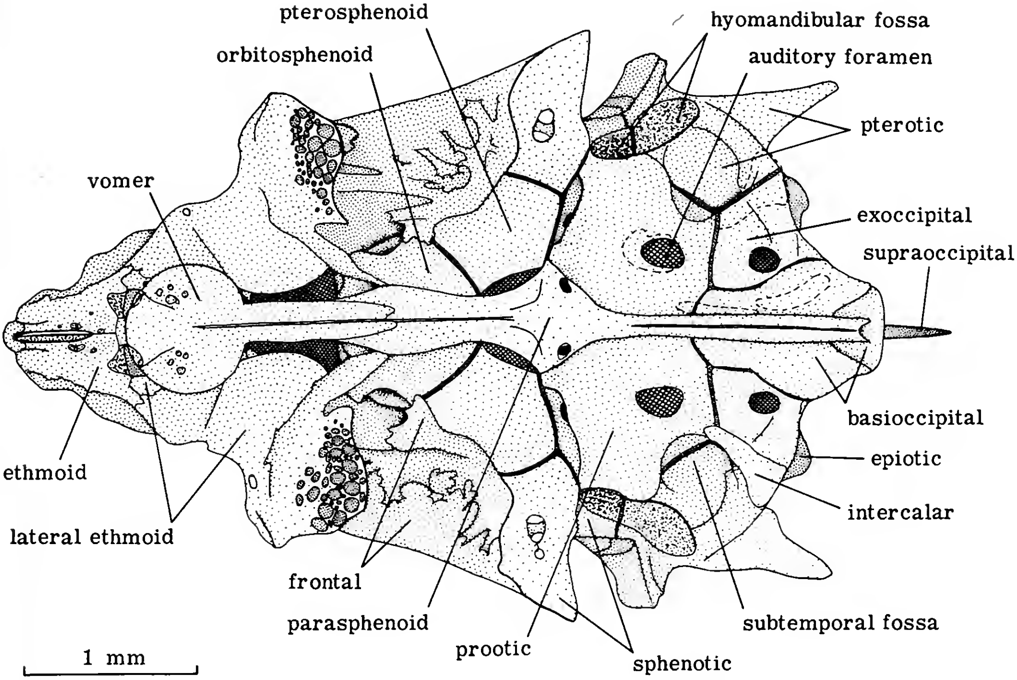

Figure 4. *Ichthyoelephas humeralis,* 102.4 mm, ventral view of cranium.

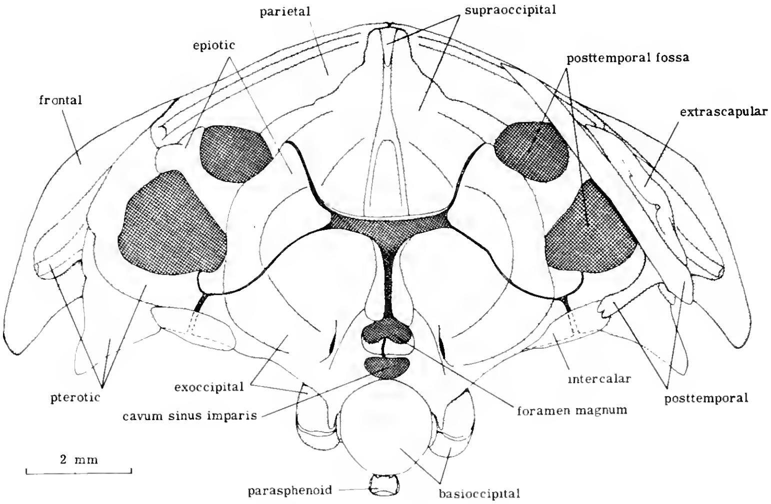

Figure 5. *Ichthyoelephas humeralis,* 102.4 mm, occipital view of cranium.

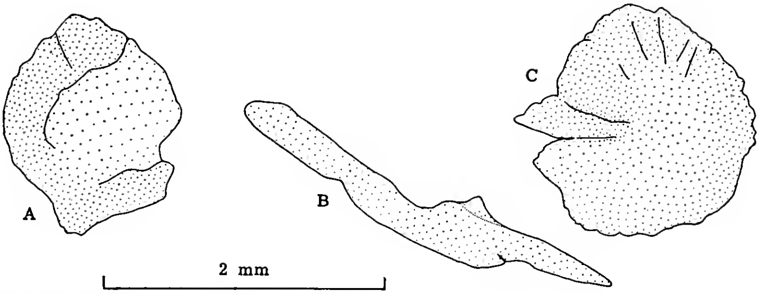

Figure 6. *Ichthyoelephas humeralis*, 102.4 mm, otoliths from left side. A. Ventral view of utriculus. B. Lateral view of sagitta. C. Lateral view of asteriscus.

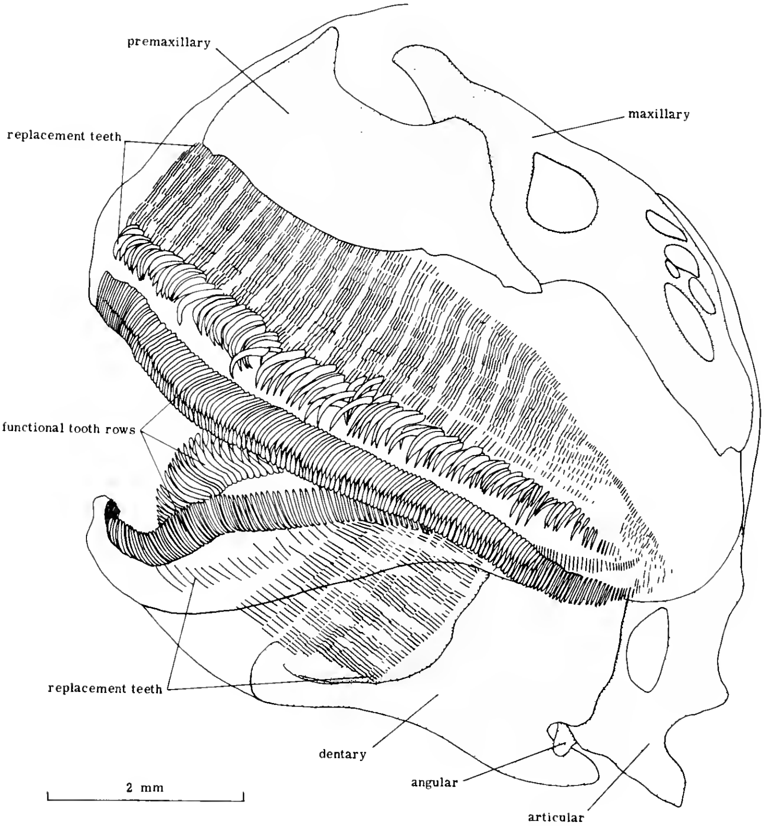

Figure 7. *Ichthyoelephas humeralis*, 97.2 mm, lateral view of jaws and dentition (internal row of teeth in upper jaw and part of lower jaw hidden from view).

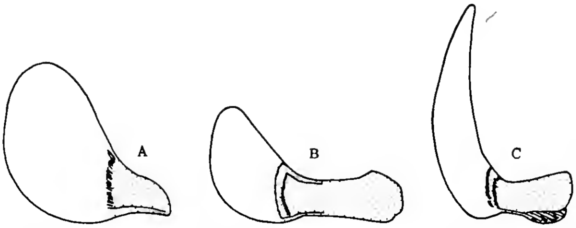

Figure 8. Form of jaw teeth in Prochilodontidae (after Mago Leccia, 1972). A. *Prochilodus.* B. *Semaprochilodus.* C. *Ichthyoelephas.*

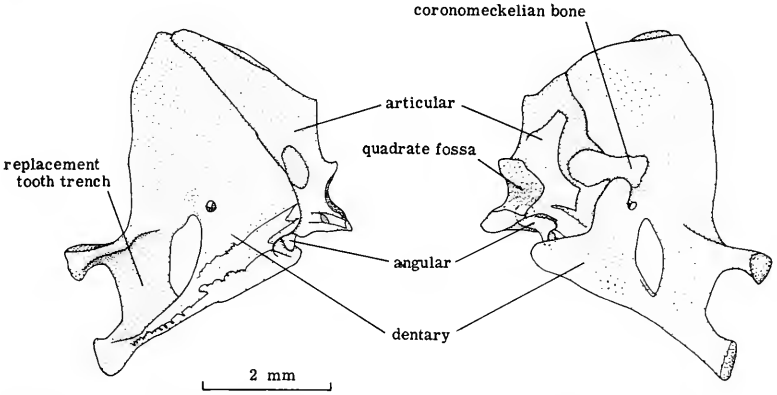

Figure 9. *Ichthyoelephas humeralis,* 97.2 mm, lateral and medial views of lower jaw.

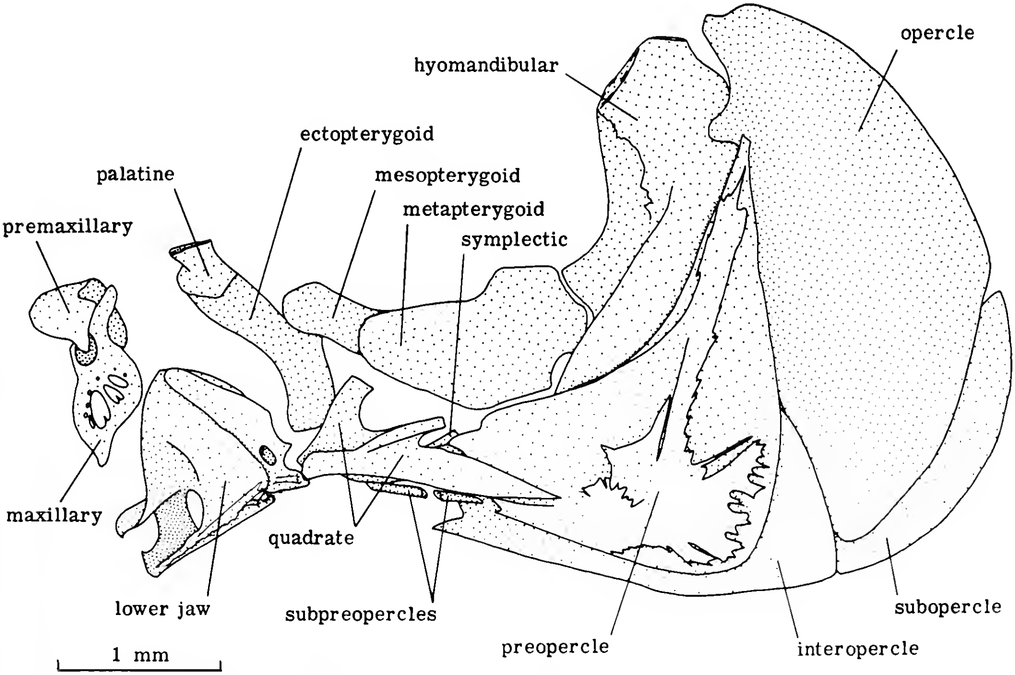

Figure 10. *Ichthyoelephas humeralis,* 97.2 mm, lateral view of jaws, suspensorium, and opercular bones.

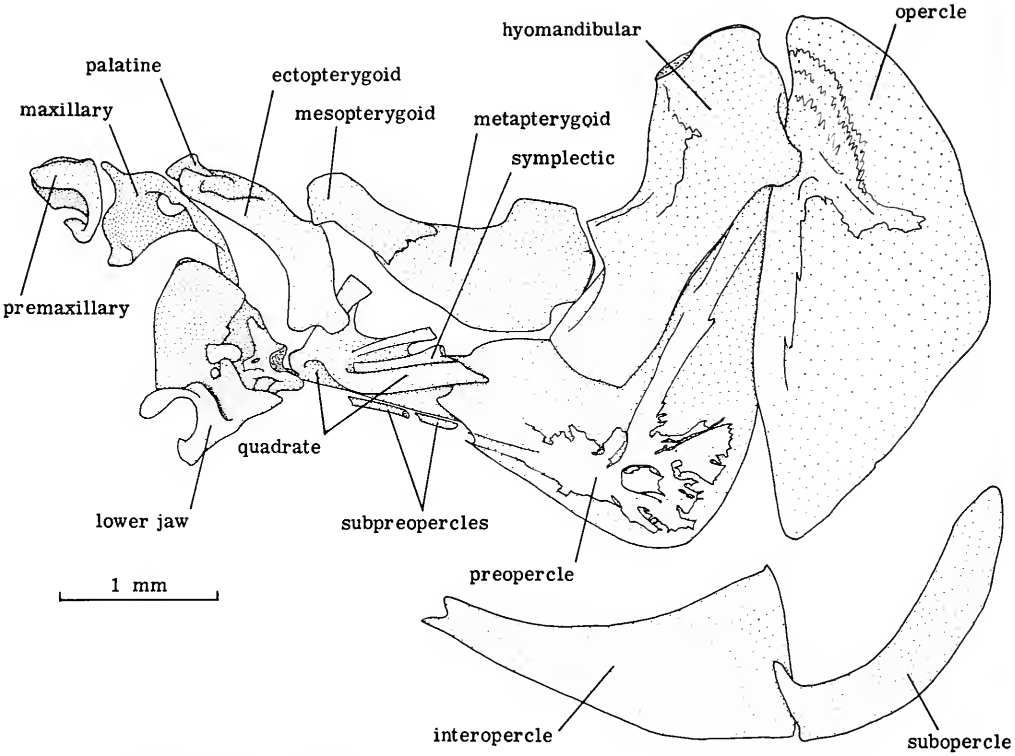

Figure 11. *Ichthyoelephas humeralis,* 97.2 mm, medial view of jaws, suspensorium, and opercular bones.

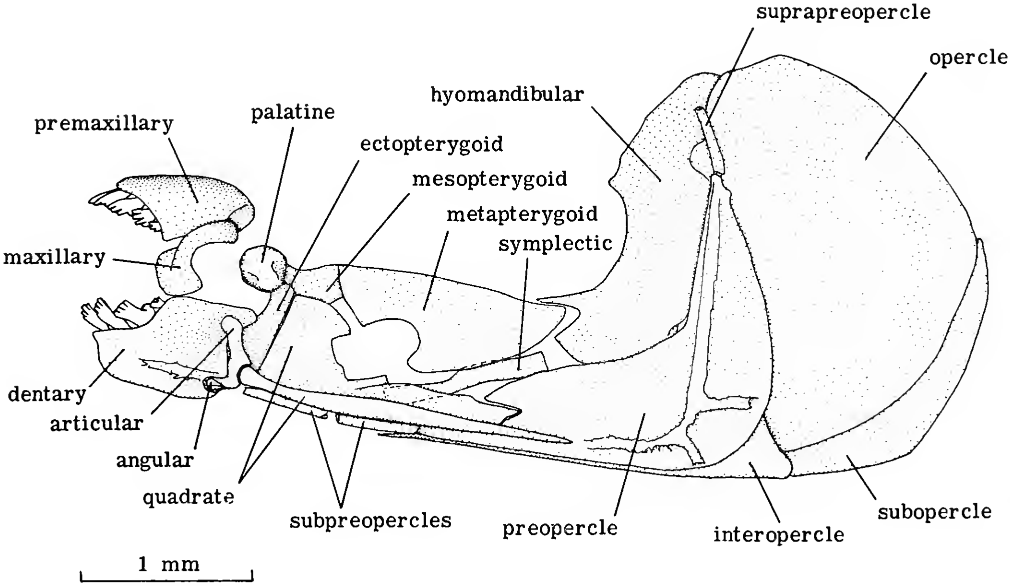

Figure 12. *Schizodon fasciatus* (Anostomidae), MCZ 46796, 95.3 mm, lateral view of jaws, suspensorium, and opercular bones.

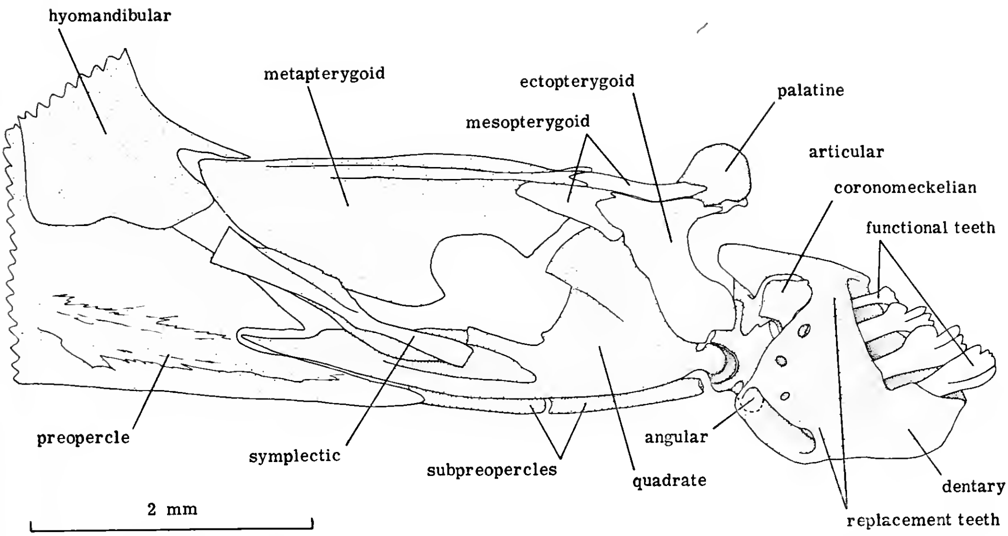

Figure 13. *Schizodon fasciatus* (Anostomidae), MCZ 46796, 95.3 mm, medial view of lower jaw and suspensorium.

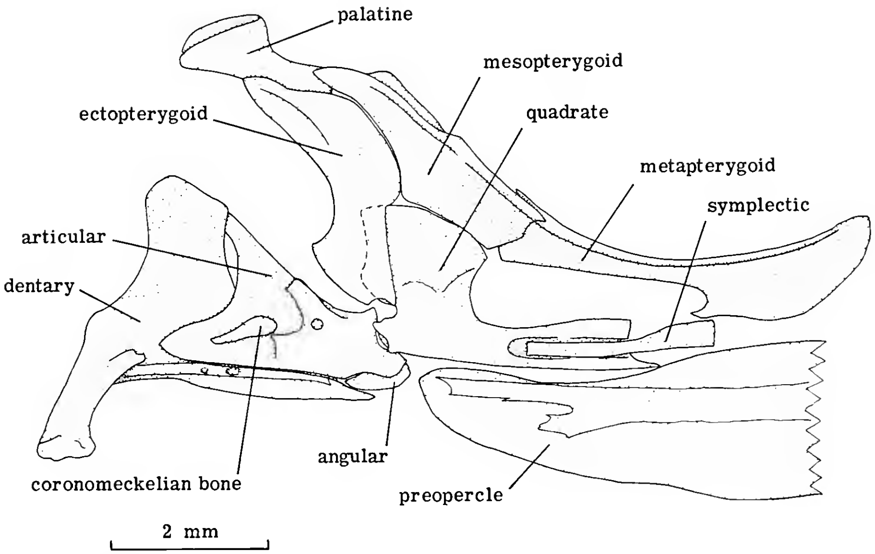

Figure 14. *Acuticurimata macrops* (Curimatidae), MCZ 46801, 69.0 mm, medial view of lower jaw and suspensorium (excluding hyomandibular).

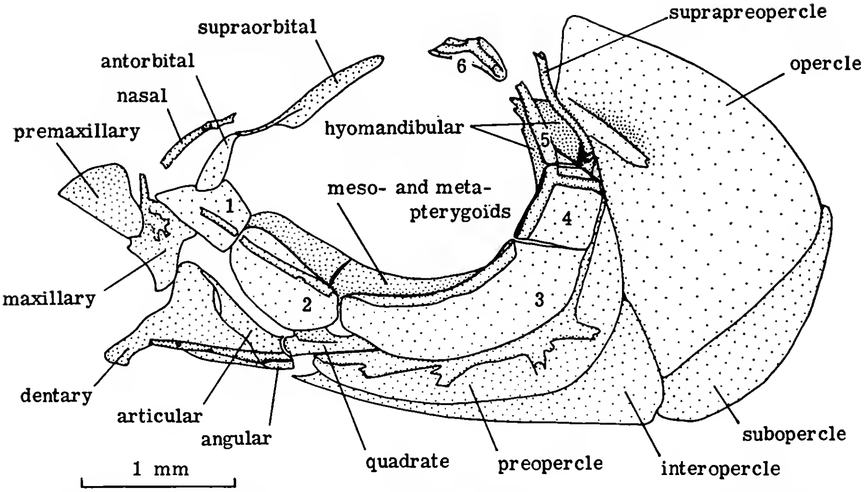

Figure 15. *Acuticurimata macrops* (Curimatidae), MCA 46801, 69.0 mm, lateral view of jaws, facial bones, opercular bones, and suspensorium.

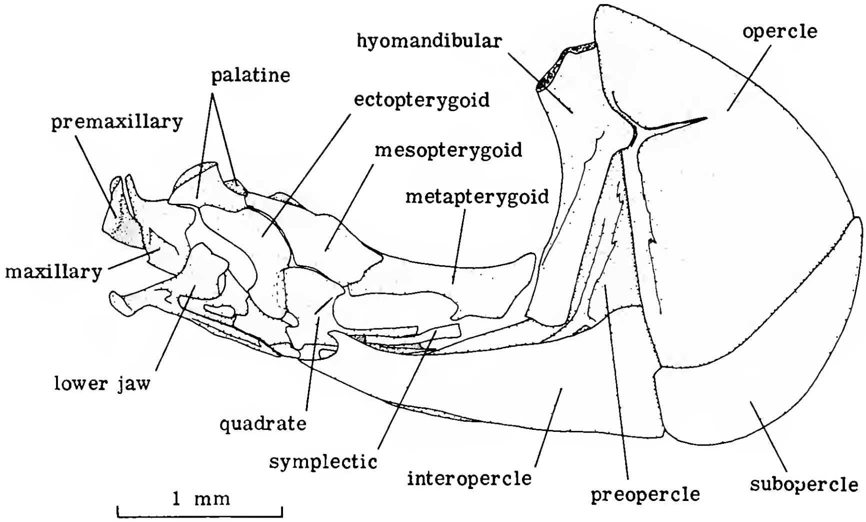

Figure 16. *Acuticurimata macrops* (Curimatidae), MCZ 46801, 69.0 mm, medial view of jaws, suspensorium, and opercular bones.

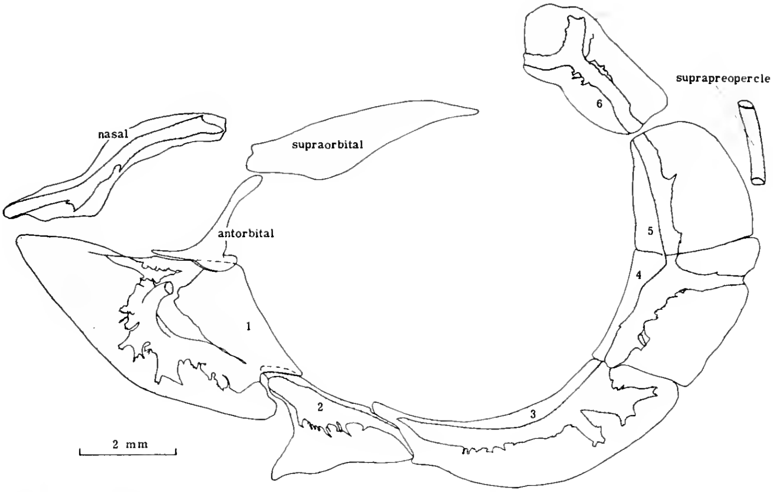

Figure 17. *Ichthyoelephas humeralis,* 97.2 mm, lateral view of nasal, antorbital, circumorbital, and suprapreopercular bones.

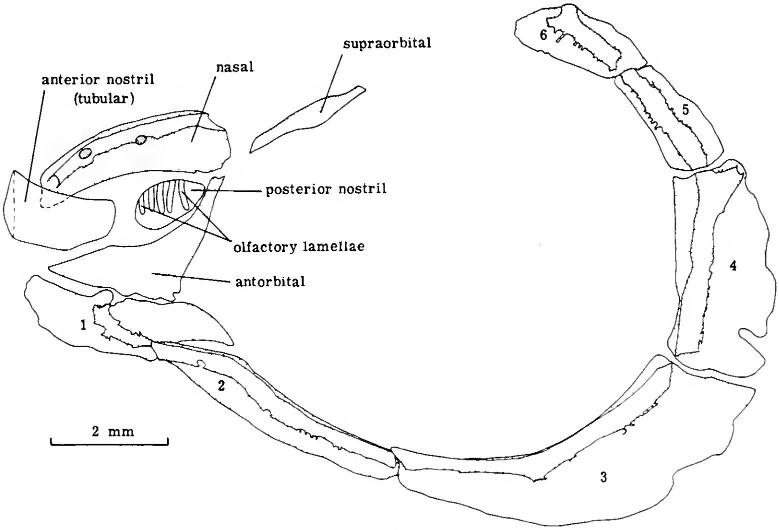

Figure 18. *Schizodon fasciatus* (Anostomidae), MCZ 46796, 95.3 mm, lateral view of nasal, antorbital, and circumorbital bones.

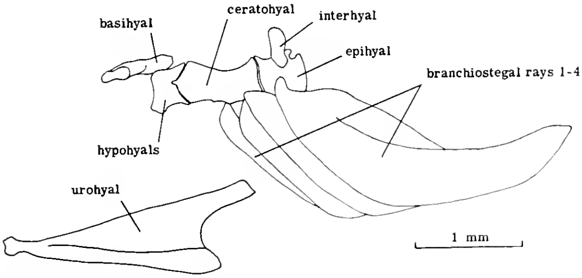

Figure 19. *Ichthyoelephas humeralis,* 102.4 mm, lateral view of urohyal, hyoid bar, and branchiostegal rays.

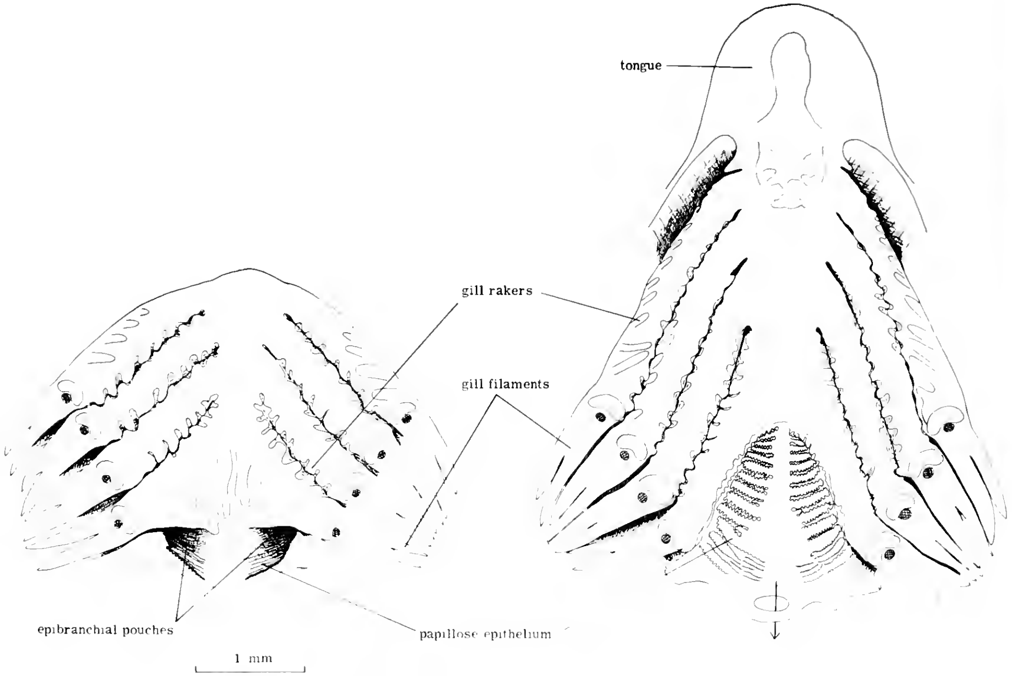

Figure 20. *Ichthyoelephas humeralis,* MCZ 48805, 137.5 mm, ventral view of upper half of gill structures and dorsal view of lower half of gill structures, showing specialized epithelium and epibranchial pouches.

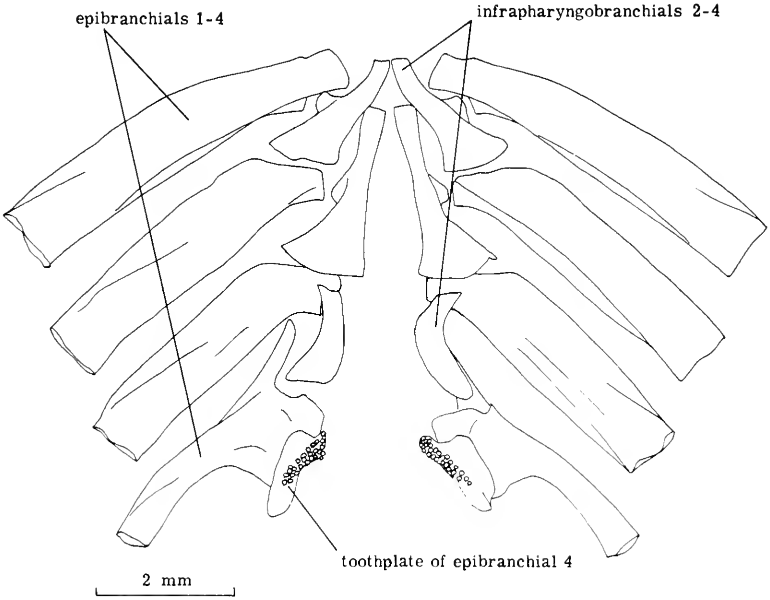

Figure 21. *Ichthyoelephas humeralis,* 102.4 mm, ventral view of dorsal half of gill arches.

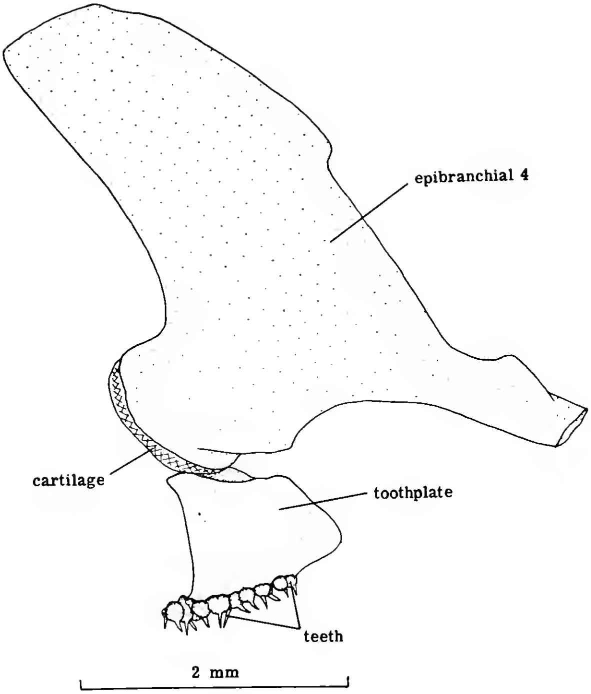

Figure 22. *Ichthyoelephas humeralis,* 102.4 mm, posterior view of epibranchial 4 and its tooth plate from right side of gill arches.

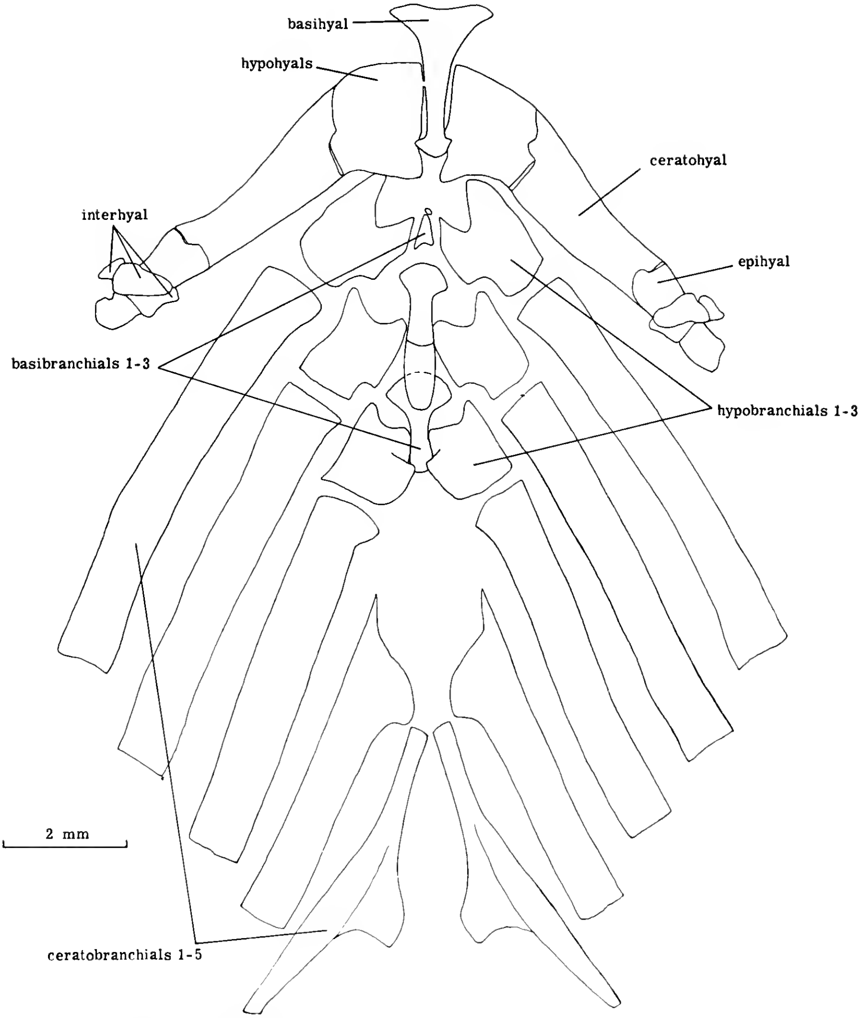

Figure 23. *Ichthyoelephas humeralis,* 102.4 mm, dorsal view of hyoid bar and ventral half of gill arches.

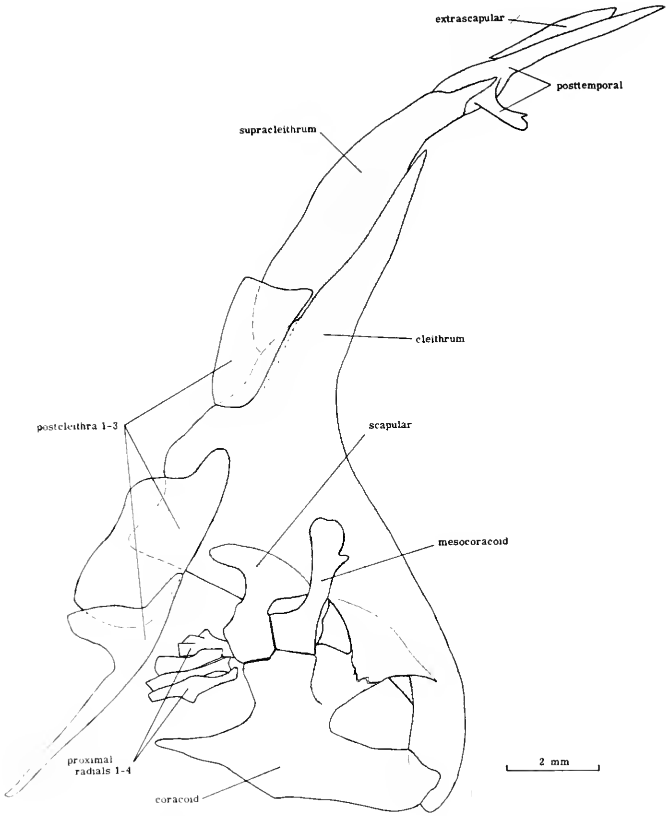

Figure 24. *Ichthyoelephas humeralis,* 102.4 mm, medial view of left half of pectoral girdle.

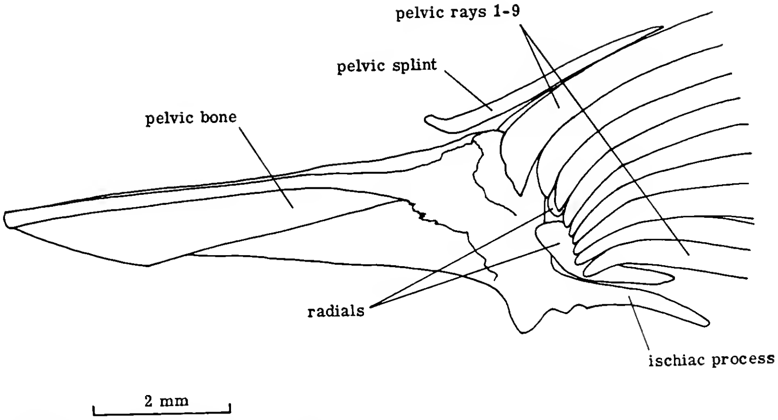

Figure 25. *Ichthyoelephas humeralis,* 102.4 mm, ventral view of right half of pelvic girdle.

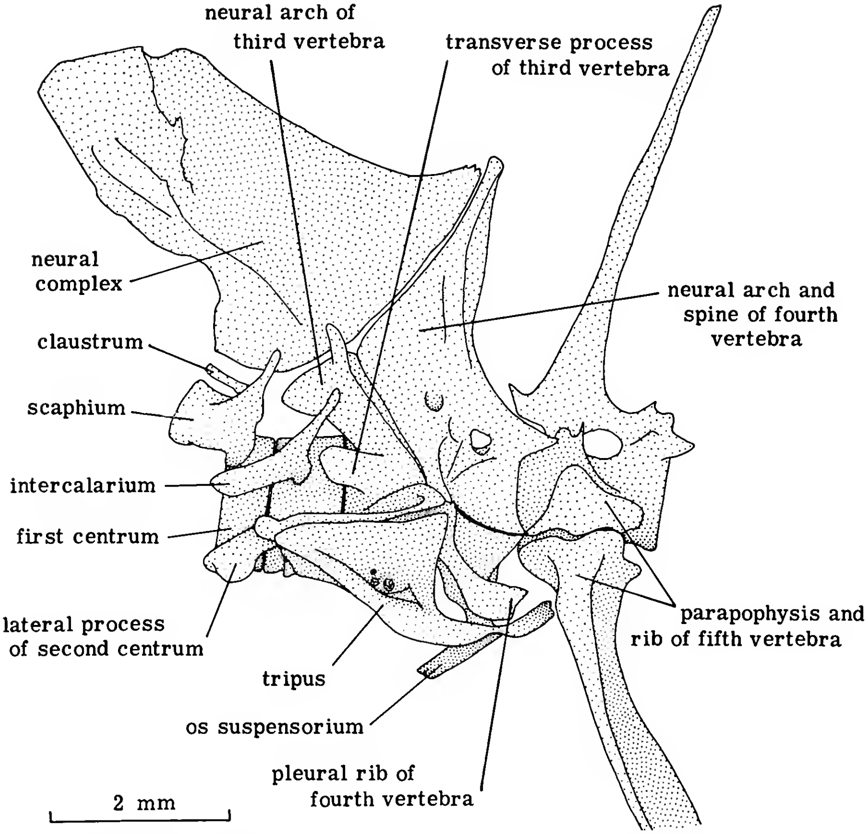

Figure 26. *Ichthyoelephas humeralis,* 102.4 mm, lateral view of Weberian apparatus.

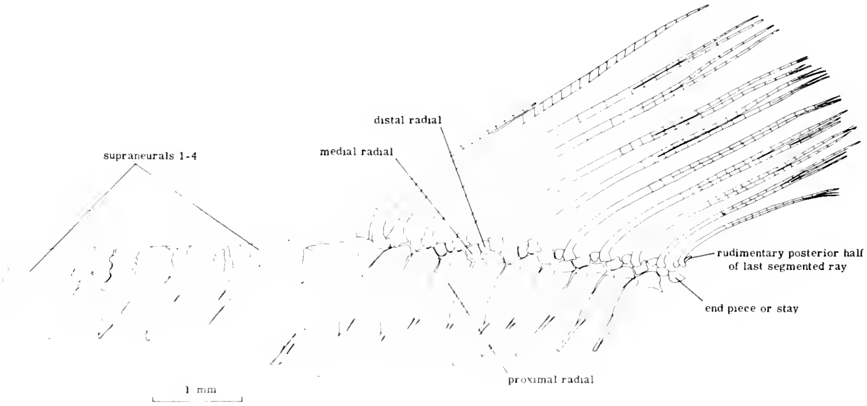

Figure 27. *Ichthyoelephas humeralis,* 102.4 mm, supraneurals and dorsal fin skeleton.

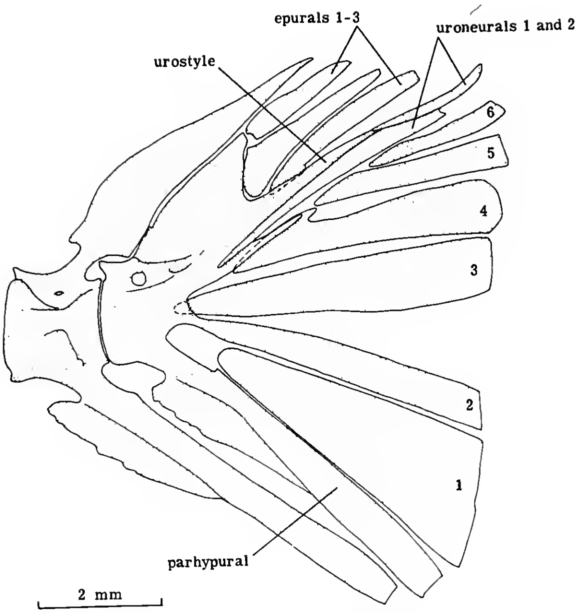

Figure 28. *Ichthyoelephas humeralis,* 102.4 mm, caudal skeleton.

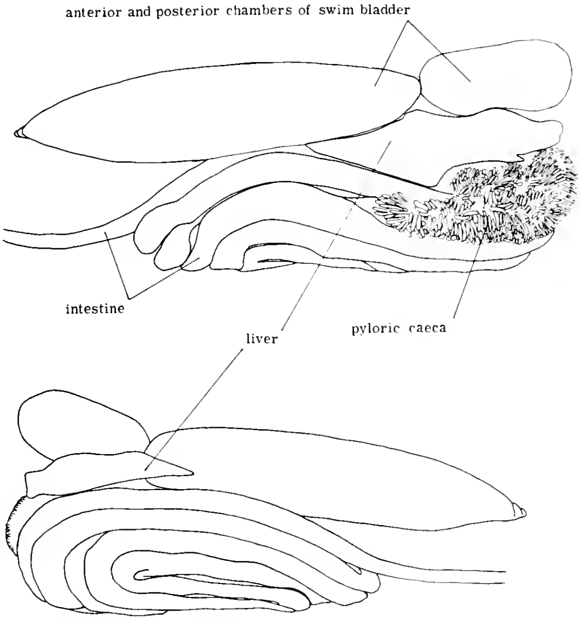

Figure 29. *Ichthyoelephas humeralis,* 102.4 mm, lateral views of viscera as seen from the right side (above) and from the left side (below).

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Studies on Deep-Sea Protobranchia (Bivalvia); Prologue and the Pristiglomidae

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STUDIES ON DEEP-SEA PROTOBRANCHIA (BIVALVIA);[1] PROLOGUE AND THE PRISTIGLOMIDAE

H. L. SANDERS[2] AND J. A. ALLEN[3]

Abstract. Great numbers of protobranch bivalves have been found through extensive and continuing sampling of the benthic fauna in the Atlantic at bathyal and abyssal depths. The many new species and varied morphologies that have been revealed indicate that the great radiation of the protobranchs took place in the deep sea. This group is being studied with regard to its comparative anatomy, both soft and hard part; functional morphology *per se* and in relation to abyssal life; changes in form with growth; mode of reproduction; and ecology. An outline classification of major protobranch taxa is given. A new family of the Nuculacea is described, the Pristiglomidae, which contains the genera *Pristigloma* (previously placed in the family Nuculanidae, here raised to superfamily) and *Microgloma*, n.g. Two species of *Pristigloma* are discussed: *P. nitens* and *P. alba*, n. sp. Although broadly distributed, they constitute less than 1% of the total fauna at any one station. They are characterized by extremely reduced gills, exceptionally large palps, and an elongate hindgut. Two new closely related species of *Microgloma*, *M. turnerae* and *M. yongei*, are described. They have a far more circumscribed distribution, both in depth and geography, than *Pristigloma*, *M. turnerae* being confined to the West Europe and Canaries basins and *M. yongei* to the Cape Verde and Angola basins. *Microgloma* are among the smallest bivalves known; miniaturization has been accomplished by reduction in cell size. In the gonads there is a drastic reduction in germ-cell numbers, only two ova maturing at any one time.

PROLOGUE

Since 1961 we have been investigating the deep-sea benthos of the Atlantic from the research vessels CHAIN and ATLANTIS II of the Woods Hole Oceanographic Institution and, to a lesser extent, from the British research vessels SARSIA and DISCOVERY. For the objectives of these studies and the methods used, see Sanders, Hessler and Hampson, 1965; Hessler and Sanders, 1967; Sanders and Hessler, 1969. One facet of our interests concerns the ecology, functional morphology, and evolution of the bivalves. The great array of species and large numbers of specimens allow us to consider for the first time a broad spectrum of morphologies within the Protobranchia from a comparative point of view. Soft-part anatomy and its function as well as shell characters form an integral part of these studies, while growth series are included whenever adequate numbers of specimens are available. All of the studies so far published on the relatively few deep-sea bivalves that were available prior to 1965 have usually considered shell characters and largely ignored the animal within. In fact, in the main, only dead shells have been collected.

The percentage of bivalves present at abyssal depths shows great variance from sample to sample with perhaps a mean of approximately 10 percent by number of the

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Woods Hole Oceanographic Institution Contribution No. 2705.

total benthic abyssal fauna (Hessler and Sanders, 1967). Usually more than 80 percent of these belong to three groups, the Protobranchia, Septibranchia, and Thyasiridae (Allen, 1971). The protobranchs are the dominant group and, in more samples than not, they account for at least 50 percent of the total number of specimens and some 45 percent of the species present. To date we have recorded at least 72 species of the Protobranchia and these encompass most of the known genera and others to be described.

Our task, after sorting the samples into individual species, was that of identification followed by the analysis of hard- and soft-part structures, their function and, in particular, the adaptations to the abyssal environment. Such an investigation is an ongoing process since new samples are continuously being collected. The material from these collections clearly demonstrates the need for a reappraisal of the taxonomic divisions within the Protobranchia. We will, within limits, use the framework of existing classification. Unfortunately, many generic names are known only from shells that have been inadequately described, and figures and existing definitions must be augmented and classified.*

In this and subsequent papers we hope to document the great radiation that has taken place in the deep sea within the subclass Protobranchia. Therefore, it is particularly important that comparative morphology should be adequately described. To begin this task, we will deal first with three extreme groups that require the creation of new family divisions and with the overt objective that they will immediately highlight the problems of identification and rational analysis of this poorly understood bivalve subclass.

To put these studies in a meaningful framework, it is first necessary to give our interpretations of phylogenetic relationships among the extant major taxa within the subclass Protobranchia. The bases for these interpretations are observations on both hard- and soft-part anatomy of the wide range of morphologies available from our deep-sea collections. No attempt here will be made to review the extensive literature on phylogenies (*i.e.*, Cox, 1959, 1960; Dall, 1895; McAlester, 1964; Purchon, 1958, 1959; Thiele, 1934–1935; Verrill and Bush, 1897; Yonge, 1939, 1959). The primary difficulties are that the different phylogenies proposed are often based on a single morphological system, that only a small subset of the diversity of soft-part anatomies are known, and that morphological features which have been thought to be conservative are not (McAlester, 1964).

Yonge (1939) has shown that within the subclass Protobranchia a greater affinity exists between the Nuculidae and Nuculanidae than between either of these and the Solemyidae. He proposed that two orders be erected, the Nuculoida to include the families Nuculidae and Nuculanidae, and the Solemyoida containing the family Solemyidae. In a recent paper (Allen and Sanders, 1969) we have pointed out that on the basis of shell and soft-part anatomy of *Nucinella serrei* Lamy the enigmatic family Nucinellidae is closest in affinity to the Solemyidae. We now propose that the Nucinellidae be included as a second family within the order Solemyoidea. A diagnosis of the major taxa of the subclass follows:

Subclass **PROTOBRANCHIA**

Bivalves with a foot sagittally and longitudinally grooved with papillate edges; ctenidial filaments flat, platelike, and unreflected.

Order *SOLEMYOIDA*

Protobranch bivalves with a minute triangular palp restricted to an area close to the mouth; ctenidia very large; globular

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* It is our intention to deposit holotypes in the Museum of Comparative Zoology, Harvard, Massachusetts (MCZ), and when sufficient material is available paratypes will be deposited in the U.S. National Museum and in the British Museum of Natural History.

opisthodetic external ligament often present.

Family SOLEMYIDAE

Shell elongate ovoid and weakly calcified, particularly at the ventral edge; hinge teeth absent; external ligament may or may not be present, dimyarian; extensive ventral mantle fusion; dorsal hood present in stomach; posterior gut diameter very narrow.

Family NUCINELLIDAE

Shell triangulate or nuculid in shape and well calcified; teeth present, composite of series of cardinals and elongate laterals; buttress present on shell around anterior adductor; large external ligament present; monomyarian or extreme heteromyarian, anterior adductor very large; mantle not fused ventrally; dorsal hood absent; posterior gut diameter not markedly narrow.

Order **NUCULOIDA**

Protobranch bivalves having large palps and palp proboscides, ctenidia not large; external ligament when present never globular.

Hitherto the relationships within the Nuculoida have not been well understood. In contrast to the Nuculidae, which are a sharply circumscribed and well-defined morphological group, the Nuculanidae contain an assemblage of varied morphologies. The problem is further compounded because many of the genera included within the Nuculanidae are known only from their shells. In view of the array of morphological diversity shown by bathyal and abyssal protobranchs, we feel that it is necessary to raise the families Nuculidae and Nuculanidae to superfamily status.

Superfamily NUCULANACEA new superfamily

Type genus: *Nuculana*, Link, 1807

Posterior inhalent current; posterior mantle fusion or development of posterior muscular and/or sensory folds with the formation of posterior siphons, apertures and/or papillae; mucus glands on mantle, if present, posterior; tentacle present; mouth not at posterior dorsal limit of anterior adductor muscle but at a varying distance from the muscle; ctenidia primarily oriented horizontally; filaments arranged alternately; palps elongate; foot elongate and with narrow neck, papillae moderate in size, heel not sharply separated from the sole; ligament either internal, external, or both; anterior mantle sense organ present; visceral and cerebral ganglia about equal in size.

The tindarid protobranchs represent an anomalous group and, as will be shown, differ in a number of ways from the majority of the Nuculanacea. However, since they agree with the Nuculanacea in many more respects than they do with the Nuculacea, they are tentatively retained within this superfamily.

Superfamily NUCULACEA

Type genus: *Nucula* Lamarck, 1799

Anterior inhalent current; no mantle fusion siphons absent; mucus glands on mantle, if present, anterior; tentacle absent; mouth close to posterior dorsal limit of anterior adductor muscle; ctenidia primarily oriented dorsoventrally or transversely, filaments arranged oppositely; large, broad, deep, almost square palp; foot relatively square and broad-necked, grossly papillate, heel sharply separated from sole; ligament always internal; hypobranchial glands present; anterior sense organ absent; visceral ganglion always smaller than cerebral.

Family PRISTIGLOMIDAE new family

From the review of the protobranchs making up our collections it is apparent that members of the genus *Pristigloma* should be removed from the superfamily Nuculanacea and placed together with a new genus, *Microgloma*, as a second family in a superfamily Nuculacea. They agree with the Nuculacea in all respects. Thus, there is an anterior rather than a posterior inhalent current; lack of mantle fusion; mucus glands of the mantle anterior, not posterior; siphons absent; tentacle absent; mouth at dorsal limit and adjacent to anterior adductor muscle; ctenidia oriented primarily transversely, not horizontally; ctenidial filaments opposite rather than alternate; palp large, broad, deep and almost square rather than elongate; foot relatively square and broad-necked rather than elongate with narrow neck; grossly rather than moderately papillate along margins of the sole of the foot; heel sharply separated from the sole; ligament internal; hypobranchial glands present; visceral ganglion smaller rather than equal in size to the cerebral ganglion.

The two families of Nuculacea can be separated according to the following criteria:

Nuculacid protobranch bivalves that are triangular in shape; ctenidia moderately large with many filaments; cerebral ganglion elongate; hindgut restricted to right side and tightly convoluted . . . . Family Nuculidae.

Nuculacid protobranch bivalves that are rounded in shape; ctenidia small with reduced number of filaments; cerebral ganglion rounded; hindgut either looped or coiled about both sides of stomach . . . . Family Pristiglomidae.

We can provide no data as to whether a nacreous layer is present in the pristiglomid shell.

Genus *Pristigloma* Dall, 1900

Glomus Jeffreys, 1876; *non* Gistel, 1848. Dall, 1900: 44. [Type species: *P. nitens* (Jeffreys), original designation.]

Shell fragile, smooth, with at most weak concentric lines; unequal number of teeth on either side of umbo, teeth lamellar or chevron-shaped, anterior teeth few or absent and, when present, confined well medial to level of anterior adductor muscle; umbos raised and posteriorly directed; large internal opisthodetic ligament which is narrow and elongate; hindgut loops rather than coils around stomach; several eggs present in ovary.

Specifically excluded from this genus by the present definition, on the basis of the number, structure, and positioning of the teeth and the shape of the shell, are *Pristigloma* (=*Glomus*) *simplex,* (Smith, 1885) and *Pristigloma* (=*Glomus*) *inaequilateria* (Smith, 1885). The soft parts of these forms are not known.

Pristigloma nitens (Jeffreys, 1876)

Figures 1–6

Glomus nitens Jeffreys, 1876: 433 (Type locality: PORCUPINE Expedition, Station 31; type specimen: U.S. National Museum); 1879: 573, plate XLV, fig. 5. Verrill, 1884: 231; 1885b: 576. Smith, 1885: 248. Dall, 1889: 46. Verrill and Bush, 1897: 53, figs. 1, 2; 1898: 848, plate XCVII, figs. 1, 2.

Pristigloma nitens (Jeffreys). Dall, 1900: 44.

Previous records. Depth range *in* Clarke (1963) = 2933–3477 m. Basins: Labrador, 1 station; North America, 1 station; Argentine, 1 station [Verrill, 1884; Smith, 1885 (as *Glomus*)].

Present records. Depth range = 2022–4853 m: Table I.

Little needs to be amended to the descriptions of shell morphology of this species as given by Jeffreys (1876) and Verrill and Bush (1898). We can add that the narrow, elongate opisthodetic internal ligament extends well posteriorly and is ventrally opposed to and more than half the length of the posterior hinge plate. The anterior plate is very short and thick (Figs. 1, 2).

The soft parts have not been described to date. The mantle edge is not fused, neither is it apposed posteriorly to form exhalent and inhalent apertures. There are three mantle lobes, the inner sensory lobe being moderately produced but nonpapillate. No anterior sense organ and no single posterior mantle tentacle is present. Mantle glands are present lateral and medial to the anterior half of the palps and these extend forward to the mantle edge. Hypobranchial glands are present but these are more circumscribed than in *Nucula* (Atkins, 1936; Yonge, 1939), being restricted to the base of the gill axis and epithelium overlying the ventral surface of posterior adductor muscle. No other specialized gland cells

TABLE I. RECORDS FOR *Pristigloma nitens* (Jeffreys).

Cruise	No.	Sta.	Depth (m)	Specimens	Latitude	Longitude	Gear	Date
NORTH AMERICA BASIN								
Chain	58	103	2022	1	39°43.6′N	70°37.4′W	*ES	5.4.66
Atlantis II	30	131	2178	5	39°38.5′N– 39°39.0′N	70°36.5′W– 70°27.1′W	ES	18.12.66
Chain	50	76	2862	1	39°38.3′N	67°57.8′W	ES	29.6.65
Atlantis II	12	72	2864	6	38°16′N	71°47′W	ES	24.8.64
Atlantis II	24	126	3806	4	39°37.0′N– 39°37.5′N	66°47.0′W– 66°44.0′W	ES	24.8.66
Chain	50	78	3828	4	38°0.8′N	69°18.7′W	ES	30.6.65
Chain	50	85	3834	4	37°59.2′N	69°26.2′W	ES	5.7.65
Atlantis II	12	70	4680	4	36°23′N	67°58′W	ES	23.8.64
Atlantis II	40	175	4667– 4693	2	36°36′N	68°29′W– 68°31′W	ES	29.11.67
Chain	50	84	4749	4	36°24.4′N	67°56′W	ES	4.7.65
Atlantis II	24	121	4800	3	35°50.0′N– 35°52.0′N	65°11.0′W– 64°58.0′W	ES	21.8.66
Atlantis II	24	122	4833	3	35°52.0′N	64°58.0′W	ES	21.8.66
Atlantis II	24	123	4853	2	37°29.0′N	64°14.0′W	ES	22.8.66
WEST EUROPE BASIN								
Sarsia		S-50	2379	5	43°46.7′N	3°38′W	ES	18.7.67
CANARIES BASIN								
Discovery		6710	2670	2	27°23.6′N	15°39.6′W	ES	19.3.68
Discovery		6711	2988	1	27°14.9′N	15°36.3′W	ES	19.3.68
BRAZIL BASIN								
Atlantis II	31	156	3459	2	00°46.0′S– 00°46.5′S	29°38.0′W– 29°24.0′W	ES	14.2.67
ANGOLA BASIN								
Atlantis II	42	194	2864	3	22°54′S	11°55′E	ES	17.5.68
Atlantis II	42	195	3797	9	14°49′S– 14°40′S	9°56′E– 9°54′E	ES	19.5.68
Atlantis II	42	197	4565– 4595	3	10°29′S	9°04′E	ES	21.5.68
Atlantis II	42	196	4612– 4360	2	10°29′S	9°04′E	ES	21.5.68
Atlantis II	42	198	4559– 4566	5	10°24′S	9°09′E	ES	21.5.68
ARGENTINE BASIN								
Atlantis II	60	256	3906– 3917	3	37°40.9′S	52°19.3′W	ES	24.3.71

are present except for the typical subepithelial mucus glands concerned with transport of particulate matter within the mantle cavity. The moderately large adductor muscles are relatively ventral in position, more or less oval in shape and clearly divided into "quick and catch" portions. The mouth lies opposite to the inner dorsal edge of the anterior adductor (Fig. 3).

The ctenidia are suspended transversely across the posterior mantle cavity close to the anteroventral border of the posterior adductor muscle. They do not extend anteriorly over the viscero-pedal mass. Relatively few gill plates are present; the number varies with the size of the animal but is usually between 8 and 13. The gill plates lie opposite and do not alternate on each side of the axis of the ctenidium. The inner plates of each axis do not appear to meet

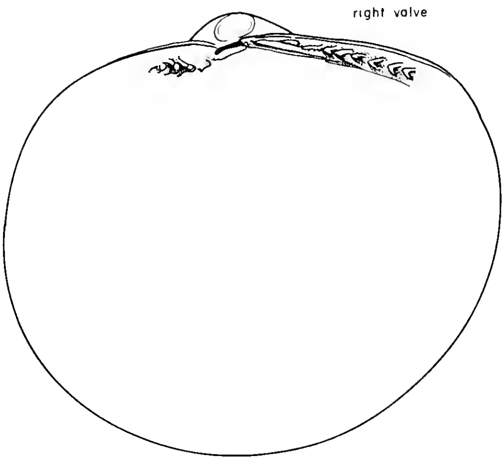

Figure 1. ***Pristigloma nitens*** **(Jeffreys). Internal view of the right valve of a specimen from the original type collection (Specimen 197414, U.S. National Museum, Jeffreys Collection, PORCUPINE Expedition, Station 31, 1381 fathoms).**

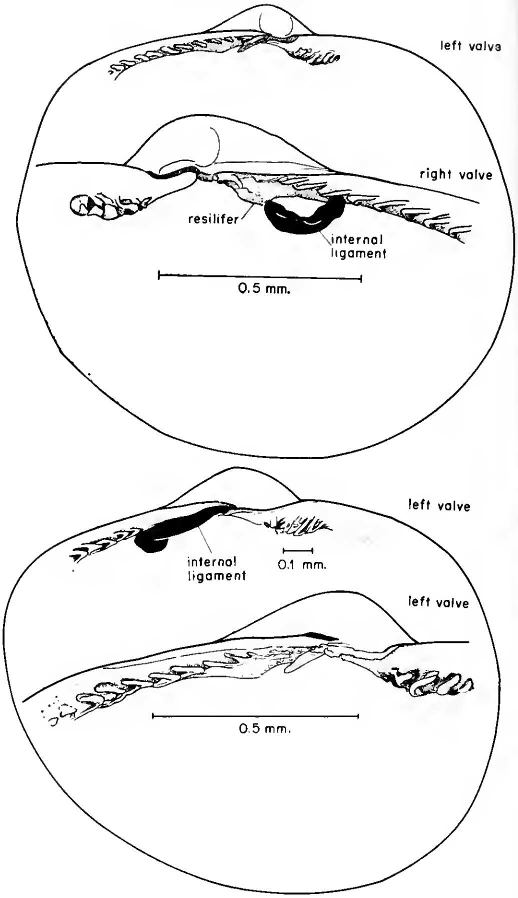

Figure 2. ***Pristigloma nitens*** **(Jeffreys). Internal view of left and right valves of specimens from the Gay Head-Bermuda transect, with enlargements to show detail of hinge structure.**

permanently in the midline but hang downwards as very short fingerlike processes. The ctenidial axis is not muscular. It extends posteriorly beyond the first pair of gill plates as a free, tapering projection. Thus the hypobranchial cavity is not entirely separated off from the remainder of the mantle cavity. The paired palps are large and broad and extend from either side of the mouth to the posterior edge of foot; the palp proboscis originates at the posterior dorsal junction of each palp. The contraction of palps and palp proboscides in preserved specimens makes their use in taxonomy questionable. The inner faces of the palps have a large number of folds (22–25) with a morphology essentially similar to that described by Stasek (1961) for *Acila.* The foot is broad with a divided sole; it is moderately large with numerous papillae along the margins. The sole of the foot is ciliated, densely so along central groove and just lateral to it, while the remainder of the sole is sparsely ciliated. A so-called "byssal" gland is present. It is moderately large, ovoid in structure with a central cavity enclosed by glandular secreting cells, and partitioned in a longitudinal, sagittal plane. Each half opens, side by side, ventral to the heel of foot just posterior to the limit of the divided sole.

The mouth lies close to, but not abutting, the anterior adductor muscle. The oesophagus passes *anteriorly* and dorsal to adductor before turning posteriorly to join a relatively huge stomach lying centrally within the body. The style sac is ventral to the stomach and the hindgut initially extends dorsally and then loops behind the stomach on both sides of the body (Figs. 3, 4a). Four loops are present on each side, *i.e.*, eight sections to each side in a specimen

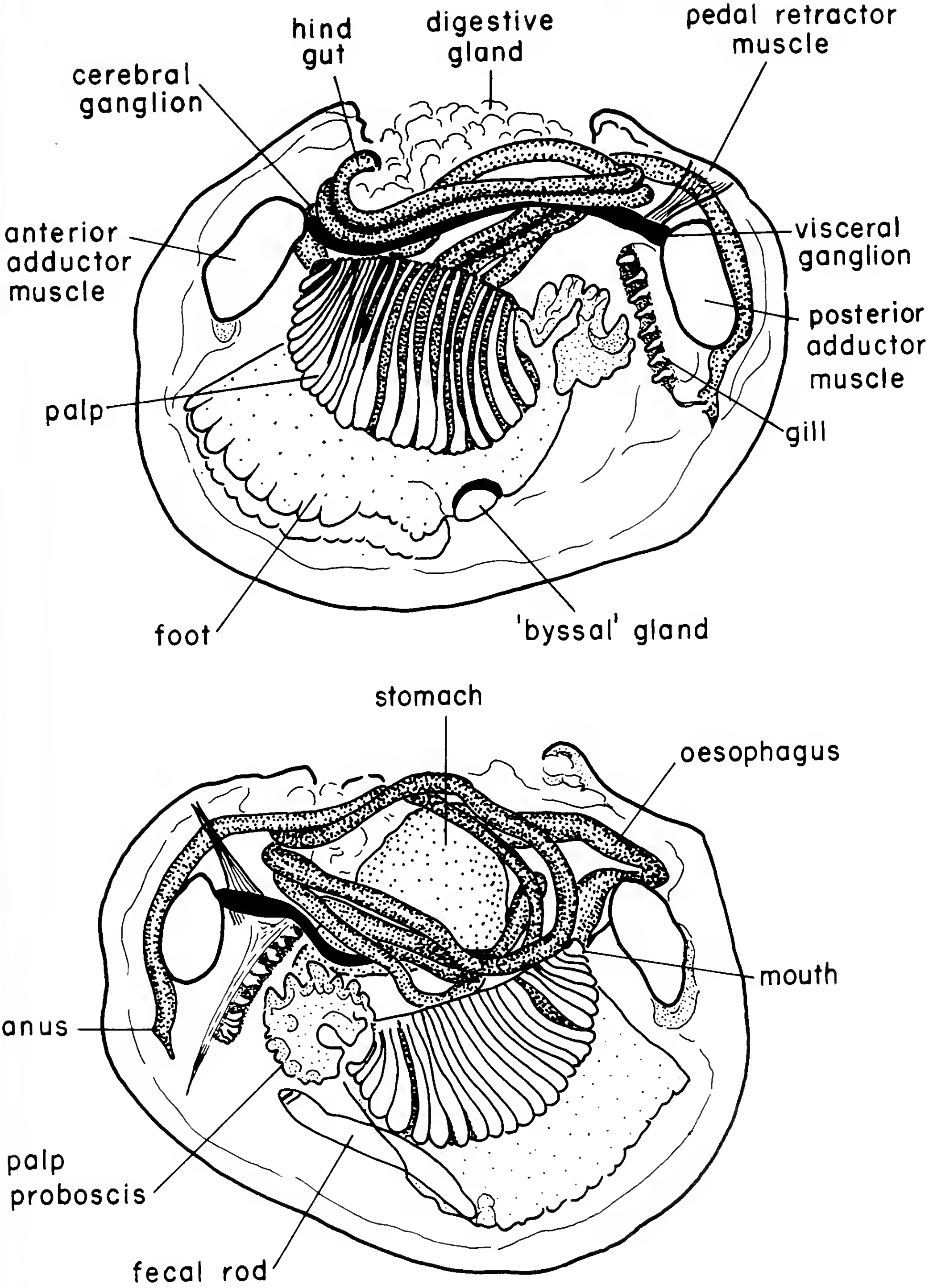

Figure 3. *Pristigloma nitens* (Jeffreys). Left and right lateral, semidiagrammatic views of the body and mantle organs.

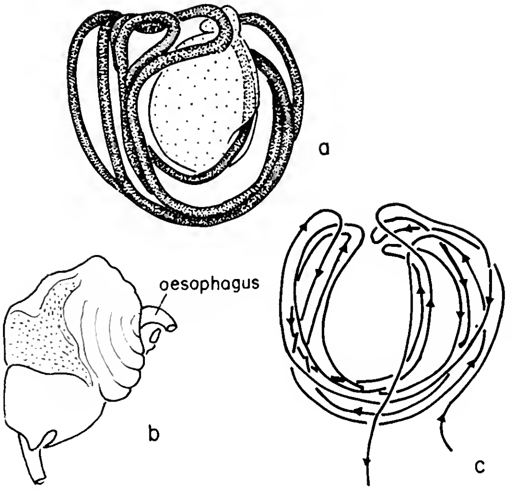

Figure 4. a) Ventral, semidiagrammatic view of the stomach and hindgut of *Pristigloma nitens;* b) lateral view of the stomach of *P. nitens;* c) diagram to show the course of the hindgut of *P. alba,* as seen from the dorsal side of the animal.

transversely sectioned. The terminal loop is on the right side and its distal limb extends posteriorly along the mid-dorsal line over the posterior adductor to the anus, situated above the space between the posterior extensions of the ctenidial axis. The stomach has six sorting ridges and two ducts to digestive diverticula. The visceral ganglia are large and well defined, and, like the cerebral ganglia, rounded. The pedal ganglia are exceptionally large.

Pristigloma nitens shows little proportional change with increasing size (Fig. 5), maintaining a height-to-length ratio of about 0.87 within the length interval of 1.10 mm to 2.72 mm. The maximum length recorded from our samples is 3.54 mm. The prodissoconch in *P. nitens* measures 260 μ in length and the egg size is 190 μ, indicating a direct mode of reproduction (Fig. 6). Nearly 200 eggs at similar stages of development are present in a single specimen, 2 mm, total length. The species is hermaphroditic with concurrently mature eggs and sperm that in the mature animal occupy the greater part of the body space.

Pristigloma alba new species

Figures 4, 7–9

Type locality: ATLANTIS II, Cruise 24, Station 122, in 483 m. Holotype: MCZ 271976. Depth range = 2178–4833 m. We construe *Pristigloma* to be feminine. **Records:** Table II.

Shell small, fragile, tumid, white, smooth with faintly discernible lines, obliquely rounded in outline but extended anteroventrally; dorsal margin straight; posterior margin short and regularly convex; anterior edge long, with the dorso-anterior margin extended and weakly convex and the ventro-anterior margin short and strongly convex; ventral edge gradually sloping ventroanteriorly; umbos proportionately large and swollen with beaks directed slightly posteriorly; no lunule, escutcheon, or external ligament present; opposing edges of valves raised both posterior and anterior to the umbo and forming a crest. Hinge plate weak, narrow, straight, and separated by a small notch in the equally lengthened anterior and posterior parts. Teeth few, lamelliform in shape, horizontally directed, parallel and overlapping; posterior row of three teeth with the proximal member half the length of the others; anterior hinge plate devoid of teeth but with a faint furrow in the right valve and two in the left. Large internal, elongate opisthodetic ligament extends obliquely posterior as a narrow, elongate, concave resilifer immediately below the hinge to the level of the distal edge of the proximal tooth. Neither muscle scars nor pallial line evident (Fig. 7a, 7b).

Mantle similar to *P. nitens* with no fusion or adhesion to form exhalent and inhalent apertures. Adductor muscles equal, the anterior extending below the level of the mouth. Hypobranchial gland cells present in the region of the gill axis and dorsally overlying the floor of kidney anterior to the posterior adductor muscle. The position of the palps and ctenidia is similar to *P. nitens* but their relative proportions differ greatly. Ctenidia considerably reduced, being restricted to two pairs of oppositely placed

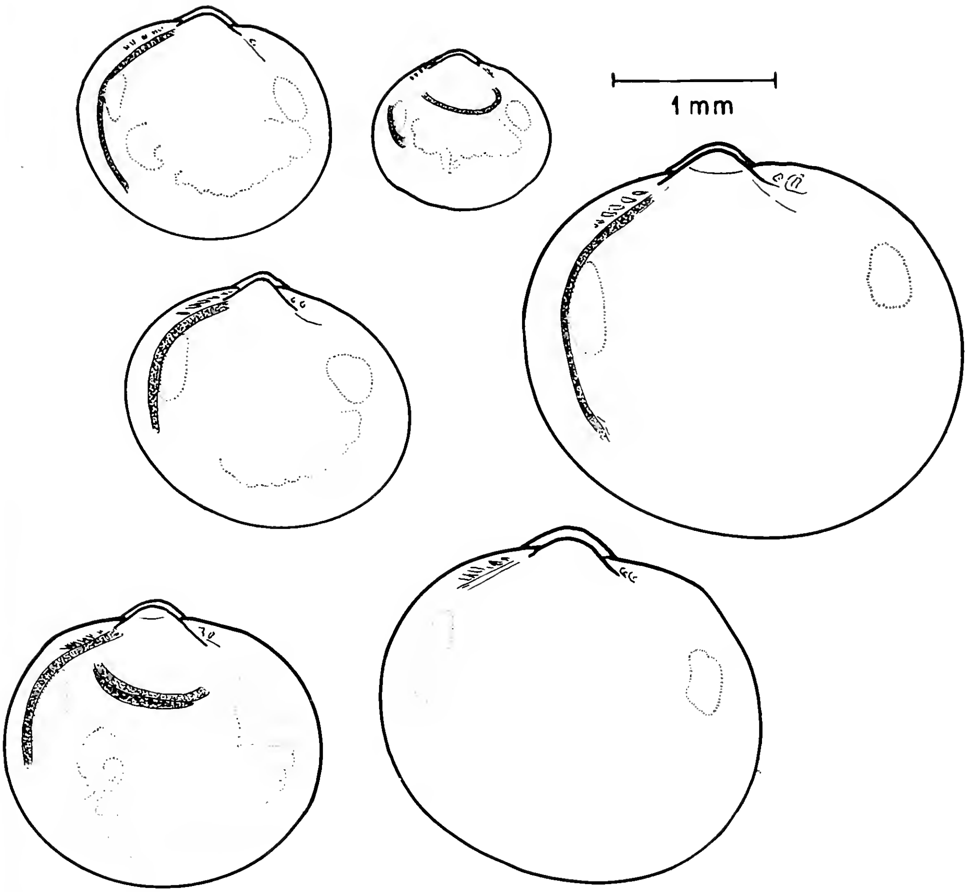

Figure 5. Lateral views of a series of specimens of *Pristigloma nitens* to show changes in shape with increasing size. Features of the soft-part anatomy, seen through the shell, are indicated.

plates. Palps very large (with approximately 17 ridges) and take up much of the lateral area of the mantle, and cover most of the lateral surface of the body/foot; palp proboscides, in a contracted state, short and thickened. Foot large, differing from *P. nitens* in that the sole is very broad and the fringing papillae are relatively large and few in number (Fig. 8), consisting of 5–6 broad laterals, 4–5 smaller posterolaterals on each side and 5 smaller frontal papillae; heel very large, hooked ventrally, and widely separate from foot; "byssal" gland large, from which an elongate groove extends and terminates at the center of the sole of foot.

The configuration of the gut is similar to that of *P. nitens*, except that there are five pairs of hindgut loops closely applied to each other* (Fig. 4c). Oesophagus lacks an anterior loop above adductor muscle and the anus does not extend as far into hypobranchial space as it does in *P. nitens* (Fig. 8). Stomach relatively large yet simple with but two sorting ridges. Ganglia

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* It is difficult to determine both from sections and from whole mounts whether some parts of the hind gut encircle the stomach rather than form loops as in *P. nitens*. Nevertheless, as far as can be seen there are no encircling sections, but the loops to the right and left of the body overlap in front of the stomach.

TABLE II. RECORDS FOR *Pristigloma alba* NEW SPECIES.

Cruise	No.	Sta.	Depth (m)	Specimens	Latitude	Longitude	Gear	Date
				NORTH AMERICA BASIN				
Atlantis II	30	131	2178	2	39°38.5′N– 39°39.0′N	70°36.5′W– 70°37.1′W	ES	18.12.66
Atlantis II	12	72	2864	2	38°16′N	71°47′W	ES	24.8.64
Atlantis II	12	64	2891	1	38°46′N	70°06′W	ES	21.8.64
Atlantis II	24	126	3806	2	39°37.0′N– 39°37.5′N	66°47.0′W– 66°44.0′W	ES	24.8.66
Chain	50	85	3824	4	37°59′N	69°26.2′W	ES	5.7.64
Atlantis II	40	175	4667– 4693	6	36°36′N	68°29′W– 68°31′W	ES	29.11.67
Chain	58	100	4743– 4892	2	33°56.8′N	65°47′W	ES	1.5.66
Atlantis II	24	121	4800	3	35°50.0′N– 37°24.0′N	65°11.0′W– 65°54.0′W	ES	21.8.66
Atlantis II	24	125	4825	1	37°26.0′N– 35°50.0′N	65°50.0′W– 64°57.5′W	ES	23.8.66
Atlantis II	24	122	4833	10	35°52.0′N	64°58.0′W	ES	21.8.66
				CANARIES BASIN				
Discovery		6709	2351	2	27°29.8′N	15°20.1′W	ES	18.3.68
Discovery		6711	2988	1	27°14.9′N	15°36.3′W	ES	19.3.68
				BRAZIL BASIN				
Atlantis II	31	156	3459	2	00°46.0′S– 00°46.5′S	29°28.0′W– 29°24.0′W	ES	14.2.67
				ANGOLA BASIN				
Atlantis II	42	195	3739	8	14°49′S– 14°40′S	9°56′E– 9°54′E	ES	19.5.68
Atlantis II	42	197	4592– 4597	1	10°29′S	9°04′E	ES	21.5.68
Atlantis II	42	198	4559– 4566	7	10°24′S	9°09′E	ES	21.5.68
				ARGENTINE BASIN				
Atlantis II	60	242	4382– 4405	2	38°16.9′S	51°56.1′W	ES	13.3.71

(including visceral) are well defined and rounded.

The species is hermaphroditic with concurrently mature eggs and sperm; about 20 mature eggs, 115 μ in diameter,[**] were present in a specimen 1.2 mm total length with a prodissoconch 190–200 μ in length. Egg and prodissoconch lengths suggest that *P. alba* has a lecithotrophic mode of reproduction (Ockelmann, 1965).

There is no obvious change in size dimensions with growth within the range of lengths available, 0.45 to 1.90 mm, although the larger specimens may be proportionately less elongate (Fig. 9). The approximate length:height:breadth ratio is 1.00: 0.79:0.63.

This minute clam can be separated from all other known species of nuculoid protobranch bivalves by its inflated shape, large umbos, very fragile shell, absence of teeth on the anterior hinge plate, lamellar form and horizontal positioning of the posterior teeth, and by the broad foot with few large papillae, and the closely packed hindgut loops.

[**] The eggs are considered mature in that they occupy the total available space, there being a very large quantity of yolk present together with a mature nucleus and large, heavily staining nucleolus.

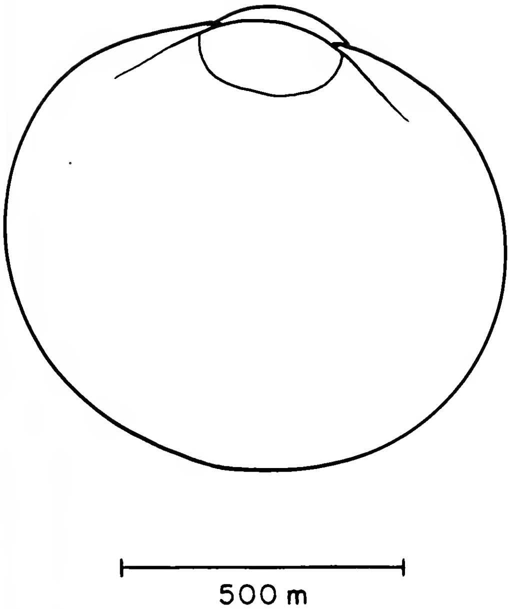

Figure 6. Lateral view of a young specimen of *Pristigloma nitens* with a well-defined prodissoconch.

Genus *Microgloma* new genus

Type species: *Microgloma yongei* (new species). We construe *Microgloma* to be feminine.

Minute; strong, robust shell with concentric ridging; equal number of teeth on either side of the umbo; teeth taxodont and extend along the hinge to the level of the posterior edge of the adductor muscles; umbos low in profile and medially directed; internal ligament amphidetic and bean-shaped; hindgut coils rather than loops about stomach; at most two mature eggs present in ovary.

This genus differs from *Pristigloma,* in that the hinge is symmetrical on either side of the umbo, having a robust shell, chevron-shaped teeth only and an internal amphidetic ligament. The soft anatomy differs in having the hindgut coiling rather than looping about the stomach.

Only two species are known of this genus and these are restricted to the eastern Atlantic.

Microgloma yongei new species

Figures 10–14, 21

Type locality: ATLANTIS II, Cruise 42, Station 200, in 2644–2754 m. Holotype: MCZ 271971. Depth range = 1964–2031 to 2754 m. **Records:** Table III.

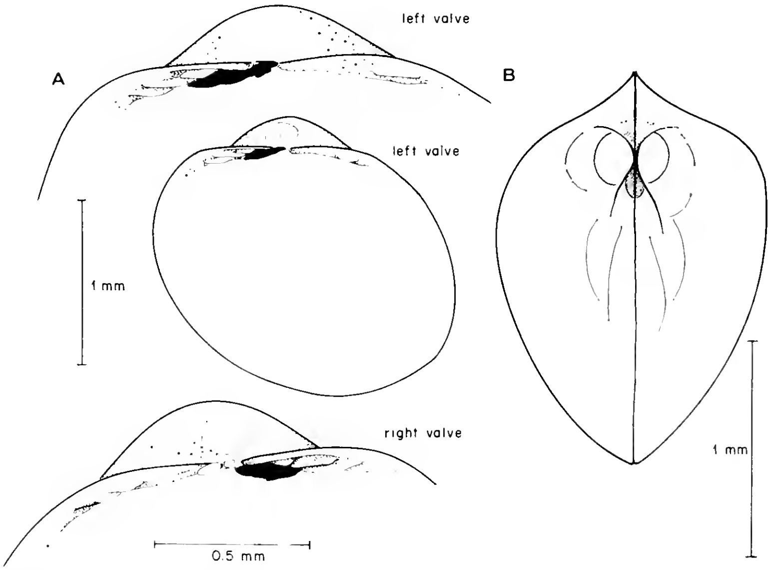

Figure 7. *Pristigloma alba* (Sanders and Allen). a) Lateral internal view of left valve and enlarged hinge detail of right and left valves; b) dorsal view of shell.

Table III. Records for *Microgloma yongei* new species.

Cruise	No.	Sta.	Depth (m)	Specimens	Latitude	Longitude	Gear	Date
CAPE VERDE BASIN								
Atlantis II	31	145	2185	19	10°36.0′N	17°49.0′W	ES	6.2.67
ANGOLA BASIN								
Atlantis II	42	200	2644–2754	90	9°41′S–9°43.5′S	10°55′E–10°57′E	ES	22.5.68
Atlantis II	42	201	1964–2031	18	9°29′S–9°25′	11°34′E–11°35′	ES	23.5.68

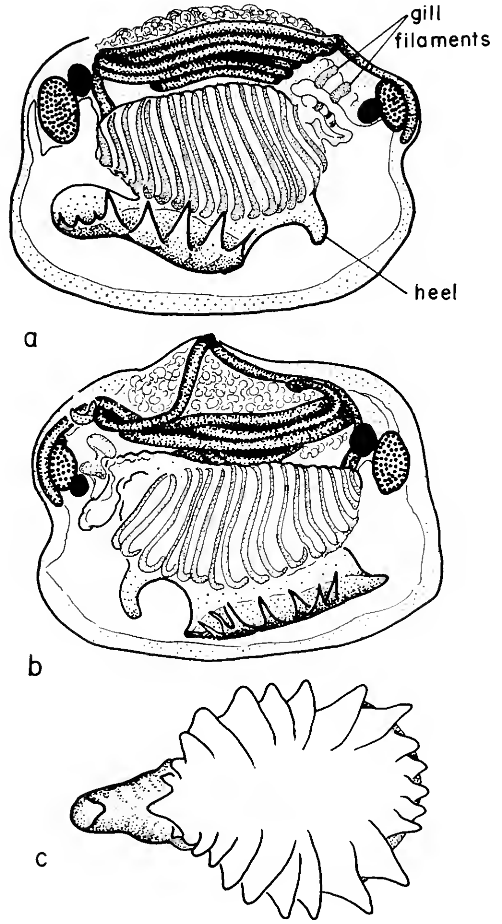

Figure 8. a) Left and b) right lateral, semidiagrammatic view of the body and mantle organs, and c) ventral view of the papillate foot, of *Pristigloma alba.*

Shell minute, robust, with strong concentric ridges at the margins that gradually become less obvious towards umbonal region; elongate oval in outline and extended anteriorly; dorsal margin slightly curved; posterior margin short and smoothly but strongly rounded; anterior margin long with both dorso- and ventro-anterior margins weakly convex and evenly rounded; umbos small, very low in profile, posterior in position, and medially directed; no escutcheon or lunule. Hinge plate with a narrow, elongate, amphidetic internal ligament; posterior hinge plate slightly shorter and straighter than the anterior; three or four chevron-shaped teeth present in the anterior and posterior tooth series (Fig. 10).

Neither inhalent or exhalent apertures present nor an anterior mantle sense organ. Adductor muscles equal in size. Few hypobranchial gland cells present in the epithelia of the ctenidial axes. No specialized mantle glands present. Gills set transversely across the posterior part of the mantle cavity, anterior to the posterior adductor; six pairs of fingerlike gill plates, each pair oppositely attached to axis; posterior axial extension present as in *Pristigloma.* Palps large, not rectangular, but somewhat fan-shaped, each with 12 internal ridges, and extend to the posterior edge of foot. Mouth set slightly behind the anterior adductor muscle. Stomach moderately large with 3 sorting ridges and 2 ducts to the digestive glands; style sac moderately large with a combined midgut from which the hindgut passes dorsally. Subsequently the hindgut is arranged so that there is 1 loop on left side of body, 3 coils encircling the stomach and 1 loop on right side of body in that sequence. The final arm of the last loop is me-

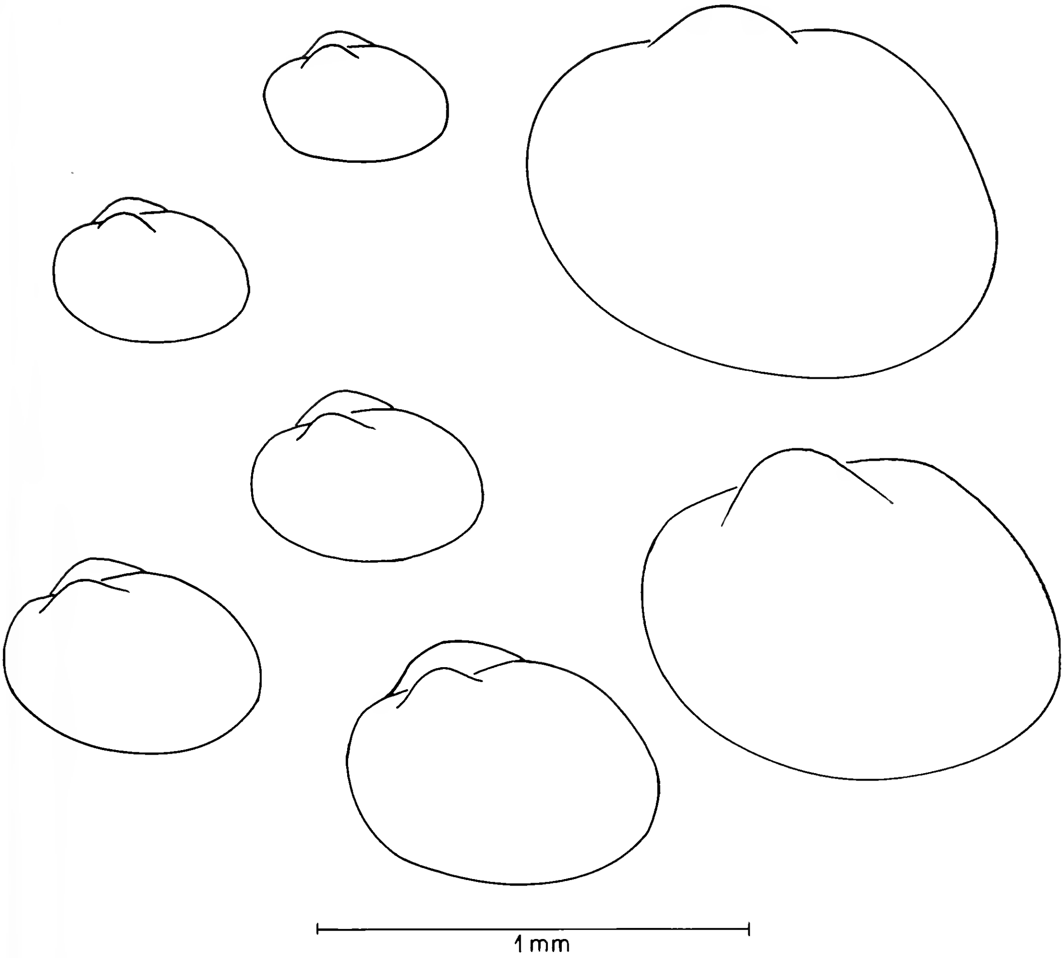

Figure 9. *Pristigloma alba* (Sanders and Allen). Lateral views of a series of specimens to show changes in shape with increasing size.

dian dorsal in position and leads to the anus. Anteriorly, the coils of the hindgut pass from left to right in front of oesophagus thus displacing it posteriorly. Foot broad with 12–14 fringing papillae to the right and left margins of the sole; heel very prominent, pointed and distinct from the sole; a moderately developed "byssal" gland internal to where foot and heel join. Nervous system similar to that in *Pristigloma* except that the visceral ganglia are as large and as well defined as the cerebral (Figs. 11, 12).

Hermaphroditic with but 2 concurrently mature eggs, one very slightly in advance of the other in its development; sperm relatively few in number, forming cap to the outside of the ova (Figs. 13, 19). Prodissoconch length of 290 μ (Fig. 10c); size of mature egg 120 μ.

M. yongei shows no obvious proportional changes with growth (Fig. 14), having a height-to-length ratio of about 0.76 and a breadth-to-length ratio of 0.55, reaching a maximum length of 1.1 mm. The absolute size range in our sample was 0.76 to 1.11

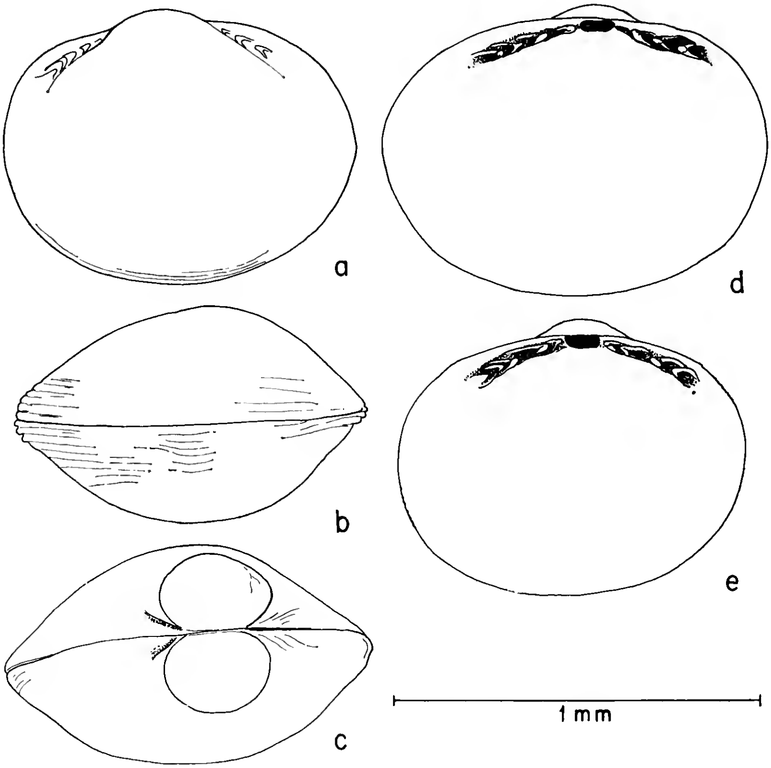

Figure 10. *Microgloma yongei* (Sanders and Allen). Shell characters, a) lateral view of right side; b) ventral and c) dorsal view of shell, showing the prodissoconch; d and e) internal views of the left valves showing individual variation in form.

mm; the shape of the histogram (Fig. 21) indicates that the larger sizes were adequately sampled but that increasing proportions of the smaller sizes were lost through the meshes of the net.

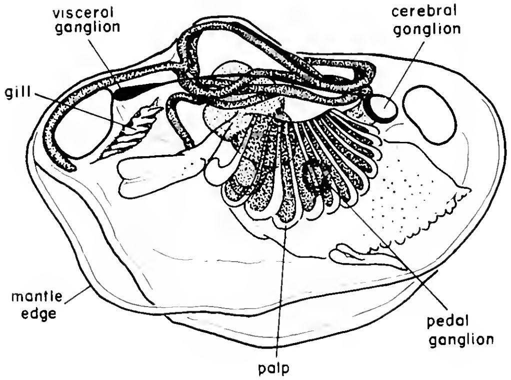

Figure 11. Right lateral, semidiagrammatic view of the body and mantle organs of *Microgloma yongei*.

The species is named in honor of Sir Maurice Yonge, a leading scholar and outstanding mentor in Malacology.

Microgloma yongei can be separated from the closely related *M. turnerae* by its proportionately greater length, the less oblique descent of the dorso-anterior margin, the lower profile of the umbo, the smaller internal ligament, the narrow hinge plate, and the larger prodissoconch.

Microgloma turnerae new species

Figures 15–21

Type locality: SARSIA Cruise, Station S-65, in 1922 m. Holotype: MCZ 271972. Depth range = 952–2351 m. Records: Table IV.

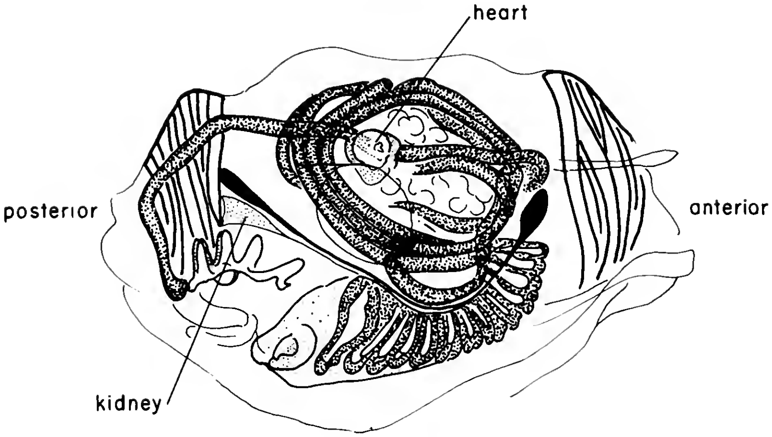

Figure 12. Dorsal, semidiagrammatic view of the body and mantle organs of *Microgloma yongei.*

Shell minute, robust, with strong concentric lines particularly along the shell margin and with faint radiating striae; subovate in outline and extended anteriorly; dorsal margin straight; posterior margin short and smoothly rounded; anterior edge long, with the dorso-anterior margin weakly convex and slightly longer than the more convex ventro-anterior edge; ventral margin weakly though evenly convex; umbos not prominent, low in profile, posterior in position and medially directed; neither lunule nor escutcheon present. Hinge plate moderately strong with a large, bean-shaped amphidetic internal ligament; posterior hinge plate shorter and straighter than the slightly ventrally sloping anterior hinge plate. Three moderately strong chevron-shaped

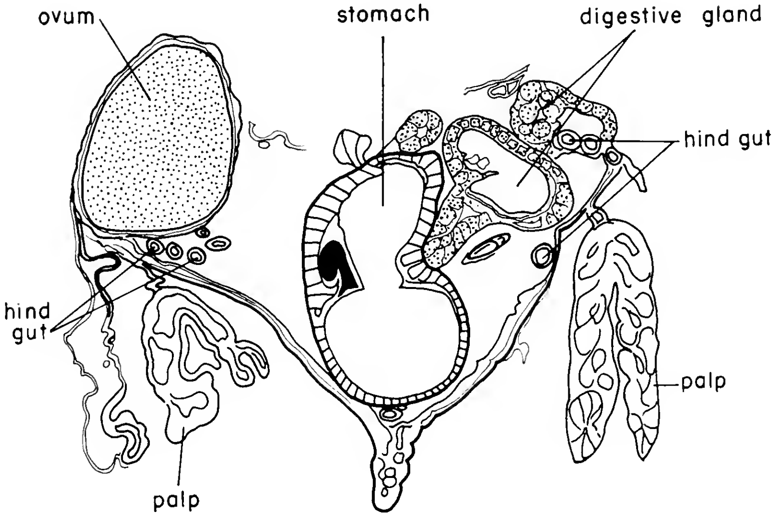

Figure 13. *Microgloma yongei* (Sanders and Allen). Transverse section through stomach, digestive gland, hindgut, ovum, and palp.

TABLE IV. RECORDS FOR *Microgloma turnerae* NEW SPECIES.

Cruise	Sta. No.	Depth (m)	Specimens	Latitude	Longitude	Gear	Date
			WEST EUROPE BASIN				
Sarsia	S-61	952	2	46°20.5′N	4°36′W	ES	19.7.67
Sarsia	S-44	1739	11	43°40.8′N	3°35.2′W	ES	16.7.67
Sarsia	S-65	1922	148	46°15′N	4°50′W	ES	25.7.67
			CANARIES BASIN				
Discovery	6709	2351	5	27°29.8′N	15°20.1′W	ES	18.3.68

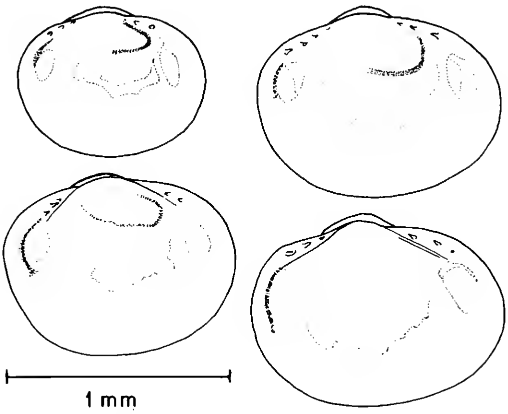

Figure 14. Lateral views of a series of specimens of *Microgloma yongei* to show changes in shape with growth.

teeth and a distal incipient protuberance on both the anterior and the posterior hinge plate (Fig. 15).

The soft parts are similar to those of *M. yongei.* The mantle characters differ only in that the adductor muscles are appreciably larger (average muscle scar/lateral mantle area ratio in *M. turnerae* 0.44/1, and in *M. yongei* 0.52/1). The palps are somewhat smaller than those of *M. yongei,* each with 13–14 ridges. The basic plan of the hindgut is similar in the two species except that all the coils are adjacent and ventral to the digestive gland in *M. turnerae,* whereas in *M. yongei* part of one coil lies dorsal to the digestive gland on the right side and alongside the final section of gut leading to anus (Figs. 11, 16, 17, 18, 19).

Microgloma turnerae shows little proportional change with growth (Fig. 20), maintaining a height-to-length ratio of about 0.80 and a breadth-to-length ratio of 0.54. It reaches a maximum length only slightly greater than 1 mm, and we believe that this may be the smallest known free-living bivalve. Its absolute size range in our samples is from 0.72 to 1.03 mm. The shape of the histogram in Figure 21, with a precipitous drop in numbers at lengths greater than 0.98 mm and a rapid though more gradual decline in numbers at lengths less than 0.94 mm, suggest that the larger sizes were adequately sampled but the progressively smaller sizes were lost through the meshes of the net (0.5 mm openings at the cod end) in ever-increasing proportions.

M. turnerae is hermaphroditic with two concurrently maturing eggs. The sperm are relatively few in number and cup the outside of the ova. A prodissoconch length of 260 μ (Figs. 15c, 18, 19) would indicate direct development (Ockelmann, 1965), yet the egg size of 120 μ falls within the size range of lecithotrophic development. Possibly the remarkably small size of both species of *Microgloma* imposes a severe limitation on the egg diameter that can pass through the oviduct, yet, with an egg number of two, development is likely to be direct if the species is to survive. Such an interpretation is consistent with the finding that the prodissoconch length is disproportionately large when compared with the actual egg size.

This species is named in honor of Dr. Ruth Turner of the Museum of Comparative Zoology, Harvard University, a dedicated and enthusiastic scientist and re-

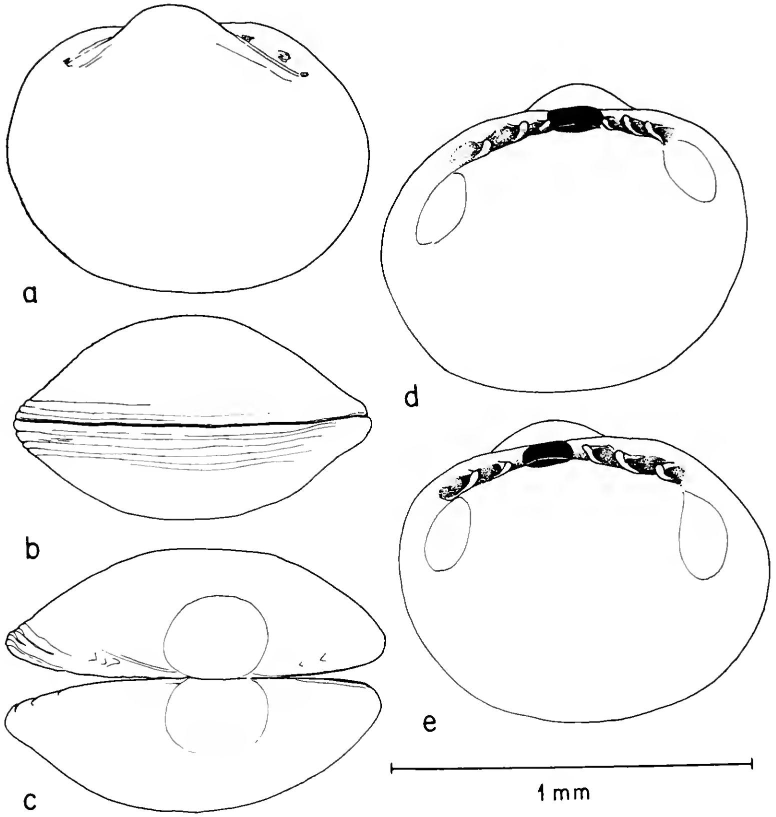

Figure 15. *Microgloma turnerae* (Sanders and Allen). Shell characters, a) outer lateral view of right valve, b) ventral view and c) dorsal view of shell, showing the prodissoconch; internal view of d) right and e) left valves.

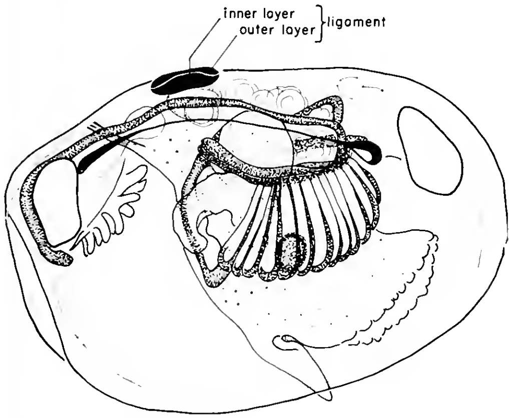

Figure 16. Right, lateral, semidiagrammatic view of body and mantle organs of *Microgloma turnerae*.

spected colleague, for her significant contributions to malacology.

FUNCTIONAL MORPHOLOGY OF THE SOFT-PART ANATOMY IN THE PRISTIGLOMIDAE

No organ system evolves in isolation; it can only be understood in relation to its interaction with other systems and structural units. Animal form and function are the resultants of such interdependent relationships in response to environmental stimuli. Thus, in the case of the family Pristiglomidae, the rounded form can be correlated, in part, with the absence of mantle fusion or modification. Since neither siphons nor tentacles are present, there is

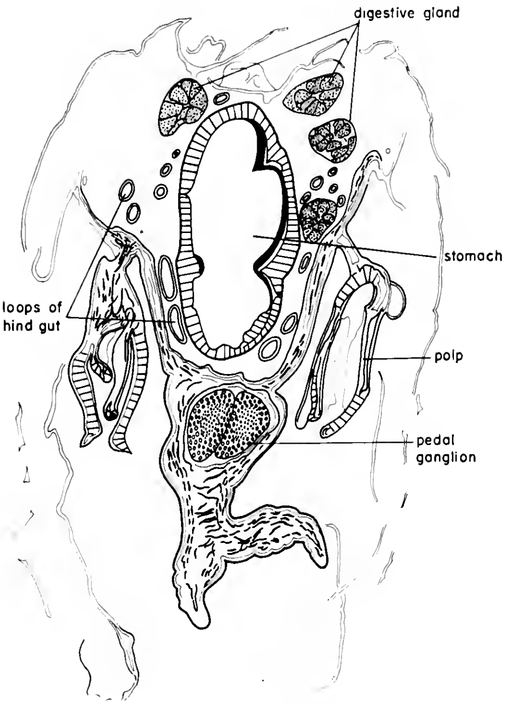

Figure 17. *Microgloma turnerae* (Sanders and Allen). Transverse section through stomach, digestive gland and pedal ganglion.

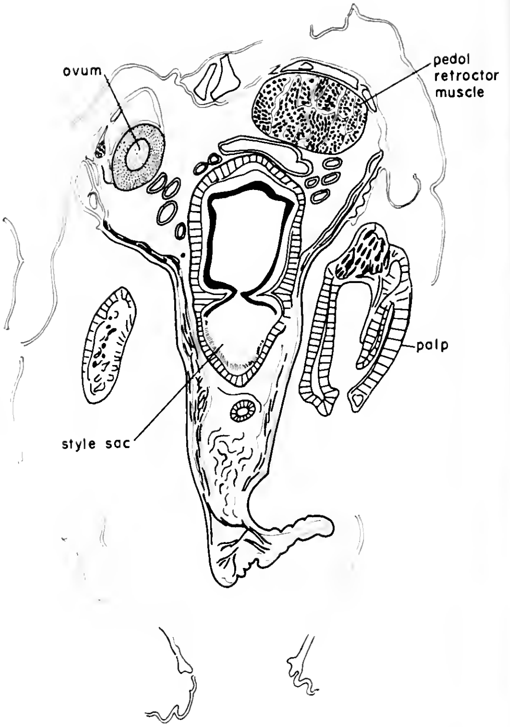

Figure 18. *Microgloma turnerae* (Sanders and Allen). Transverse section through stomach and second ovum.

no morphological reason for the shell to be rostrate and posteriorly elongate. Because the inhalent current must be anterior and ventral and the exhalent current posterior, a direct one-way flow system results.

Flow patterns within the mantle cavity of those species with an anterior and ventral incurrent, such as *Pristigloma* and *Microgloma,* seem to be related both to the ventral positioning of the anterior adductor muscle and the position of the mouth close to the posterior dorsal edge of that muscle (Allen, 1958, 1968). The adductor may act as a baffle or wall, which regulates the direction of flow of the adjacent currents away from the region of the mouth and broadly directs the flow of water away from the anterior and towards the posterior part of the palps, thus ensuring that maximum sorting takes place at the palp surfaces.

The position of the ctenidial axis is also related to the position of the inhalent current area. In the Nuculanacea the inhalent current is posterior and concentrated in a narrow intake diameter and flows immediately along and directionally parallel to the length of the ctenidia, whereas in the Nuculacea, and in *Pristigloma* and *Microgloma* in particular, the incurrent flow is broad, less directional, and not adjacent to the ctenidia. The position of the ctenidia in the Nuculacea are distant from the point of entry and set at right angles to the flow (Fig. 22).

It was shown earlier (Allen and Sanders, 1966) that, in the tellinacean *Abra,* there is an inverse relationship between size of palp and size of ctenidium, and that when the species of *Abra* are arranged in increasing depth range, there is a progressive reduction in ctenidium size. In general, this relationship also holds for the Nuculacea.

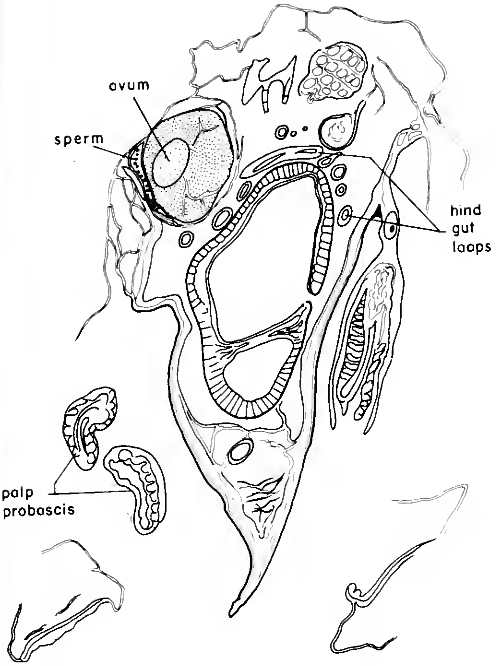

Figure 19. *Microgloma turnerae* (Sanders and Allen). Transverse section through stomach and gonad (including first ovum).

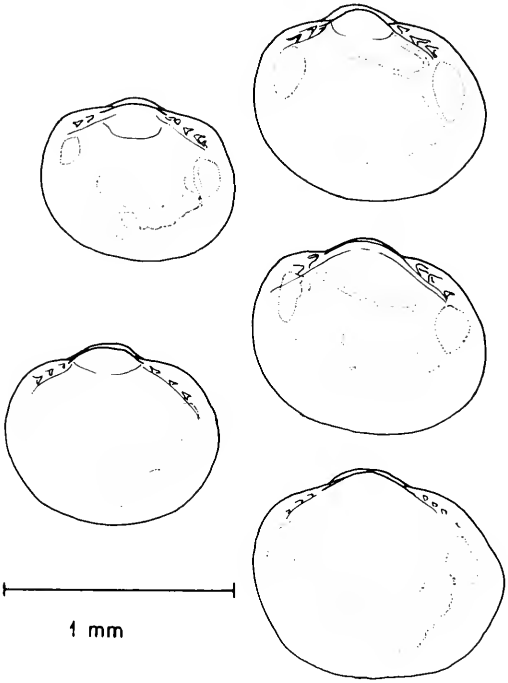

Figure 20. Lateral view of a series of specimens of *Microgloma turnerae* to show changes in shape with increasing size.

Respiratory needs perhaps diminish with increasing depth, and an increase in palp size with consequent increase in ciliation compensates for loss of ctenidial ciliation. It may also reflect a loss of sorting ability of the gills which again is compensated for by an increase in the sorting area of the palp. This latter correlation is perhaps not so significant in abyssal deposit-feeding bivalves since organic matter in sediments are refractory in the deep sea and deposit feeders must process large quantities of material. It might be noted that in the Nuculanacea, where the ctenidial axis is muscular and gills may form a pump diaphragm, progressive reduction of the ctenidium with increasing depth, while occurring, is not so great.

The small size of the Pristiglomidae in itself may be a modifying factor in their respiratory needs. Simple diffusion across a small body volume may supply much of the oxygen required and may explain in part that *P. alba* (1.90 mm maximum total length) has only two pairs of gill filaments to each ctenidium—the least recorded for any adult bivalve—while *P. nitens* (3.54 mm maximum total length) has eight to thirteen pairs. Yet, even in *Microgloma*, which must be one of the smallest if not the smallest recorded bivalve, ctenidia are not lost altogether and there are six pairs of gill filaments in both species.

In general, because the Nuculacea are not rostrate or posteriorly elongate, the palp proboscides are relatively short in comparison with those of the Nuculanacea, particularly in those species which are greatly extended posteriorly. In *Pristigloma,* and *P. alba* especially, because of the great size of the palp in relation to the shell length and the fact that the posterior limit of the palp lies close to the mantle edge, the palp

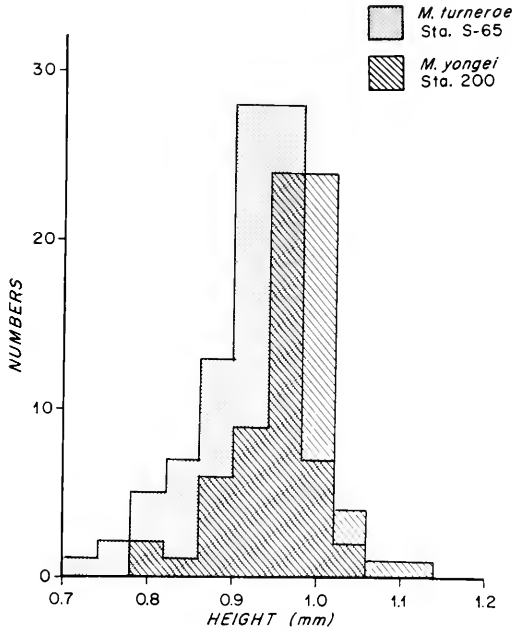

Figure 21. Size/frequency histogram of one sample each of *Microgloma yongei* and *M. turnerae*.

proboscides are proportionately shorter. In *Microgloma* the palp does not lie as close to the mantle edge as in *Pristigloma* and the palp proboscides are relatively longer than in the latter genus.

Because food is not plentiful and much is refractile (Sanders and Hessler, 1969), and probably difficult to digest, the gut of deep-sea protobranchs, and of the Pristiglomidae in particular, is modified. Thus, while the stomach is similar in design to that of shallow-water protobranchs (Yonge, 1959; Purchon, 1956), in *Pristigloma alba* and *Microgloma* sorting ridges are only two or three in number and these are not very pronounced. However, the stomach remains relatively large, as does the style sac, and together they take up most of the available body space.

The hindgut in shallow-water species such as *Nuculana* forms a single loop on the right-hand side of the stomach. In deep-sea species the hindgut is extended and, as such, poses a problem in the disposition of an elongate tube. Many different arrangements have been evolved, as will be apparent from future publications. In *Pristigloma* the hindgut is looped to the right and left of the stomach, the loops being carried from one side to the other behind the stomach. In contrast, in *Microgloma* there are three coils around the top of the stomach in a horizontal plane and also an additional loop on each side. In all protobranchs the final straight section of

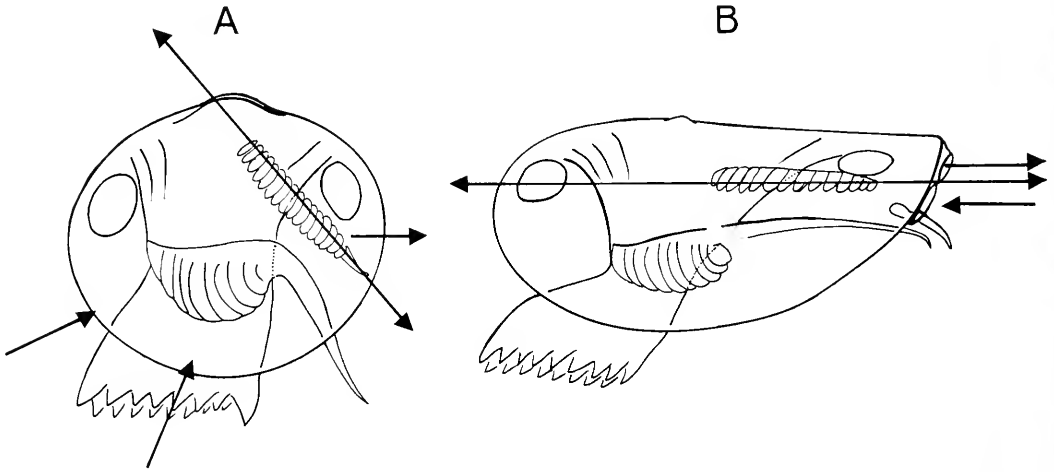

Figure 22. Relationship between water flow and the gill axis in a) the nonsiphonate Pristiglomidae and b) a generalized siphonate nuculanacean.

gut to the anus always originates on the right side. Unlike *Abra* (Allen and Sanders, 1966) the closely packed loops never coalesce into a single sac modified for the bacterial decomposition of organic matter in fecal pellets. Digestion is extracellular in the protobranchs, and enzymes from the digestive glands (and possibly elsewhere) can function in the hindgut. A bacterial flora has not been observed in the deep-sea protobranchs. The hindgut loops are usually closely packed and adjacent lengths frequently pass material in opposite directions, thus giving rise to a contra-flow effect typical of blood systems (Scholander, 1968). We are unable to determine whether diffusion takes place across the membranes of such adjacently opposed segments.

In all protobranchs, fecal material is compacted to form rods. It will be shown later that the ctenidial axes in many protobranchs act as a guide for the disposal of feces to the outside. In the Pristiglomidae, however, the extensions of the ctenidial axes are not attached and do not appear to function in this way. Thus fecal rods are frequently seen in the ventral part of the mantle cavity (Fig. 3) of pristiglomid species, and occasional specimens have been observed with a fecal rod partially extruded and extending across the gap between the ctenidial axes into the lower half of the mantle cavity. Normally, ciliary currents across transversely arranged gill plates will give rise to a posteriorly directed water flow that will tend to carry fecal material out with the exhalent current. However, the ctenidia are so reduced in the pristiglomid species that this flow is probably too weak to function in this way. It seems possible that the enlarged heel of the foot of the Pristiglomidae is used in ejecting the rods posteriorly from the mantle cavity. The position of the rods behind and adjacent to the heel is such that the normal foot movement of the animal will eject them posteriorly.

The function of the "byssal" gland is obscure; it is universally present but varies in size within the Protobranchia. In the Pristiglomidae it is well developed with no evidence that byssus threads are produced. The detailed histology of this gland in the Protobranchia as a whole will be the subject of a later paper.

FUNCTIONAL MORPHOLOGY OF THE HARD-PART ANATOMY IN THE PRISTIGLOMIDAE

The ventral position of the adductor muscles (in relation to the height of the shell) reduces the tendency of the valves to shear. The relative size of the adductors, the robustness of the shell, the thickness of the hinge plate, the number and structure of the teeth and the size of the ligament are interrelated. The adductor muscles are proportionately larger in the heavier-shelled microglomids, which possess a relatively strong hinge plate, well-developed chevron teeth, and a large amphidetic internal ligament. In contrast, the thin-shelled pristiglomids have a weak hinge line and few teeth, some or all of which are low and lamellar in form. The differences between the two genera are particularly apparent when *Pristigloma alba* is compared with *Microgloma* (to which it is similar in size). Thus, *P. alba* has small adductor muscles, an inflated and very fragile shell, and a thin weak hinge line. The hinge area is further differentiated by the posterior plate bearing three reduced lamellar teeth and the anterior hinge plate with one or two weak ridges.

The internal ligament differs in the two genera. The large amphidetic, bean-shaped ligament of *Microgloma* correlates with the shell symmetry, the equal size of the adductor muscles, and the symmetry of the few low chevron-shaped teeth on the hinge plates. The large, somewhat ventrally sloping, opisthodetic ligament of *Pristigloma* is correlated with the asymmetry of the body (there being a larger proportion of the animal anterior to the umbo), the larger size of the anterior as compared to the posterior adductor muscle, and the shallow, asymmetrical hinge plates. Again, these characters are more developed in *P. alba* than in *P. nitens.* The horizontal oval and elongate form of both ligaments counteracts shearing.

MINIATURIZATION

The species of *Microgloma,* although perhaps the smallest of bivalves, remain complex morphologically and structurally. Restraints towards reducing the length of the hindgut are imposed by the poor feeding conditions for these and other deposit feeders in the deep sea. The sediments are uniformly low in organic matter (Sanders, Hessler, and Hampson, 1965) and, more important, such organic matter that is present is refractory (Sanders and Hessler, 1969). Therefore, deposit-feeding bivalves process large quantities of sediment with the result that the hindgut is relatively long, and in *Microgloma,* the elongate hindgut is manifested by its complex looping and coiling about the stomach.

The microglomid response to miniaturization has not been an obvious reduction in cell number but rather a marked diminution in cell size. On a tissue-by-tissue comparison with *Nucula cortica* (a small species, 2.5 mm total length), body cells in *Microgloma turnerae* are only 8.5 percent as large by volume. A similar trend can be shown for *Pristigloma* (8.7%) (Table V).

TABLE V. MEAN CELL MEASUREMENTS OF VARIOUS TISSUES (AVERAGED DIMENSIONS (μ) OF TEN CELLS) OF THREE SPECIES OF DEEP-SEA PROTOBRANCHIA

	Microgloma turnerae	*Nucula granulosa*	*Pristigloma nitens*
Style sac			
Height	9.6	21.2	17.2
Width	7.8	11.2	5.4
Hindgut			
Height	5.2	25.9	6.1
Width	4.9	16.8	4.4
Palp epithelium			
Height	8.4	15.9	7.4
Width	4.1	9.0	5.1
Foot epithelium			
Height	7.8	23.7	10.4
Width	6.8	10.0	5.8

The single major exception to this generalization is in the reproductive system. Only two mature eggs are present in the oviducts of *M. turnerae* and *M. yongei,* certainly the smallest egg number yet reported for a bivalve. However, such a pronounced reduction in egg number is attributable to the absence in the protobranchs of the planktotrophic mode of reproduction with its production of small eggs. In bivalves with lecithotrophic development, eggs are at least 90 μ in length (Ockelmann, 1965). With such an astonishingly low reproductive potential, mortality must be drastically reduced to allow sufficient numbers of young to reach sexual maturity and so maintain the species. Mortality can be reduced by the suppression of a planktonic stage and the adoption of direct development; such an evolutionary strategy together with miniaturization of the genus may explain the apparently anomalous findings of a lecithotrophic egg size of 115–120 μ in *M. turnerae* and *M. yongei* coupled with a prodissoconch size of 260 μ and 290 μ respectively, indicative of *direct* development. The size of the gonadal apertures in the minute microglomids imposes a rigid upper limit on the size dimensions of an egg that can be passed. Egg sizes that are correlated with direct development, 150 μ–200 μ (Ockelmann, 1965), are too large to pass through the oviduct. We suggest that the largest egg size that can be so discharged falls within the size range given for the lecithotrophic egg although the very small clutch size dictates a direct mode of development, and this is supported by the large size of the prodissoconch. Egg production is probably continuous and the larvae may be lecithotrophic for a very short period of time. The restricted patterns of distribution in the microglomids are certainly compatible with a direct mode of development.

DISTRIBUTION PATTERNS

The two genera of the Pristiglomidae have contrasting patterns of distribution. Both *Pristigloma nitens* and *Pristigloma alba* are broadly distributed vertically at depths between 2000 m and 5000 m and they are present at many of the stations in these depths. Yet despite the fact that they are consistent elements of the fauna, these bivalves are never represented by more than a few individuals and they usually comprise less than 1 percent of the Protobranchia in the sample. They also have broad horizontal or zoogeographical distributions. We have now collected *P. alba* from the North American Basin, the Canaries Basin, the Angola Basin, the Brazil Basin, and the Argentine Basin and *P. nitens* from the same five basins as well as the West Europe Basin.

Microgloma turnerae and *Microgloma yongei*, on the other hand, appear to be narrowly distributed both horizontally and vertically. *M. turnerae* has been collected from mid-bathyal to upper abyssal rise depths at but three stations in the West Europe Basin and a single locality in the Canaries Basin. *M. yongei* is known from three upper abyssal rise–lower slope stations, one in the Cape Verde Basin, and two in the Angola Basin. Yet, when they are present, the microglomids are often numerically major constituents of the protobranch bivalves. At station S-65, *M. turnerae* comprised more than 50 percent of the sample while *M. yongei* comprised almost 15 percent of the protobranchs at station 175 and 58 and 9.5 percent at stations 200 and 201.

SUMMARY

Extensive and continuing sampling of the benthic fauna at bathyal and abyssal depths of the Atlantic has yielded very great numbers of protobranch bivalves. Examination of these collections has revealed many new species and many varied morphologies, indicating that the great radiation of this group has taken place in the deep sea. Such unique and varied material makes possible comprehensive studies of this relatively poorly known subclass. Some of the components of these investigations are the comparative anatomy of both soft and hard parts, functional morphology *per se* and in relation to abyssal life, changes in form with growth, mode of reproduction, and ecology.

To put subsequent studies in perspective an advance outline classification of the major taxa is given. This is followed by the analysis of a new family of the Nuculacea, the Pristiglomidae, which comprises the genera *Pristigloma* (previously placed in the family Nuculanidae, here raised to superfamily status), and *Microgloma*, a new genus.

Two species of *Pristigloma* are found in the samples, *P. nitens* and the new species *P. alba*. Both are broadly distributed, vertically and horizontally, in the deep Atlantic, being most frequently found between 2500 m and 5200 m. Despite their wide range and frequent presence, they usually constitute less than 1 percent of the total protobranch fauna at any one station. They are characterized by extremely reduced gills (two pairs of gill plates only in *P. alba*), exceptionally large palps, and an elongate hindgut that makes at least four separate loops to either side of the body.

The genus *Microgloma* is also represented by two species, both new, *M. turnerae* and *M. yongei*. These are closely related and, in contrast to *Pristigloma*, have a much more circumscribed distribution in depth and geography. *M. turnerae* is restricted to the West Europe and Canaries basins at 1000–2300 m and *M. yongei* is found only in the Cape Verde and Angola basins at 2000–2700 m. Unlike *Pristigloma*, *Microgloma* is present at relatively few stations but may make up a significant fraction of the total protobranch population. They are among the smallest bivalves known and miniaturization has been accomplished largely by reduction in cell size. However, in the case of the gonads there is a drastic reduction in germ-cell numbers, with only two ova maturing at any one time.

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Studies on Deep-Sea Protobranchia (Bivalvia); The Families Siliculidae and Lametilidae

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STUDIES ON DEEP-SEA PROTOBRANCHIA (BIVALVIA);[1] THE FAMILIES SILICULIDAE AND LAMETILIDAE

J. A. ALLEN[2] AND H. L. SANDERS[3]

Abstract. Two new families are erected, the Siliculidae and the Lametildae. Both are characterized by laterally elongate hinge teeth, but each having a suite of distinguishing features. Two new species of Silicula are described and one species each of the new genera *Lametila* and *Prelametila*.

It is argued that the elongate, laterally compressed form of *Silicula* and the anteriorly directed and well-developed foot are features of a fast-burrowing animal and are in direct contrast to the globular lametilids with their ventrally directed foot.

While the two species of the family Lametilidae are totally abyssal, the species of *Silicula* range from upper slope depths to the abyss.

Unlike other protobranch families (*e.g.*, Pristiglomidae), in the Siliculidae and Lametilidae sexes are separate. Males are larger than females and *Lametila* is probably protogynous. This may well be of considerable importance in sparse abyssal faunas, that maximum sperm density is achieved through the large size of the adult.

The present paper forms part of the continuing investigation on the deep-water Protobranchia of the Atlantic Ocean. The objectives together with the specific consideration of the Family Pristiglomidae are given in the previous contribution of this series (Sanders and Allen, 1973). In this study we turn our attention to those nuculanacid protobranchs that may lack the chevron-shaped taxodont teeth, the supposed hallmark of the protobranchiate bivalve, and have instead elongate teeth running obliquely parallel to the dorsal edge of the shell on either side of the umbo. Despite the fact that four of the nuculanacid species collected in our samples share such a tooth configuration, while a fifth has taxodont teeth as well, they separate sharply into two categories that differ decisively in a considerable number of morphological features. Therefore, we propose that two new families, the Siliculidae and the Lametilidae, be erected to include these species.

The basis for creating two rather than one family for this assemblage is as follows:

(1) Shell shape
- Siliculidae—elongate and laterally compressed
- Lametilidae—rounded and somewhat tumid

(2) Ligament
- Siliculidae—internal, elongate, obliquely opisthodetic
- Lametilidae—internal, oblong, amphidetic

(3) Elongate teeth
- Siliculidae—at least four elongate teeth on the posterior and three elongate teeth on the anterior hinge plate
- Lametilidae—no more than two

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elongate teeth on either the posterior or the anterior hinge plate

(4) Gut
  Siliculidae—never more than one loop to the right and left of the body, gut penetrates deep into the foot
  Lametilidae—two or more loops to the left and the right of body, gut does not penetrate deep into foot

(5) Palp
  Siliculidae—large and elongate
  Lametilidae—smaller and broader and more anterior in position

(6) Palp proboscides
  Siliculidae—very long and narrow
  Lametilidae—large but not elongate

(7) Foot
  Siliculidae—very large and elongate, no posterior projection from the heel of foot
  Lametilidae—short and square, a triangular posterior projection from the heel of foot

(8) Ctenidium
  Siliculidae—outer gill plates half the size of the inner; frontal and laterofrontal cilia are exceptionally long and dense
  Lametilidae—outer and inner gill plates of the same size; frontal and laterofrontal cilia not exceptionally long or dense

(9) Inhalent current
  Siliculidae—through an inhalent aperture
  Lametilidae—through an inhalent siphon

(10) Tentacle
  Siliculidae—fine and attenuated
  Lametilidae—stout

(11) Visceral ganglion
  Siliculidae—below the level of the posterior adductor muscle
  Lametilidae—level with the posterior adductor muscle

(12) Kidney
  Siliculidae—short
  Lametilidae—elongate

(13) Body axis
  Siliculidae—bent through 90°
  Lametilidae—vertical

Family SILICULIDAE new family

Nuculanid protobranchs with fragile, smooth, laterally flattened, posteriorly elongate and gaping shell; hinge weak and elongate; teeth elongate; umbo small, hardly raised above the dorsal margin of the shell; lunule and escutcheon absent; ligament internal, elongate, opisthodetic, slanting posteroventrally; inhalent aperture not complete but formed by the dorsal and ventral adhesion of the mantle edges; outer gill plate half the size of the inner, frontal and laterofrontal cilia exceptionally long and dense; mouth set well back from anterior adductor muscle; pedal ganglion exceptionally large.

Genus *Silicula* Jeffreys, 1879

Type species (by monotypy): *Silicula fragilis* Jeffreys

Hinge teeth relatively few in number, 4–8 on the posterior and 3–5 on the anterior hinge plate, elongate and parallel or obliquely parallel to the hinge; posterior dorsal margin of the shell either straight or convex.

The available evidence from hard-part anatomy of shell structure, hinge line, umbo size and ligament suggests that *Silicula* probably is most closely related to the genus *Propeleda* Iredale (see Thiele, 1935) and, perhaps to a lesser degree, to *Poroleda* Tate. Iredale (1924) separated *Propeleda* from *Poroleda* on the basis of the former having fewer elongate, overlapping teeth, parallel or obliquely parallel to dorsal shell margin (as in *Silicula*) rather than numerous short teeth set diagonally across hinge plate and which do not, or just barely, overlap. Both *Propeleda* and *Poroleda* are more extended posteriorly and more rostrate than *Silicula* and have the posterior dorsal margin concave rather than straight or convex. *Silicula mcalesteri* (page 278) begins to approach the condition present in

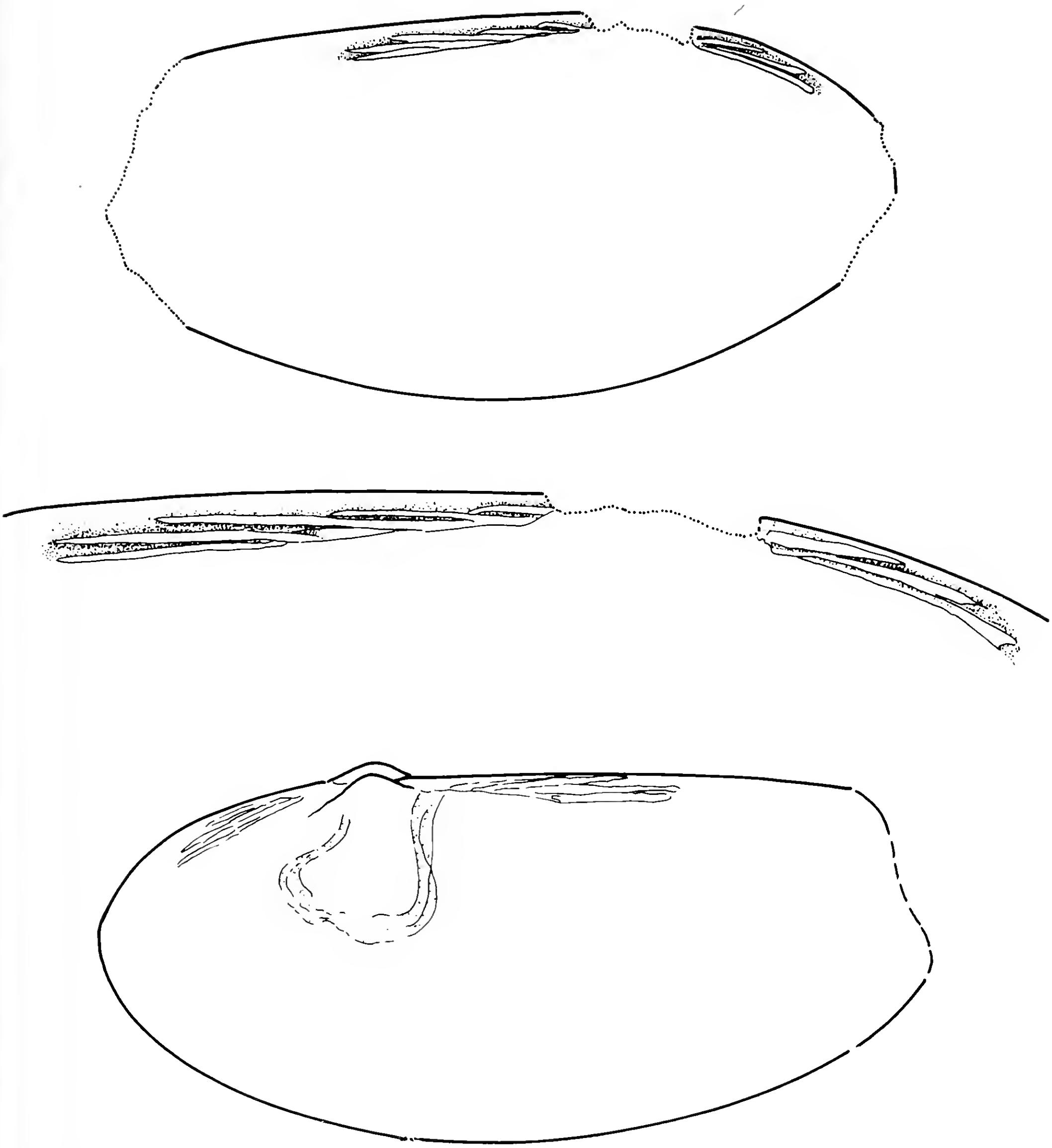

Figure 1. *Silicula fragilis* Jeffreys. Internal view of the left valve, with hinge detail in enlargement and view of right side of intact holotype (U.S. Nat. Mus. No. 197405).

Propeleda for it is both more elongate and more rostrate than the other species of *Silicula*; however, the posterior dorsal margin is convex rather than concave. Until there is information about the soft anatomy of *Propeleda* we cannot determine whether that genus can be legitimately separated from *Silicula*. We can, therefore, only tentatively place *Propeleda* and *Poroleda*, together with *Silicula*, as distinct genera within the family Siliculidae.

The nomenclature of the genus *Silicula* is not clear. Monterosato (1875) gave a brief description of a new genus which he called *Phaseolus*. Authors (*e.g.*, Dall, 1908; Dell, 1956) have overlooked this description by Monterosato (1875, Vol. 4) and considered *Phaseolus* a *nomen nudum* (Dall, 1908; Bowden and Heppell, 1966) and dated the genus *Phaseolus* from Seguenza (1877), *P. ovatus* Seguenza being the type (Thiele, 1935). Jeffreys (1879) considered the name *Phaseolus* to be preoccupied in botanical nomenclature and substituted the name *Silicula*, citing *S. fragilis* Jeffreys as the type species. Jeffreys (1879) mentions the existence of *Phaseolus ovatus* in the same paper and said that this fossil *possibly* belongs to the same genus. Nevertheless, the use of *Phaseolus* in both zoological and botanical nomenclature is no reason for substituting a new name. Later, Verrill and Bush (1897), having examined specimens of both *Silicula fragilis* and *Phaseolus ovatus*, proposed that because of the considerable differences in shell character both names should be retained. This conclusion was disputed by Dall (1908), who was of the opinion that until all the characters of the two species were known *Silicula* could hardly rank higher than a subgenus, particularly as he thought "it highly likely that species of intermediate character would be found." We have retraced these steps and have examined the holotype of *Silicula fragilis* from the Jeffreys collection in the U.S. National Museum (No. 197405) and also *Phaseolus ovatus* from the type locality in the same collection (No. 197406). We believe that Verrill and Bush (1897) were correct and that the two species are grossly different and belong to different genera. The specimen of *Phaseolus ovatus* corresponds to the descriptions of Monterosato (1875) and Seguenza (1877) and exactly with the figures of the type of this species (*e.g.*, fig. 791, Thiele, 1935). We are supported in our findings by Thiele (1935) himself as he too separates the two species. The present work shows that there are at least two distinct groups having elongate lamellar hinge teeth, one of which is typified by *Silicula fragilis*. We believe that *Phaseolus* may be included in our second group comprising the new genera *Lametila* and *Prelametila*.

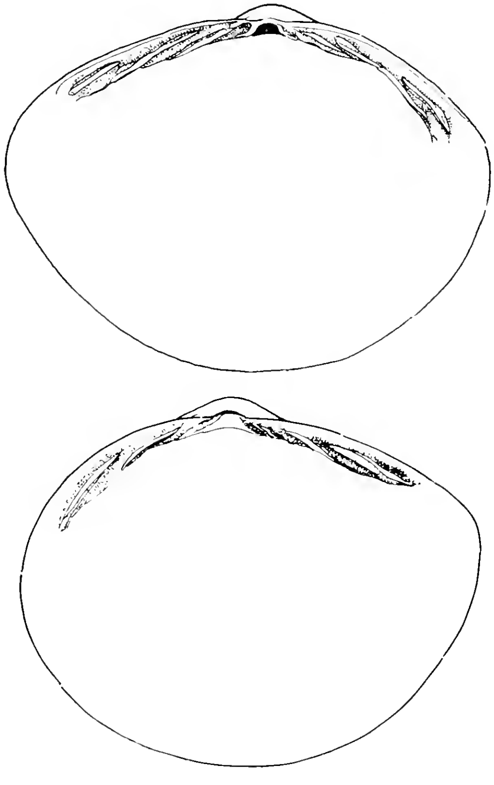

Figure 2. Internal views of left and right valves of *Phaseolus ovatus* Seguenza (U.S. Nat. Mus. No. 197406) from type locality—Fierazzi, Bougnone, Sicily.

It must be pointed out also that the genus *Phaseolus* has been misapplied by authors (Belyaev, 1972; Knudsen, 1970) and it is doubtful that *P. faba* (Knudsen, 1970) belongs to the genus.

Silicula filatovae new species

Figures 3–11

Type locality: ATLANTIS II, Cruise 17, Station 93, in 5007 m. Holotype: MCZ 271977. Depth range = 3826–5042 m. **Records:** Table I.

Shell laterally compressed, smooth, glossy, iridescent, almost transparent, fragile, with fine concentric lines; elongate oval in outline and without a pronounced posterior extension; dorsal margin long, curving al-

TABLE I. RECORDS FOR *Silicula filatovae* NEW SPECIES.

Cruise	No.	Sta.	Depth (m)	Specimens	Latitude	Longitude	Gear	Date
NORTH AMERICAN BASIN								
Chain	50	78	3826	10	38°0.8′W	69°18.7′W	ES	30.6.65
Chain	50	85	3834	55	37°59.2′N	69°26.2′W	ES	5.7.65
Chain	50	84	4749	7	36°24.4′N	67°56.0′W	ES	4.7.65
Chain	58	100	4743–4892	1	33°56.8′N	65°47.0′W	ES	1.5.66
Atlantis II	24	125	4825	1	37°24.0′N–37°26.0′N	65°54.0′W–65°50.0′W	ES	23.8.66
Chain	50	80	4970	9	34°49.8′N	66°34.0′W	ES	2.4.65
Chain	50	83	5000	2	34°46.5′N	66°30.0′W	ES	3.4.65
Atlantis II	17	93	5007	1	34°39.0′N	66°26.0′W	ES	14.12.65
Chain	50	81	5042	2	34°41.0′N	66°28.0′W	ES	8.4.65
CAPE VERDE BASIN								
Atlantis II	31	149	3861	1	10°30.0′N	18°18.0′W	ES	7.2.67
ANGOLA BASIN								
Atlantis II	42	197	4565–4595	25	10°29.0′S	9°04.0′E	ES	21.5.68
Atlantis II	42	196	4612–4630	1	10°29.0′S	9°04.0′E	ES	21.5.68
Atlantis II	42	198	4559–4566	13	10°24.0′S	9°09.0′E	ES	21.5.68

most imperceptibly downwards away from the umbo; posterior margin broad and smoothly rounded; anterior margin narrow and sharply, though evenly, rounded, anterodorsal margin slightly shorter than anteroventral margin, ventral margin long but gradually and smoothly curved; umbos very small, hardly interrupting the contour of the dorsal shell margin, posteriorly directed and slightly anterior in position, the anteroposterior umbonal ratio being about 45/55; shell gaping anteriorly and, more so, posteriorly with the valves separated along much of the dorsal margin (Fig. 3).

Hinge plate long, narrow, slanting away from dorsal edge of shell distally, with an oblong opisthodetic internal ligament which is ventroposteriorly directed. Four elongate, narrow, slightly convex teeth insert one above the other behind umbo, diverge distally, and occupy much of the ventral side of the posterior hinge plate; dorsal tooth shortest and narrowest, terminating almost at the level of the posterior adductor muscle, each of the more ventral teeth progressively more elongate, with the second reaching the distal edge of the posterior adductor muscle, the third and fourth terminating beyond the adductor muscle, close to dorsal edge of the posterior shell margin; ventral tooth forming the ventral edge of the hinge plate, very thin proximally where it is almost hidden by the overlying tooth but thicker distally in the region of posterior adductor muscle. Anterior hinge plate with three elongate, narrow teeth curved slightly to the ventral side; these teeth are almost as long as the posterior series, lying one above the other and diverging slightly; all teeth reach the level of the anterior adductor muscle, dorsal tooth shortest, the two ventral teeth thicker than the dorsal, each longer than the one dorsal to it, terminating beyond the adductor muscle where they approach the dorsal edge of the anterior shell margin; ventral tooth forming the ventral edge of the hinge plate and partially hidden proximally by the overlying tooth. Shells range in size from 1.65 mm to 5.20 mm, the height-to-length ratio changing slightly with size and ranging from .559 in the smallest

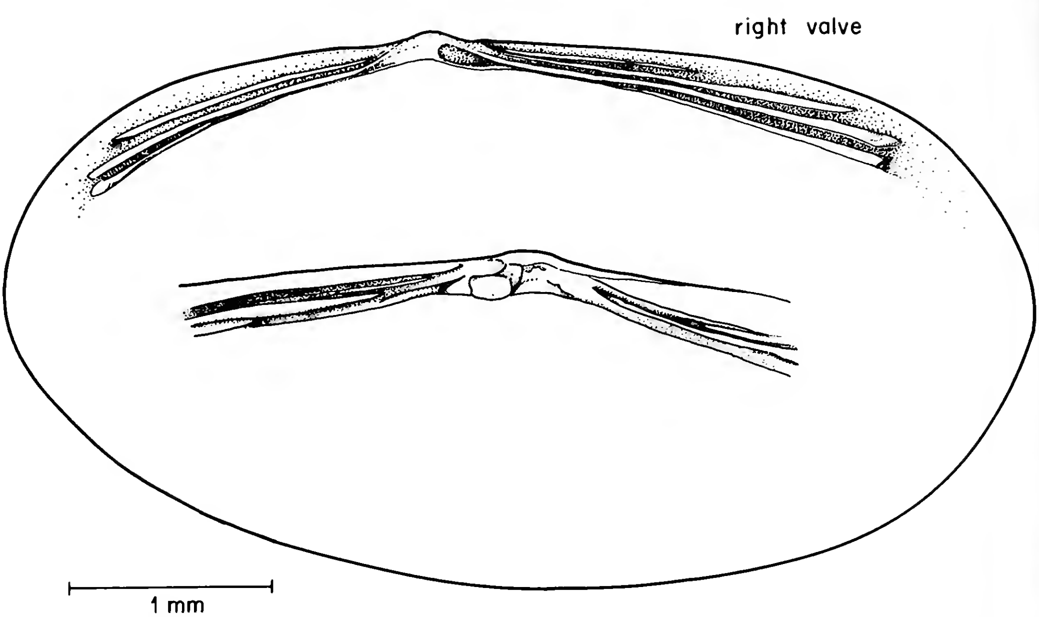

Figure 3. *Silicula filatovae* Allen and Sanders. Internal view of right valve, with hinge detail of left valve.

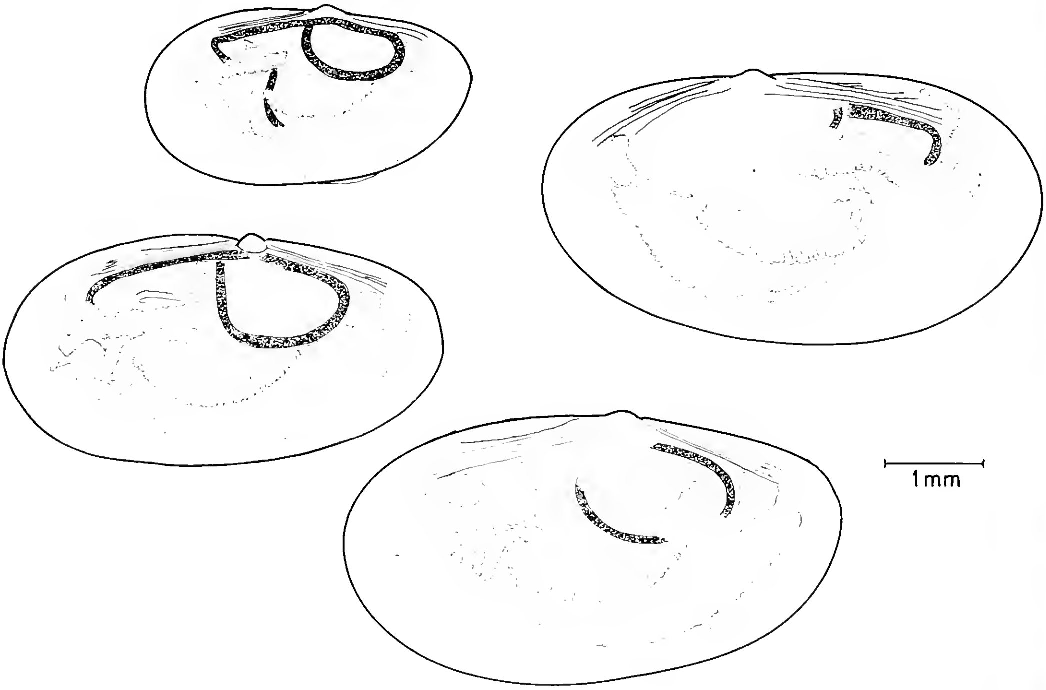

Figure 4. Lateral views of a series of specimens of *Silicula filatovae* to show changes of shape with increasing size. Features of the soft-part anatomy, seen through the shell, are indicated.

to .491 in the larger specimens (Figs. 4, 11). The width-to-length ratio is only about .17, reflecting their very flattened form (Figs. 5, 11). The prodissoconch varies from about 290 μ–310 μ, suggesting that development is direct (Ockelmann, 1965).

Posterior exhalent siphon, formed by the fusion of the inner muscular folds of the mantle, can be completely retracted within the mantle/shell; siphonal embayment shallow and almost nonexistent, the pallial line being set back from the posterior shell edge so that the inner muscular fold of the mantle is distant from the middle sensory fold, the retracted siphon lying within this space posterior to the posterior adductor muscle within the space so formed. Posterior adductor muscle set forward within the mantle cavity below the posterior limit of the hinge teeth; siphonal retractors poorly developed, extending anteriorly and ventrally below the posterior adductor; posterior inhalent aperture formed by the apposition of the somewhat extended inner muscular folds of the mantle immediately ventral to the exhalent siphon and at a point close to the posteroventral mantle/shell edge; inhalent region broad, occupying the whole of the posterior margin below the level of the posterior adductor muscle (Fig. 6); sensory lobe minutely papillate in the inhalent region, but elsewhere a simple fold; inhalent aperture may extend beyond the shell edge but clearly not to the same

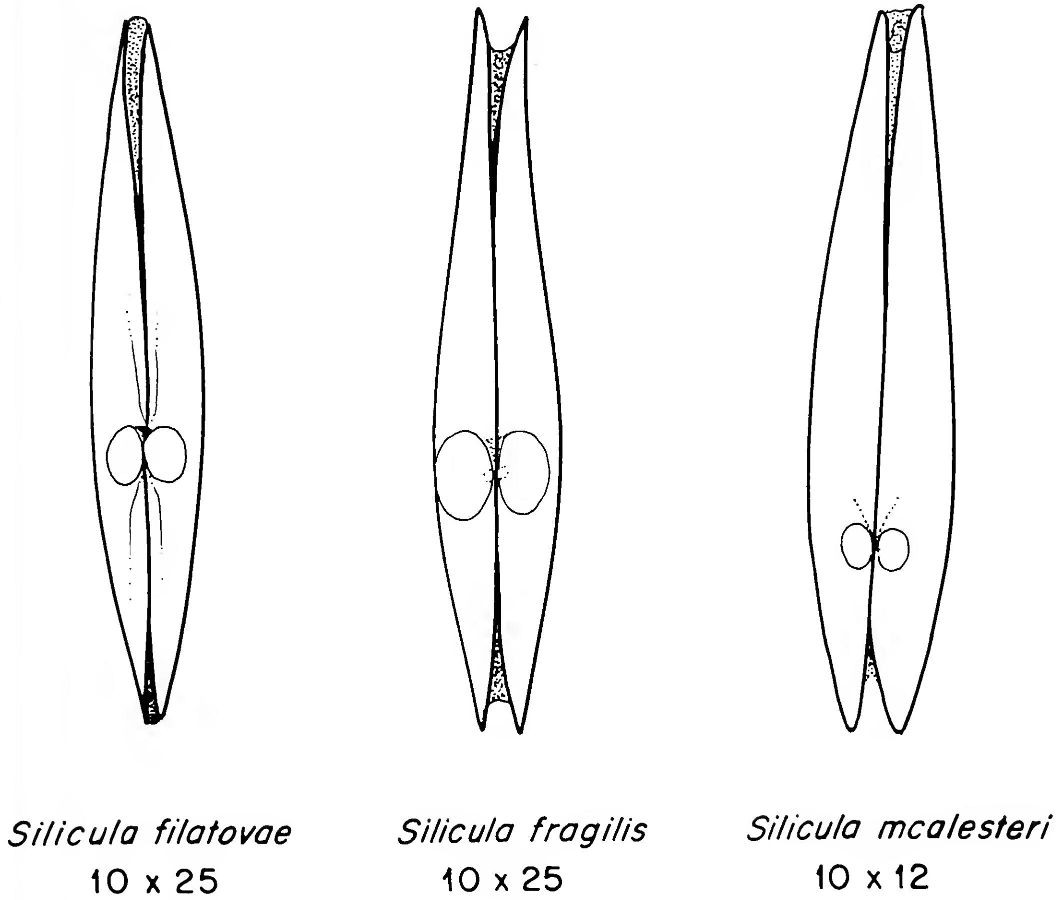

Figure 5. Comparative figures of the dorsal view of specimens of *Silicula filatovae*, *S. fragilis*, and *S. mcalesteri*.

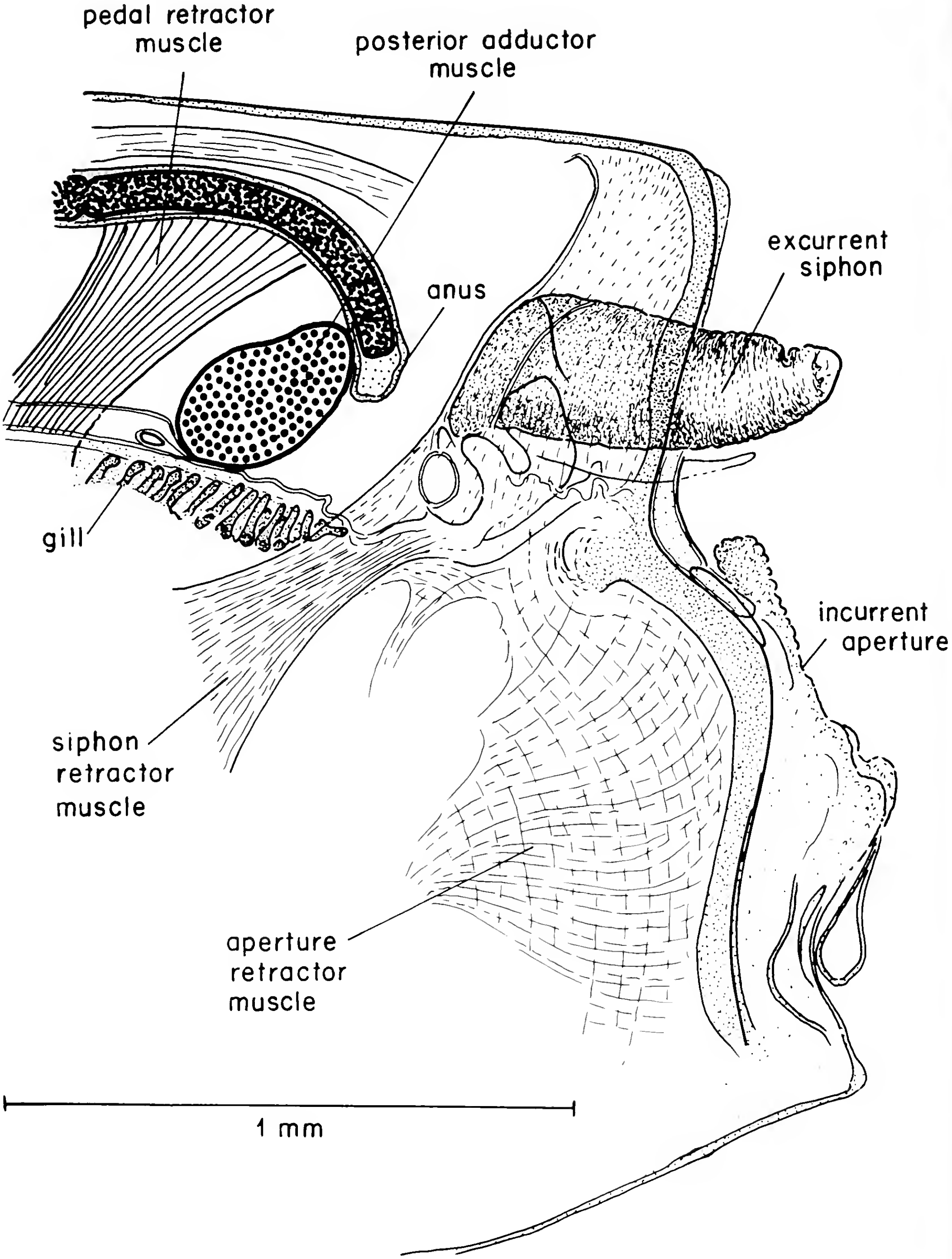

Figure 6. Siphonal region of *Silicula filatovae* as seen from the left side.

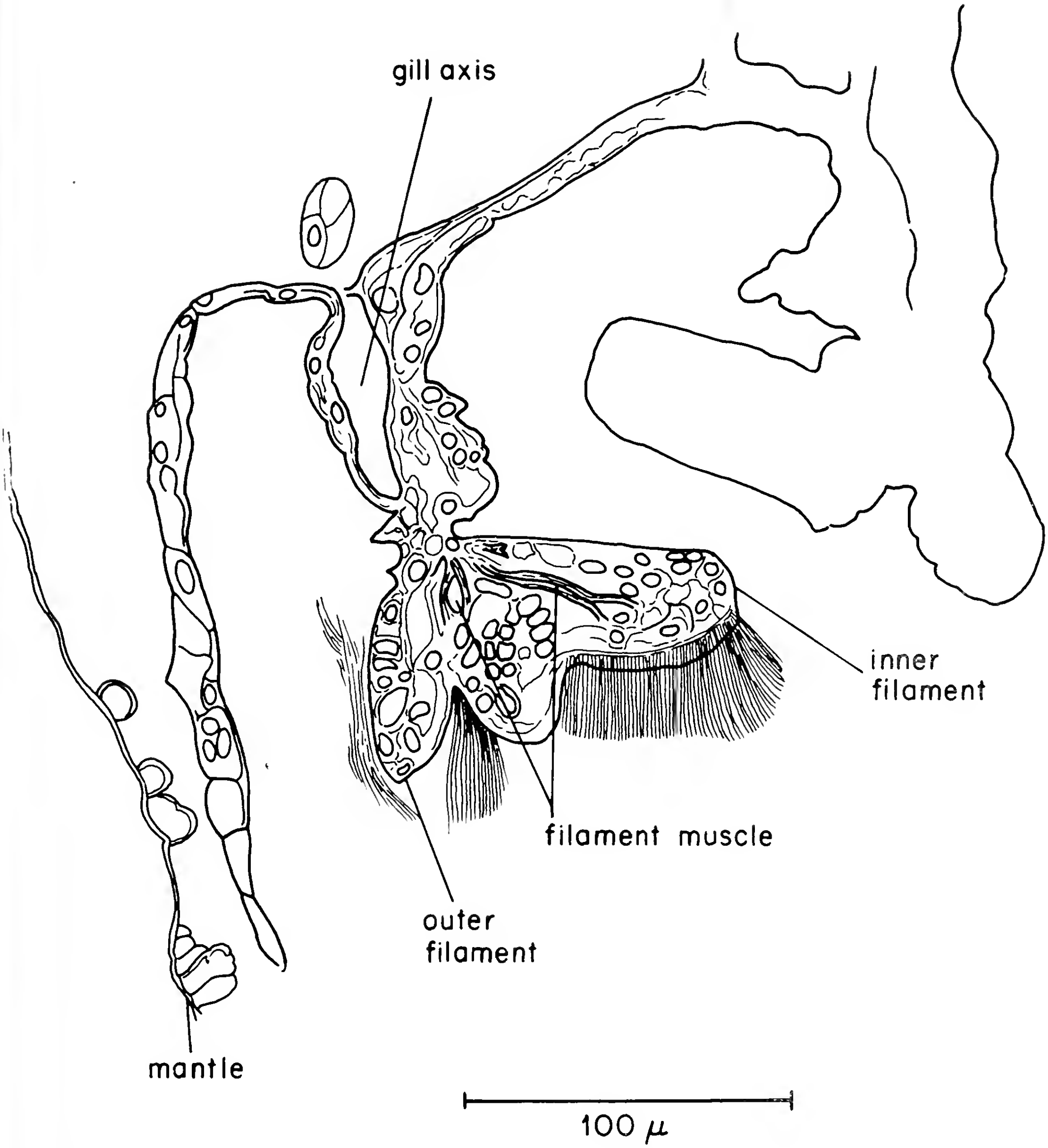

Figure 7. *Silicula filatovae* Allen and Sanders. Transverse section through a gill axis and filament of the left side.

extent as the exhalent siphon; fine retractor muscle fibers extend anteriorly into the mantle tissue behind the inhalent aperture, and numerous epithelial gland cells are present in the mantle epithelium internal to the aperture.

Anterior mantle sense organ located below the level of the anterior adductor muscle and is formed by a moderately elongate, swollen section of the middle sensory fold with an increase in the number of overlying epithelial layers and gland cells.* Single posterior, very fine, attenuate tentacle on

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* The detailed consideration of the histology of the anterior sense organ will be deferred to a later paper.

the right side, its point of origin between the base of the siphon and the dorsal limit of the inhalent aperture. Adductor muscles equal in size, both elongate although the anterior muscle is more rounded than the posterior, the long axes approximate to the anteroposterior axis of the body, "quick and catch" sections distinct.

Gill axis horizontal and parallel to anteroposterior axis of shell and extends from the ventral side of the exhalent siphon to a position one-third the distance across the body; axis attached along its whole length to the body wall and, posterior to the body, it is also attached to the mantle where there is no free posterior process as in the Pristiglomidae (Sanders and Allen, 1973); gill filaments 12–44, the number depending on the size of the animal, set alternately on either side of the axis as in *Nuculana* (Yonge, 1939); gill filaments short, the outer series half the length of the inner (Fig. 7); shorter, outer filaments make ciliary junctions with the mantle whereas the inner filaments, behind the foot, are joined by tissue adhesion. Thus, the gills separate a hypobranchial cavity from the rest of the mantle cavity. Frontal and laterofrontal cilia exceptionally long and dense, longer than the filament is deep (oral-aboral dimension); abfrontal cilia very sparse. Suspensory part of the gill axis is without muscle fibers; however, two or three bundles are present in the gill filament. The latter muscles radiate out from the dorsal side of the filament close to the axis in a fashion similar to those in other protobranchs, but are not so well defined (Atkins, 1936; Yonge, 1939).

Palps and palp proboscides relatively narrow and very elongate, even in the contracted state; palp ridges vary in number from 24–30 and, in the contracted state, the most posterior ridges fan out so that the proximal ridge lies parallel to gill axis. Mouth *not* adjacent to the anterior adductor muscle but posterior to and far removed from it (Figs. 8, 9), and thus the palp also is posterior in position within the mantle cavity.

Body and foot together take up much of the shell's space; foot deeply cleft in the sagittal plane, the peripheral papillae of the sole numerous and varying in size. "Byssal" gland* very large with a conspicuous spherical cavity which is, typically, filled with a hyaline substance, the cavity is partially divided in the sagittal plane by a tongue of tissue. Foot greatly extended posteriorly but lacking the large hooked heel found in the Pristiglomidae (Sanders and Allen, 1973). Body axis curved anteriorly through 90° so that the foot is extended anteriorly. Pedal retractors, particularly the posterior, very powerful and consist of 1 posterior and 3 anterior pairs.

The course of the gut follows the basic pattern of the Protobranchia; thus, the oesophagus, somewhat displaced to the right, leads dorsally and posteriorly to a large stomach and the combined style sac and midgut; from the latter, the hindgut makes a single loop to the right side before passing dorsally and posteriorly over the posterior adductor muscle to the anus. Stomach simple, very large, occupying much of the available dorsal body space with a broad, nonridged sorting area, dorsal hood, and an extensive chitinous lining over much of dorsal side. Digestive gland with 3 ducts (2 left and 1 right). Long axis of stomach and style sac anteroposterior. Hindgut elongate, proximally penetrating deep into the foot where it curves posterior to and then ventral to the pedal ganglion (Fig. 8) before turning dorsally alongside the proximal section and then passing to the right side of the body. Before it turns to the right there is a characteristic U-shaped bend posterior to the style sac. The loop on the right side passes forward to the posterior edge of the anterior adductor and then turns posteriorly and middorsally to the anus, thus outlining the digestive gland

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* The form and function of the protobranch "byssal" gland will be discussed in a later paper.

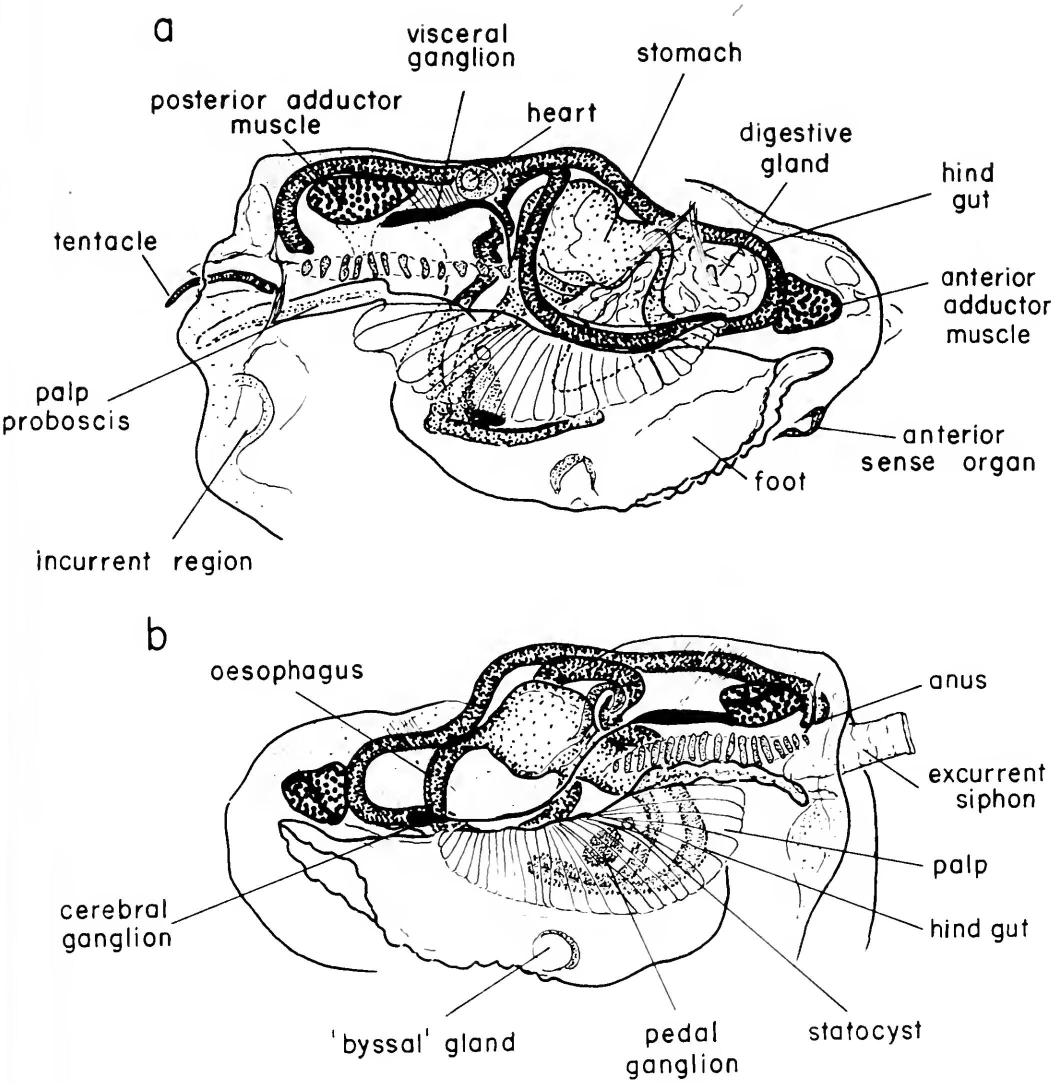

Figure 8. *Silicula filatovae* Allen and Sanders. a) Right and b) left lateral, semidiagrammatic views of the body and mantle organs.

and stomach. Lumen of hindgut relatively large, being 0.6 mm diameter in a specimen 4.0 mm total length.

Sexes separate; immature gonads lie ventral to the digestive gland and with increasing maturity extend dorsally to cover the sides of the visceral mass. Main part of the kidney, because of the anterior position of the posterior adductor muscle, compressed anteroposteriorly between well-developed posterior pedal retractors and the posterior adductor. In compensation there is an anterior extension of the kidney into the posterior part of the body cavity. Nervous system characterized by huge paired pedal ganglia each with an associated statocyst. Visceral ganglia cylindrical, elongate and, like the cerebral ganglia, relatively small.

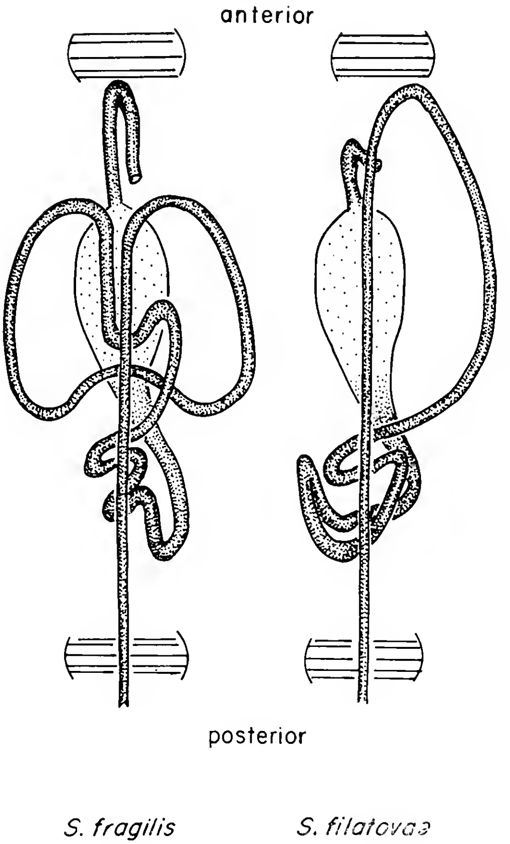

Figure 9. Diagrammatic comparison of the guts of *Silicula fragilis* and *S. filatovae* as seen from the dorsal side.

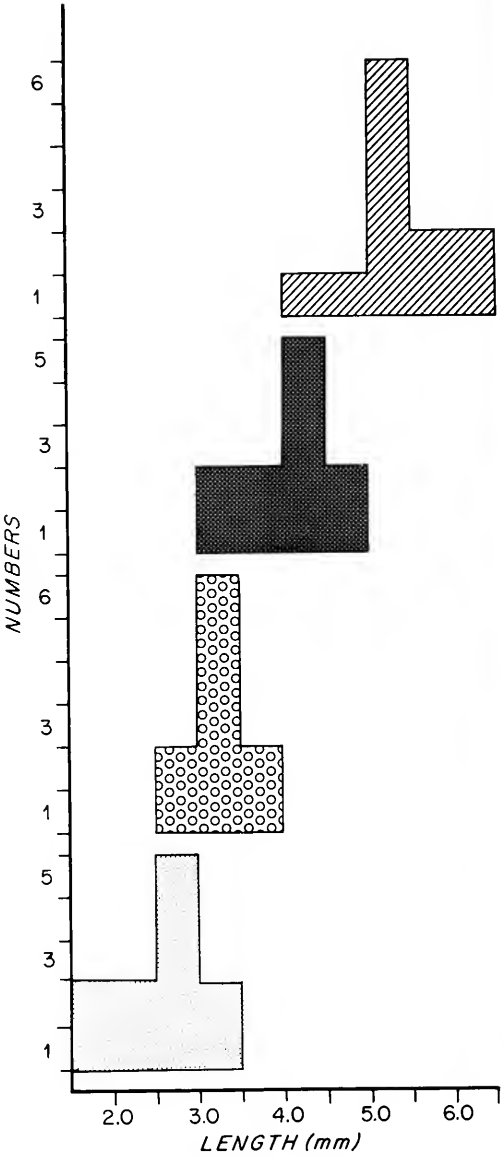

Figure 10. Size/frequency distribution of specimens of *Silicula filatovae* collected from Station 85, sorted according to sex and gonadial development.

This species is named for Dr. Z. A. Filatova of the Institute of Oceanology, Academy of Sciences, U.S.S.R., an esteemed friend and colleague, in recognition of her important ecological and malacological contributions to the understanding of the deep-sea benthos.

Because the shell is transparent, we were able to appraise the state of maturity of *S. filatovae* at Station 85. Animals without gonadal development (11) varied in length from 1.89 to 3.40 mm, those with incipient gametogenesis (10) ranged from 2.80 to 3.79 mm, and those with obvious gonad development (23) were 3.40 to 5.20 mm long (Table II and Fig. 10). The larger specimens were all mature, the smaller specimens immature, and both categories overlap, there being an intermediate size group that had incipient gonad development. Our interpretation of these findings is given later (p. 307) in the discussion.

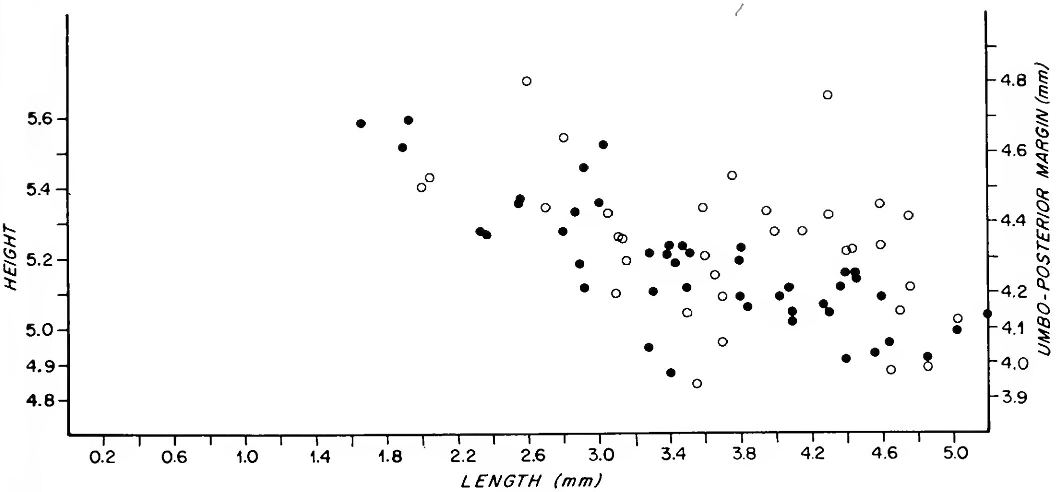

Figure 11. *Silicula filatovae* **Allen and Sanders. Graph showing height/total length (●) and umbo to posterior margin/total length (○) plotted against total length.**

TABLE II. INDEX OF BODY SPACE OCCUPIED BY THE GONAD FOR 192 INDIVIDUALS BELONGING TO SPECIES OF *Silicula* AND *Lametila*. NOTE ALL SPECIES NEED NOT HAVE THE SAME PROPORTION OF BODY SPACE OCCUPIED WHEN SEXUALLY MATURE.

Gonad stages	0	1	2	3	4	5	6	7	8	spent	Station No.
S. mcalesteri	1	1	2	4	9	3	10	9	8	—	280
S. fragilis	11	6	2	—	—	—	—	—	—	—	85
	26	3	3	4	2	3	1	2	—	—	126
S. filatovae	21	4	7	8	3	1	—	—	—	—	85
L. abyssorum	4	10	3	10	6	2	1	1	—	1	64

Silicula fragilis Jeffreys, 1897

Figures 1, 5, 12–17

Silicula fragilis Jeffreys, 1879: 574 (Type locality: PORCUPINE Expedition, 1869, Station 16; type specimen: U.S. National Museum no. 197405).

Previous records. Depth range *in* Clarke (1962) = 1493–2223 m. West Europe Basin, 2 stations (1493 and 2223 m).

Present records. Depth range = 1922–4402: Table III.

A few supplemental remarks can be added to the original description by Jeffreys (1879) of *Silicula fragilis,* for the positioning of the teeth is not elaborated in detail in the text and the illustration shows some artistic license. We have examined the type specimen carefully and find a number of major differences. The posterior teeth are much shorter than figured, they do not extend upwards to reach the dorsal margin but, instead, are straight and relatively parallel to it. The distal tooth does not remotely approach the posterior margin of the shell. Similarly, the anterior teeth are shorter, they do not reach the anterior shell margin and, rather than being somewhat concave as figured, they are slightly convex. In each of these respects, our material agrees with the holotype (Figs. 1, 12).

The basic detail of the mantle, mantle fusion, tentacle, anterior sense organ and mantle glands is similar to that of *S. filatovae* (Fig. 13). The adductor muscles are relatively smaller than in *S. filatovae* with the anterior more circular in outline, and

TABLE III. RECORDS FOR *Silicula fragilis* JEFFREYS.

Cruise	No.	Sta.	Depth (m)	Speci-mens	Latitude	Longitude	Gear	Date
				NORTH AMERICA BASIN				
Atlantis II	12	64	2891	1	38°46.0′N	70°06.0′W	ES	21.8.64
Atlantis II	24	126	3806	41	39°37.0′N–39°37.5′N	66°47.0′W–66°44.0′W	ES	24.8.66
Chain	50	85	3834	39	37°59.2′N	69°26.2′W	ES	5.7.65
				WEST EUROPE BASIN				
Sarsia		S-65	1922	2	46°15.0′N	04°50.0′W	ES	25.7.67
				ARGENTINE BASIN				
Atlantis II	60	259a	3305–3317	5	37°13.3′S	52°45.0′W	ES	26.3.71
Atlantis II	60	242	4382–4402	1	38°16.9′S	51°56.1′W	ES	13.3.71

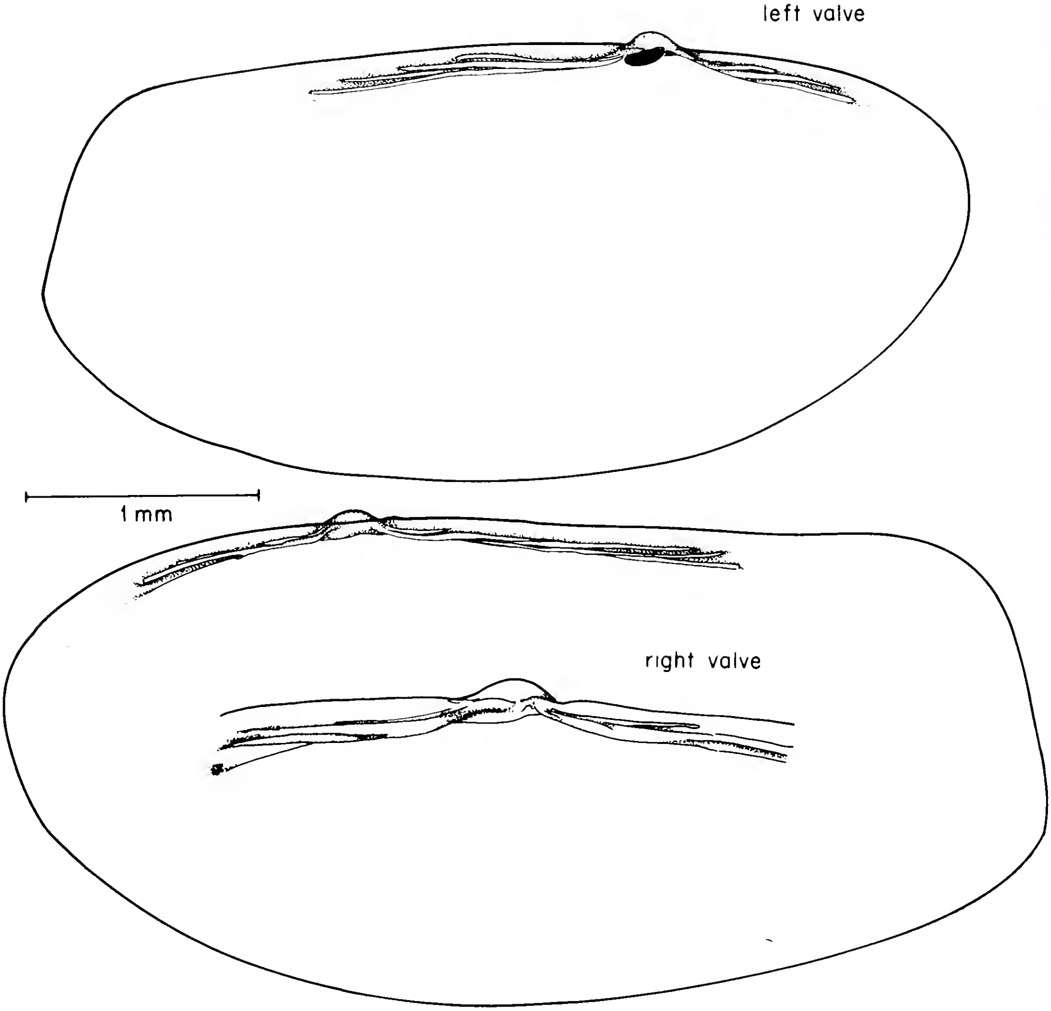

Figure 12. *Silicula fragilis* Jeffreys. Internal views of left and right valves, with enlarged hinge detail of right valve.

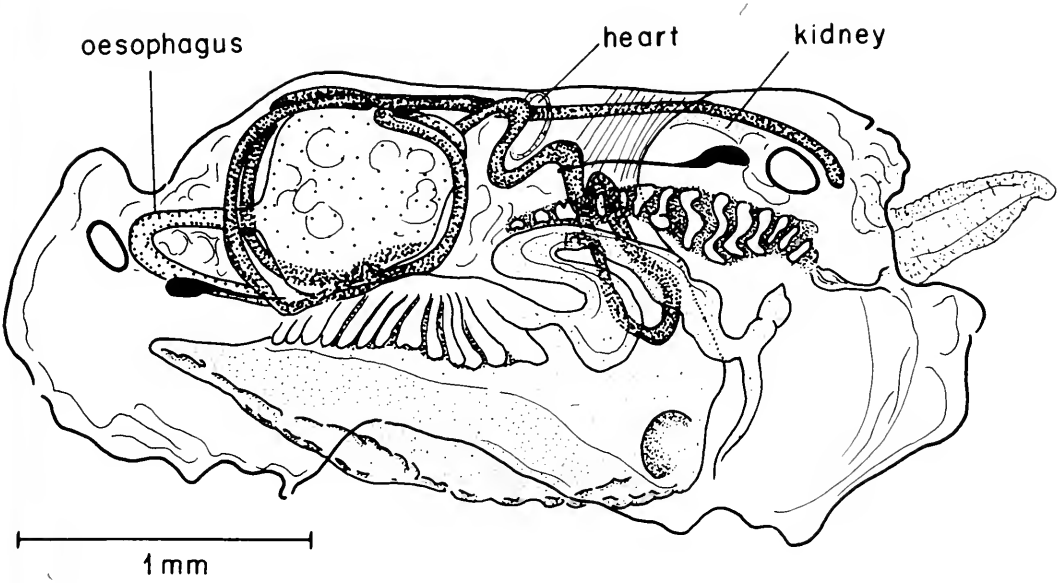

Figure 13. *Silicula fragilis* Jeffreys. Left lateral, semidiagrammatic view of the body and mantle organs.

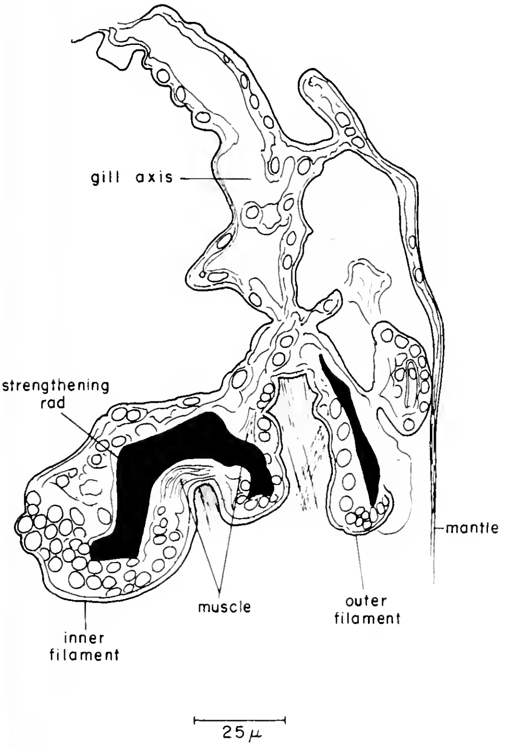

Figure 14. *Silicula fragilis* Jeffreys. Transverse section through a gill axis and filament of the right side.

the posterior set well forward within the mantle cavity. The gills are also similar in position and form; however, there are only 11–13 gill filaments and the gill does not extend as far across the body as it does in *S. filatovae*. The suspensory membrane is not muscular but there are one or two radiating muscles within the gill filament. The skeletal elements of the inner filaments are very broad (Fig. 14). The palps and palp proboscides are exceptionally attenuated, being much narrower than those of *S. filatovae* and with 14–18 palp ridges. Attenuation is accentuated because the mouth is somewhat closer to the anterior adductor muscle than it is in *S. filatovae* and because of the greater posterior extension of the mantle cavity.

In the form and arrangement of the gut *S. fragilis* differs markedly from *S. filatovae* as well as from *S. rouchi* and *S. mcalesteri*. The mouth is closer to the anterior adductor muscle and the oesophagus extends forward as far as the posterior limit of the muscle before it turns dorsally and posteriorly towards the stomach and style sac (Fig. 9). The latter are orientated in an anteroposterior direction. The hindgut is very elongate and loops to the left as well as to the right side of the body. From its junction with the midgut, the hindgut extends posterior to the pedal ganglion, but does not curve forward below the ganglion, instead it turns dorsally behind the style sac where it forms two U-bends before passing forward to the *right* of the dorsal midline. Opposite the point where the oesophagus joins the stomach, the hindgut turns to the left side of the body and forms a single loop before returning to the right-hand side dorsal to the stomach. A single loop is formed on the right side and this leads to the final middorsal posterior section which ends at the anus. The right and left loops outline the periphery of the stomach and style sac. Note, in the case of both loops, the material in the gut is passing counter-clockwise when viewed from the side. The loops do *not* extend as far as the anterior adductor muscle and the diameter of the lumen is relatively smaller than in *S. filatovae*. The pedal ganglion is huge. The "byssal" gland is relatively smaller than that in *S. filatovae*.

Remarks. Silicula fragilis can be separated readily from *S. filatovae* by the elongate rectangular shell shape (not elongate oval); the anterior position of the umbo; the straight dorsal margin behind the umbo which is not gently and smoothly convex; the broad and obliquely truncate posterior margin that slants posteriorly and ventrally rather than being smoothly rounded; the shorter, less robust teeth that parallel the dorsal margin rather than diverge from it; the presence of five rather than four teeth in the posterior series and four rather than three in the anterior series; the shell is even more fragile than in *S. filatovae;* the gut loops on both sides of the body, rather than being confined to the right side; the posterior adductor muscle and pallial line are well anterior to the posterior shell margin.

Beside the suite of familial features, *S. fragilis* shares with *S. filatovae* a shell that gapes both anteriorly and posteriorly and valves that are separated along part of the dorsal margin (Fig. 5).

Within the size range of 1.25 mm–5.09 mm, the height-to-length ratio changes with increasing length from .634 to .436 (Figs. 15, 16). The thickness-to-length ratio is only about .16, reflecting the very flattened form of *S. fragilis* (Fig. 15). The prodissoconch appears to be about 200 μ long, suggesting a lecithotrophic mode of development. Some gonad development was observed in specimens as small as 2.09 mm but the appraisal of gametogenesis is rendered difficult because the shells of many of our specimens are opaque. At Station 126, 17 of the 36 specimens available were opaque. Of the remaining 19 individuals, nine showed some development of the gonad and ten did not (Table 1 and Fig. 17). The latter group varied in length from 1.25 mm–3.03 mm while the former ranged from 2.09 mm–5.09 mm. At Station 85 where 20 specimens were available for analysis, one was opaque, ten varying in length from 2.47 mm–4.17 mm showed no gametogenesis, and eight, with a range in sizes from 2.90 mm–4.60 mm, were mature or maturing (Table II and Fig. 17). Our interpretation of these data is given in the discussion section (p. 307).

Silicula mcalesteri new species

Figures 5, 18, 20–22

Type locality: ATLANTIS II, Cruise 60, Station 280, in 275–305 m. Holotype: MCZ 271974. Depth range = 275–305 m. **Records:** Table IV.

The shell, elongate in outline with the posterior margin considerably extended, smooth, glossy, iridescent, straw-yellow, semitransparent and somewhat laterally compressed with fine concentric lines; dorsal margin long; umbo small, barely rising above the dorsal margin of the shell and placed far forward at a position about 25 to 29 percent of the distance between anterior and posterior edges; shell highest in the region of the umbo and gradually and continuously tapering posteriorly (Fig. 18);

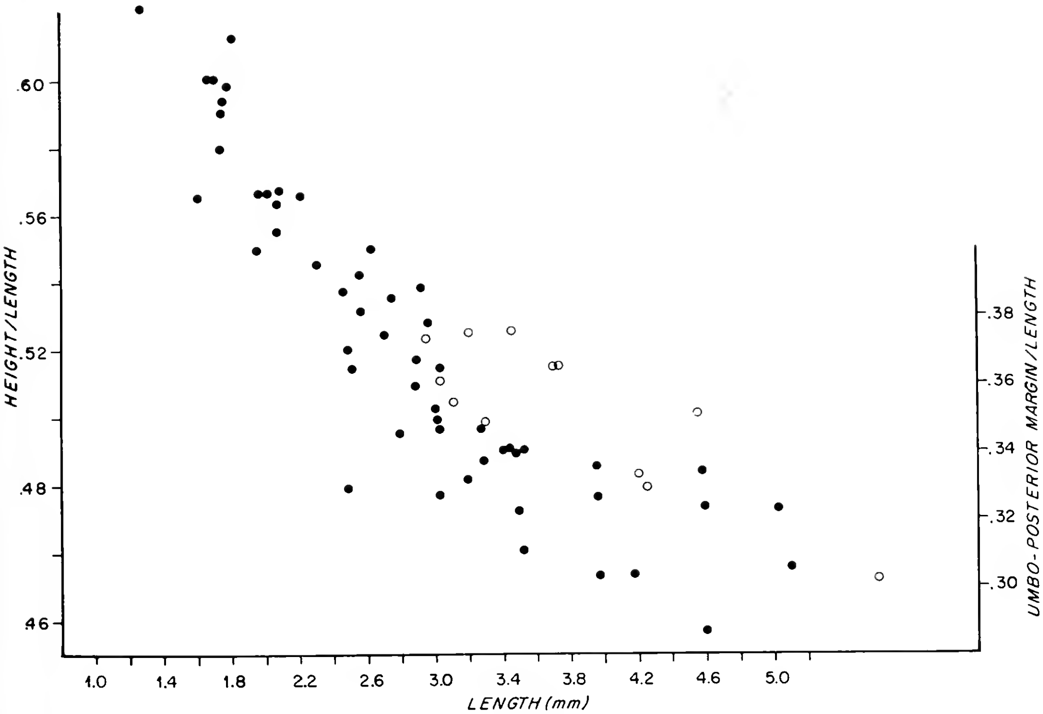

Figure 15. *Silicula fragilis* Jeffreys. Graph showing height/total length (●) and umbo to posterior margin/total length (○) plotted against total length.

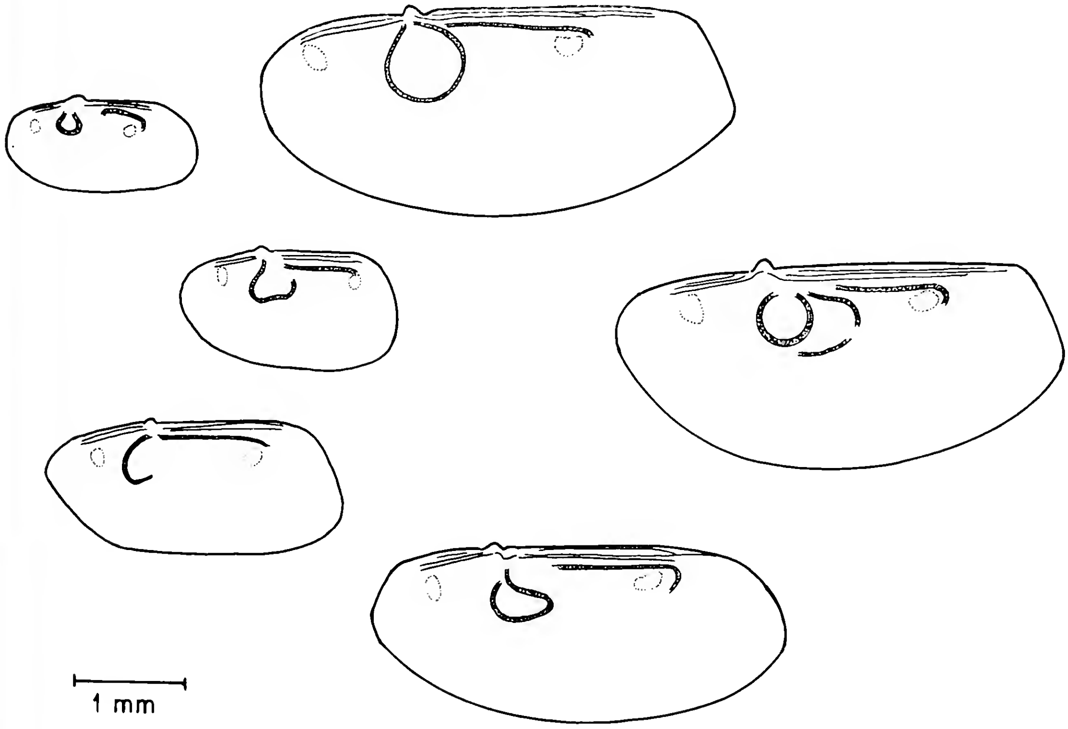

Figure 16. Lateral views of a series of specimens of *Silicula fragilis* to show changes in shape with increasing size.

TABLE IV. RECORDS FOR *Silicula mcalesteri* NEW SPECIES.

Cruise	No.	Sta.	Depth (m)	Specimens	Latitude	Longitude	Gear	Date
				ARGENTINE BASIN				
Atlantis II	60	280	275–305	39	36°18.0′S–36°19.0′S	53°24.5′W	ES	29.3.71

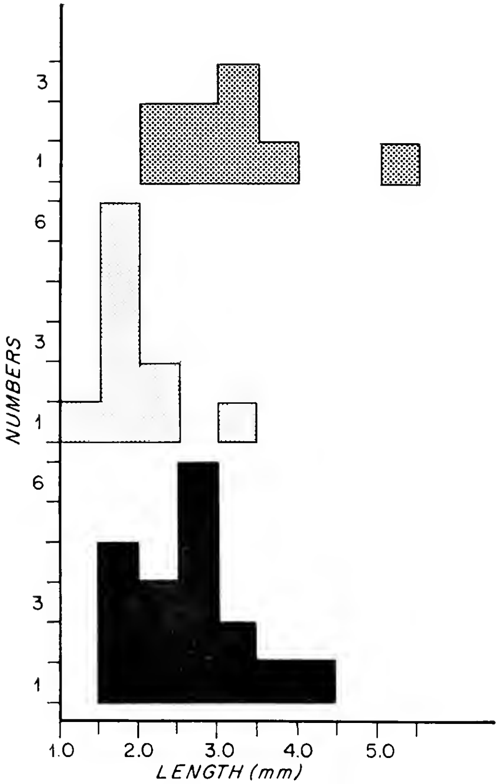

Figure 17. Size/frequency distribution of specimens of *Silicula fragilis* collected from Stations 126 and 85 and sorted according to sex and gonodial development.

dorsal margin behind the umbo convex in front of the umbo, slanting abruptly downwards to the anterior limit of the shell, such that the dorsal and ventral margins merge in a smooth curve; shell margin, immediately anterior and posterior to the umbo forming small concavities; posterior margin narrowly truncate; anterior margin sharply and evenly rounded; ventral margin long and gently curving; shell gaping anteriorly and posteriorly, the valves separated along part of the dorsal margin (Figs. 5, 18).

Hinge plate long, thin, and weak; posterior hinge plate long, straight, and paralleling the dorsal shell margin; anterior hinge plate short, straight and angled ventro-anteriorly. Opisthodetic ligament large, elongate, originating below the umbo and directed transversely in a ventroposterior direction. Posterior hinge plate with 6–8 very narrow, elongate teeth, only the largest specimens having 7 and 8 teeth; the most proximal tooth small, being readily overlooked, and rising from the thickened hinge plate immediately behind the umbo and above the ligament; the second tooth is also small, but three times the length of the first, and positioned on the hinge plate immediately below and behind the first, above the distal end of the ligament, and slanting posteriorly and dorsally away from the hinge line towards the dorsal margin; remaining teeth considerably longer, and continuously overlapping, on hinge line and, excepting the distal tooth, directed slightly anteriorly towards the dorsal shell margin; the terminal tooth forms the distal hinge line; in specimens with 6 teeth, 1 to 5 are sequentially more elongate, teeth 4 and 5 extending more than half the length of the posterior hinge plate, and tooth 6 half the length of tooth 5; anterior hinge plate with 5 overlapping teeth which arise from the anterior hinge line and are considerably shorter than all but the two most proximal of the posterior hinge series; teeth 1–4 diverge from the hinge line, tooth 5 forms the distal hinge line, the most proximal tooth is smallest and slightly concave; teeth 3 and 4 are longest and slightly convex, pallial line present and with a pronounced embayment below the posterior adductor muscle scar.

The 49 specimens of *S. mcalesteri* from Station 280 varied from 3.55 mm–11.38 mm

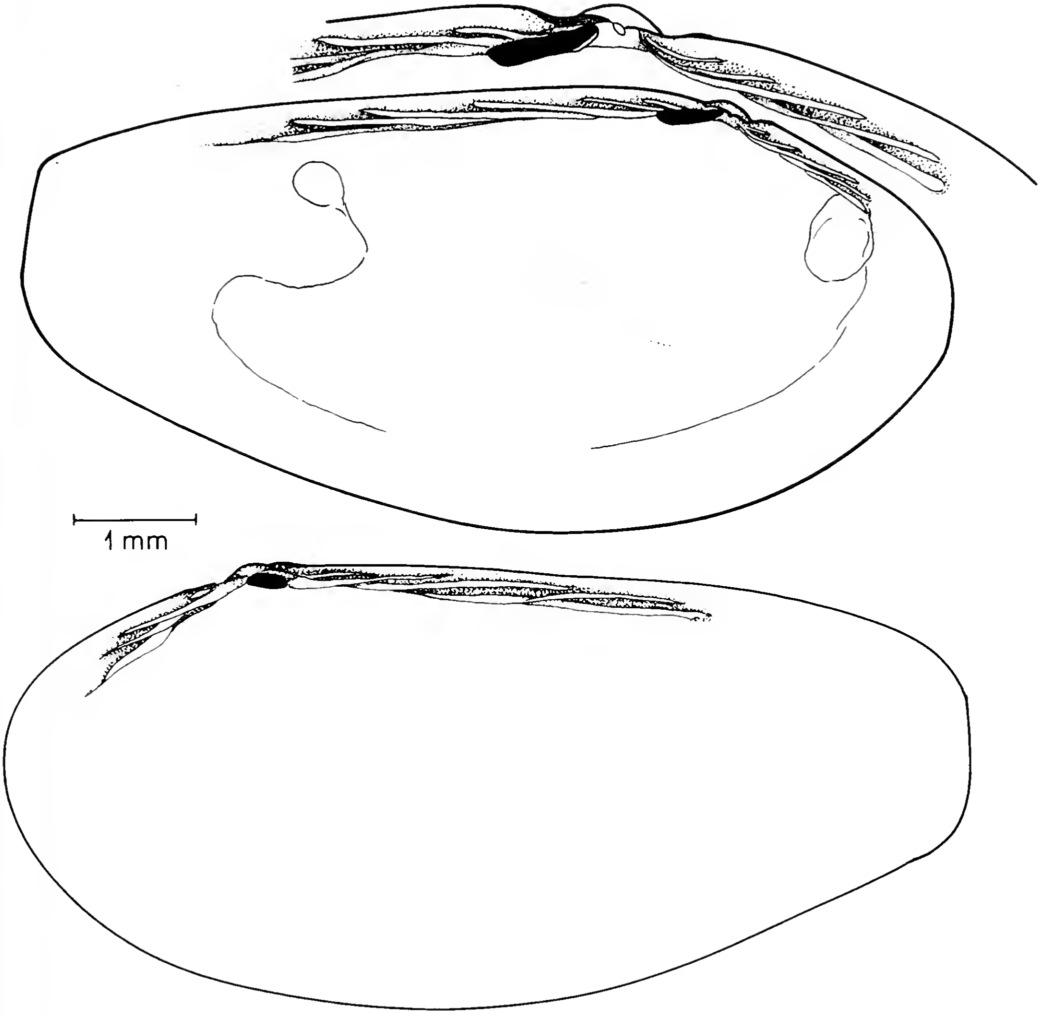

Figure 18. *Silicula mcalesteri* Allen and Sanders. Internal views of the left and right valves, with enlarged hinge detail of the left valve.

in length. Within the length range of 4.0 mm–11.38 mm, the height-to-length ratio remains relatively constant, 0.43–0.48. The two smallest specimens, less than 4 mm, have a height-to-length ratio of 0.56 and 0.52 (Figs. 19, 20). With a width-to-length ratio of 0.27, S. *mcalesteri* does not have the extreme flattened form of either S. *filatovae* (0.17) or S. *fragilis* (0.16).

S. *mcalesteri* exhibits the greatest posterior elongation of the mantle/shell of the species described. Exhalent siphon very well developed with a well-defined siphonal embayment; siphonal retractor muscles form 5–6 bundles. Similarly, the muscular inner fold of the mantle edge in the region of the inhalent aperture is particularly well developed. Anterior sense organ small but well defined. Both adductor muscles small, but the posterior muscle is somewhat smaller than the anterior, and, as in the other species, is set far forward in mantle cavity, where it still stands opposite the end of the hinge plate.

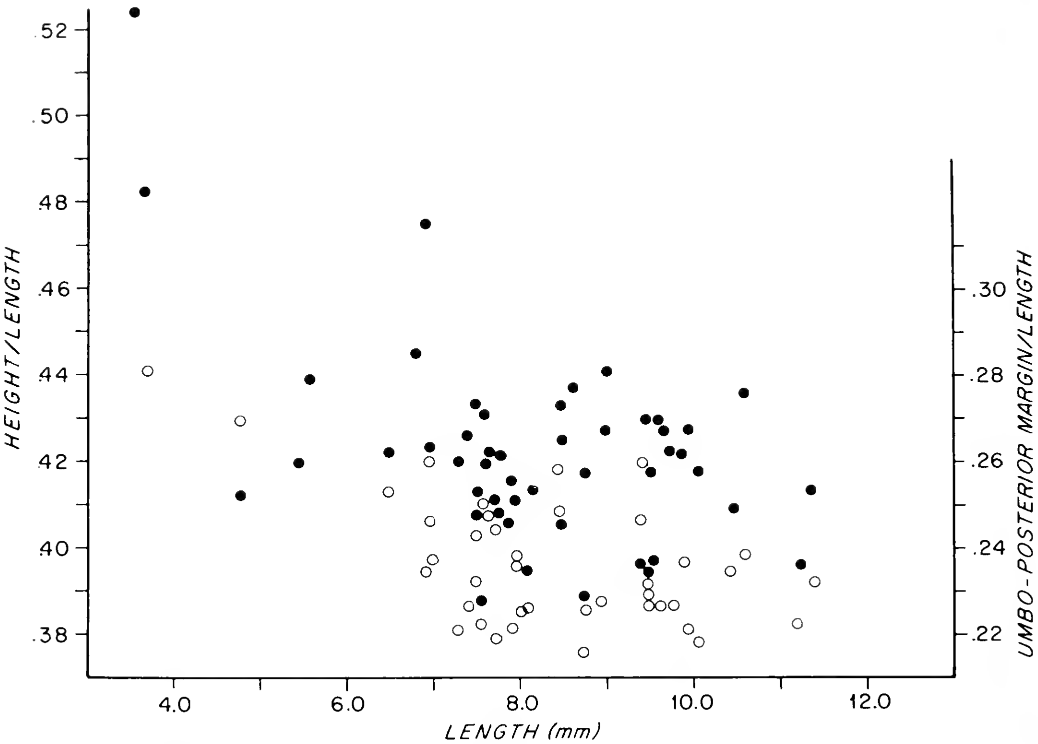

Figure 19. *S. mcalesteri* Allen and Sanders. Graph showing height/total length (●) and umbo to posterior margin/ total length (○) plotted against total length.

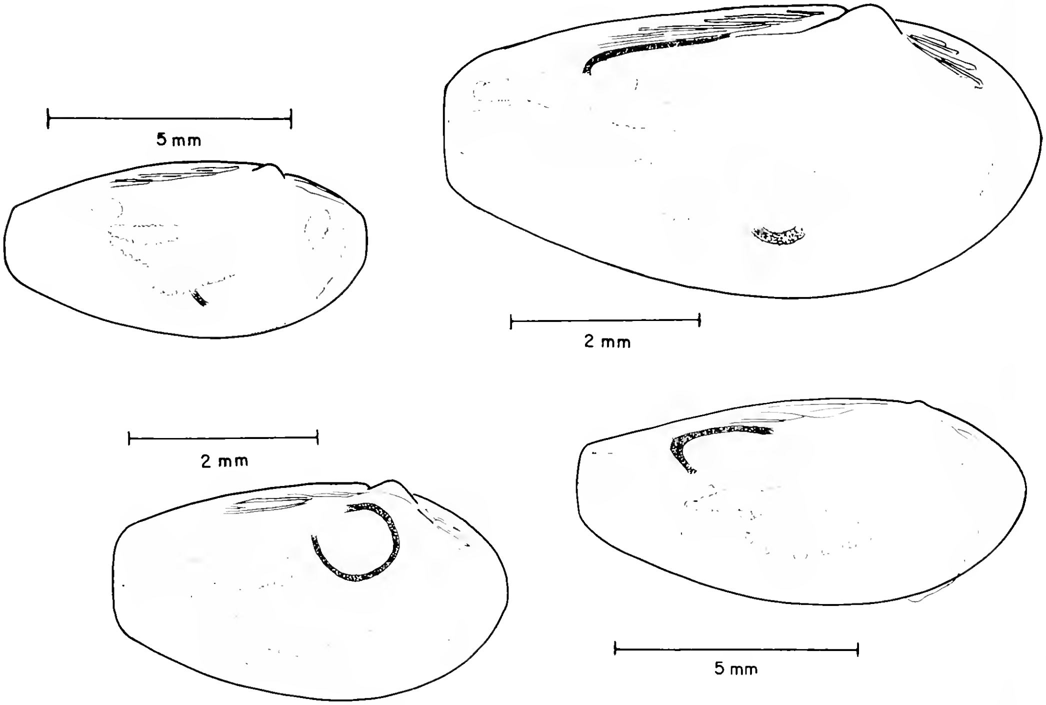

Figure 20. Lateral views of a series of specimens of *S. mcalesteri* to show changes in shape with increasing size.

Gills well developed with 27–35 plates to each side of the axis, and extend along the body to a position opposite the posterior limit of the stomach; no muscles in the suspensory part of the axis and in sectioned specimens the axial blood space is exceptionally large (Fig. 22). Palps, bearing about 35 ridges, centrally located in the mantle cavity and lie relatively close to the ventral edge of the shell. Body and foot large, the dorsoventral axis turned through 90°. "Byssal" gland moderately large and the fringing papillae of the foot variable but relatively small in size.

Mouth set far back from the anterior adductor muscle; the oesophagus extends diagonally anteriorly and dorsally towards the anterior adductor; however, unlike *S. fragilis,* it turns short of the posterior edge of the muscle towards the stomach. Stomach large, but proportionately smaller than in other species of *Silicula.* Combined style sac and midgut large and elongate, the long axis oriented in a more dorsoventral direction than in the previous two species. Hindgut curving downwards anteriorly towards the pedal ganglion before passing dorsally to the right side of the body where it forms a single, small loop. There is no U-bend in the hindgut behind the style sac. Both cerebral and visceral ganglia small, elongate and cylindrical in shape. Kidney more extensive than in *S. filatovae* and *S. fragilis,* invading the body behind the stomach (Fig. 21).

Remarks. Silicula mcalesteri is possibly conspecific with *Silicula patagonica* (Dall). We have examined the type specimen of *S. patagonica* (U.S. Nat. Mus. No. 96914; Fig. 23) and the single valve lacks the umbonal region together with the proximal parts of the anterior and posterior hinge plates. In addition, the posterior shell margin is badly eroded, and the anterior shell

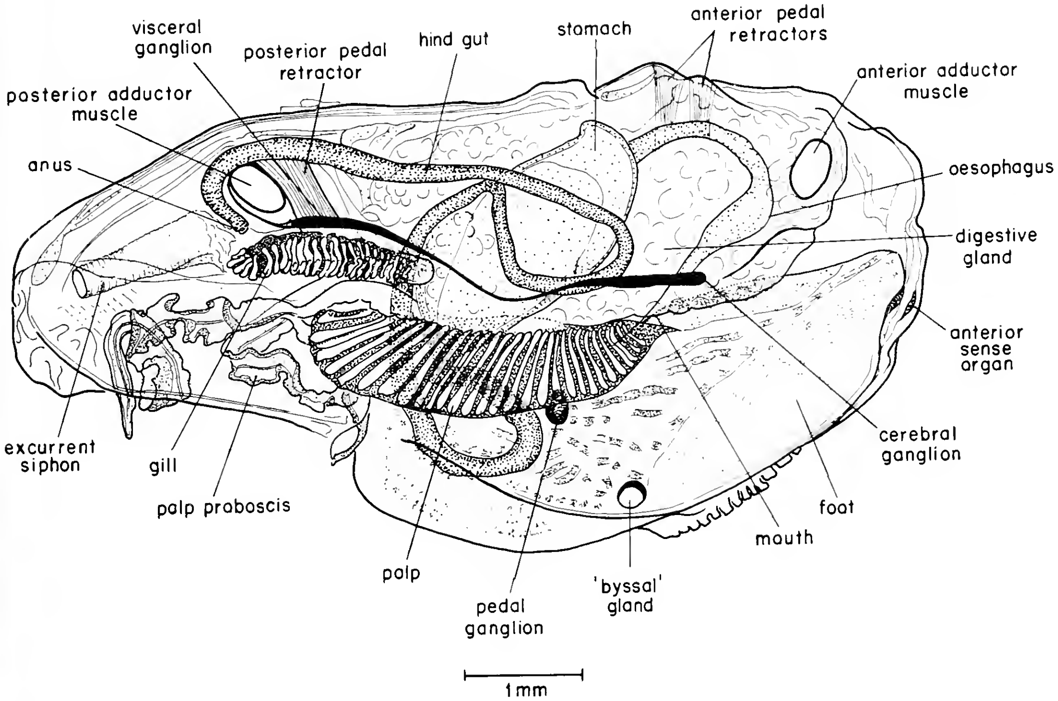

Figure 21. *Silicula mcalesteri* Allen and Sanders. Right lateral, semidiagrammatic view of the body and mantle organs.

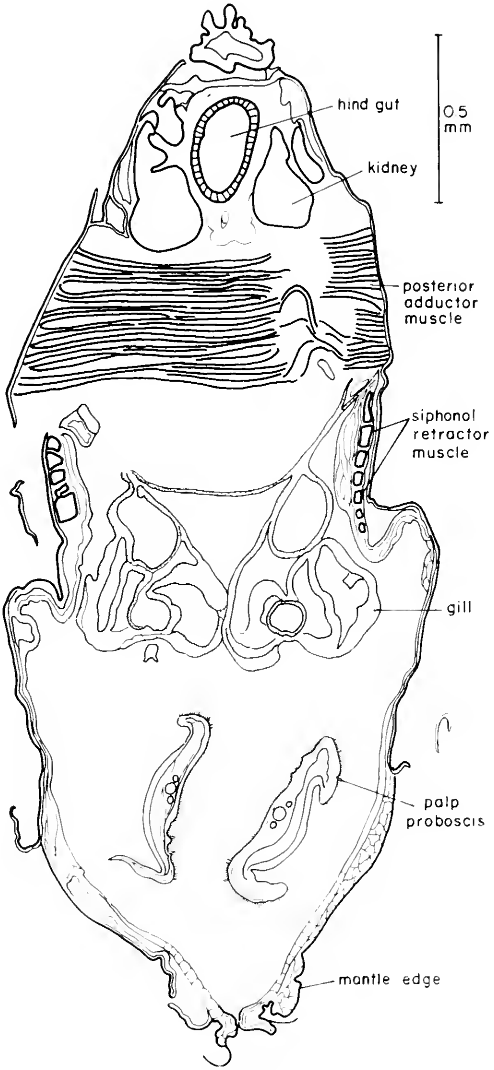

Figure 22. *Silicula mcalesteri* Allen and Sanders. Transverse section through posterior adductor muscle, gills and palp proboscides.

margin is not intact. Though the type is reminiscent of *S. mcalesteri* the teeth appear thicker and, because *S. patagonica* is from the eastern Pacific, we decided to consider these as separate entities.

The present species is named in honour of Dr. A. Lee McAlester, Department of Geology and Geophysics, Yale University, for his keen and perceptive contributions to the evolutionary history of the protobranch bivalves.

The shell of this species is sufficiently transparent for us to appraise the state of maturity and sex of the animals in our sample. Only the two specimens smaller than 4 mm were not mature; one was immature and the other showed incipient gonad development. The sexes are separate and present in our sample in essentially equal numbers, 23 females and 24 males. In the region of broad overlap, 6.5 mm–10.0 mm, males and females were equally abundant (Fig. 24). The three mature specimens smaller than 6.5 mm were females and each of the five individuals larger than 10.0 mm were males, suggesting a possible size differential in the sexes. The mature egg is small (90 μ) for a protobranch and according to the criteria of Ockelmann (1965) this size would make it barely lecithotrophic. We estimate that about 1,000 ripe eggs were present in the one specimen examined.

Silicula rouchi Lamy, 1910

Figures 25–27

Silicula rouchi Lamy, 1910: 394 (Type locality: Alexander Island, Antarctica; type specimen: Mus. natl. Hist. nat., Paris); 1911: 30. Hedley, 1916: 18. Soot-Ryen, 1951: 6. Carcelles, 1953: 208. Powell, 1958: 171; 1960: 171. Dell, 1964: 147. Nicol, 1966: 15. Dell, 1969, folio 11.

Although this species is not represented in our collections, we include it since it completes the known species of the genus. Through the kindness of John Taylor we were able to borrow preserved material of *S. rouchi* from the British Museum of Natural History (B.M. No. 196526W) and study the soft-part anatomy.

Concerning the shell, little needs to be added to the descriptive information provided by Lamy (1910), Dell (1964), and Nicol (1966). In shell morphology, tooth structure, and shape, it is more similar to *S. fragilis* than the other species. However, *S. rouchi* differs from *S. fragilis* by having a relatively smaller and more anteriorly placed umbo, an anterior dorsal margin

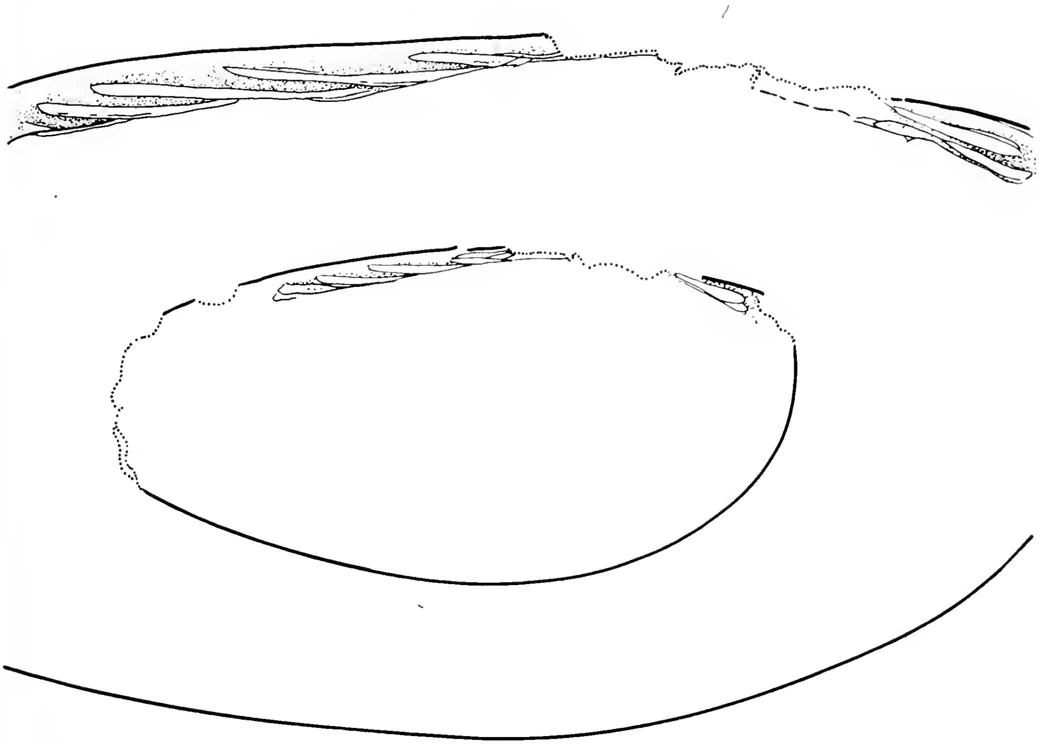

Figure 23. Two lateral views (left valve), one an enlargement of holotype of *Silicula patagonica* Dall. (U.S. Nat. Mus. No. 96914, Station 2783, west coast of Patagonia.)

which initially curves dorsally in front of the umbo rather than being straight, and an anterior hinge that is shorter and more ventrally curved which bears shorter though thicker teeth (Figs. 25, 27).

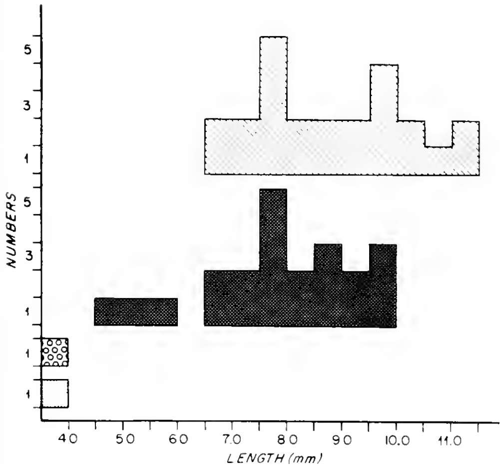

Figure 24. Size/frequency distribution of specimens of *S. mcalesteri* collected from Station 280, and sorted according to sex and gonadial development.

The soft parts are very similar to *S. filatovae*, with differences being a matter of degree. The adductor muscles are relatively large, ovoid, and equal in size. The long axis of the anterior adductor muscle is dorsoventral, that of the posterior approximately anteroposterior. The exhalent siphon is well developed with a slight but noticeable siphonal embayment. The inhalent aperture, as in all species of the genus, is formed by the apposition of the inner muscular mantle layers, but involves *no* fusion. A single tentacle on the right side is inserted between the inhalent aperture and the exhalent siphon. The gill is horizontal with 35–40 gill filaments to each side of the axis of each demibranch, the outer filaments being half the size of the inner. The palps, with approximately 18 ridges, are relatively

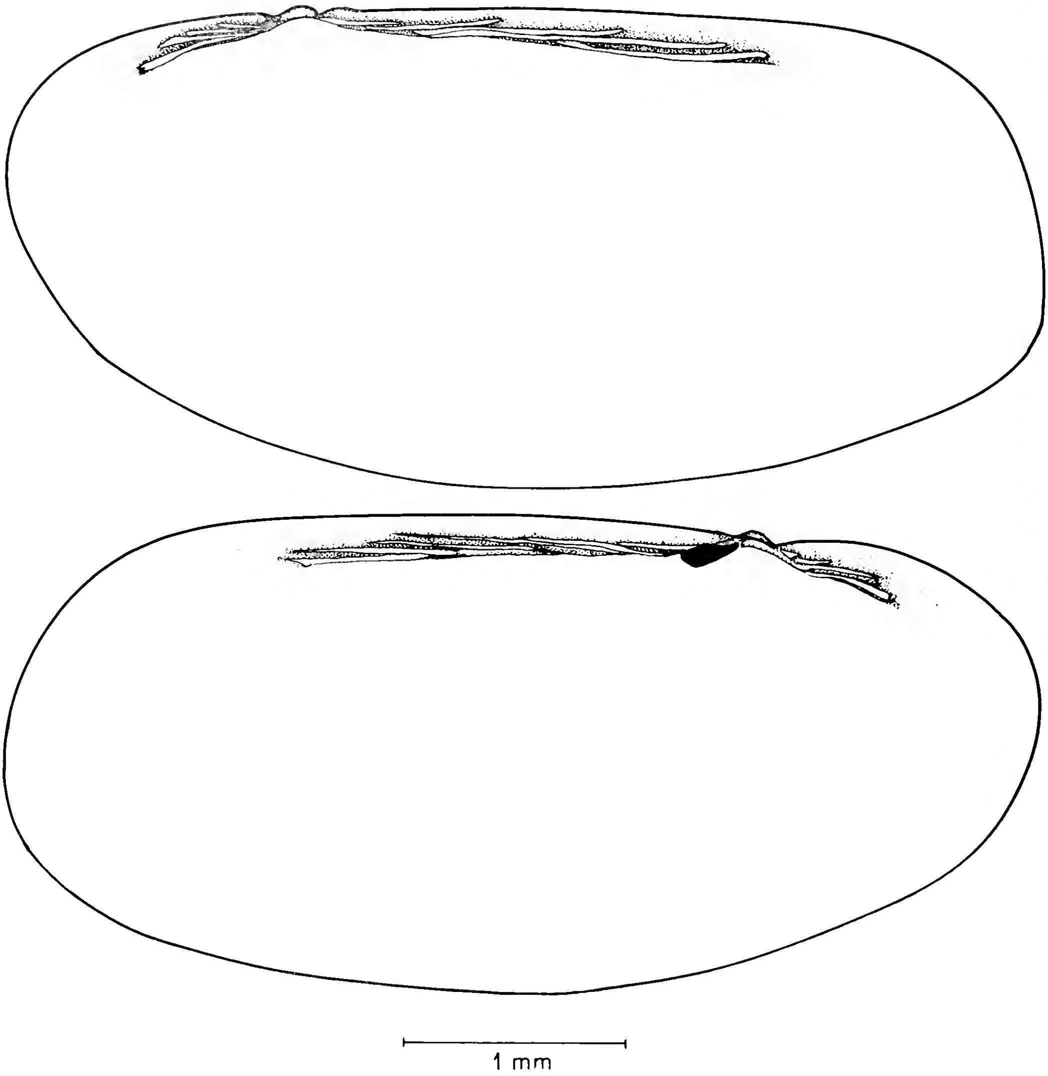

Figure 25. *Silicula rouchi* Lamy. Internal views of left and right valves.

shorter and narrower than those of other species and barely extend across the length of the body. Because the mouth is set so far posterior to the anterior adductor muscle, the palps occupy a central position within the mantle cavity. The palp proboscides are exceptionally long, reflecting the increased posterior extension of the mantle cavity. The foot is relatively small and the body axis is not turned anteriorly to the same extent as in the previous species. However, the foot remains very muscular with powerful anterior and posterior retractor muscles.

The mouth is positioned about one-third the length of the body posterior to the anterior adductor and, as in *S. fragilis,* the course of the oesophagus is forward to the anterior adductor muscle before turning posteriorly towards the stomach. The stomach is not as large as in the other members of the genus, nor does it take up as much

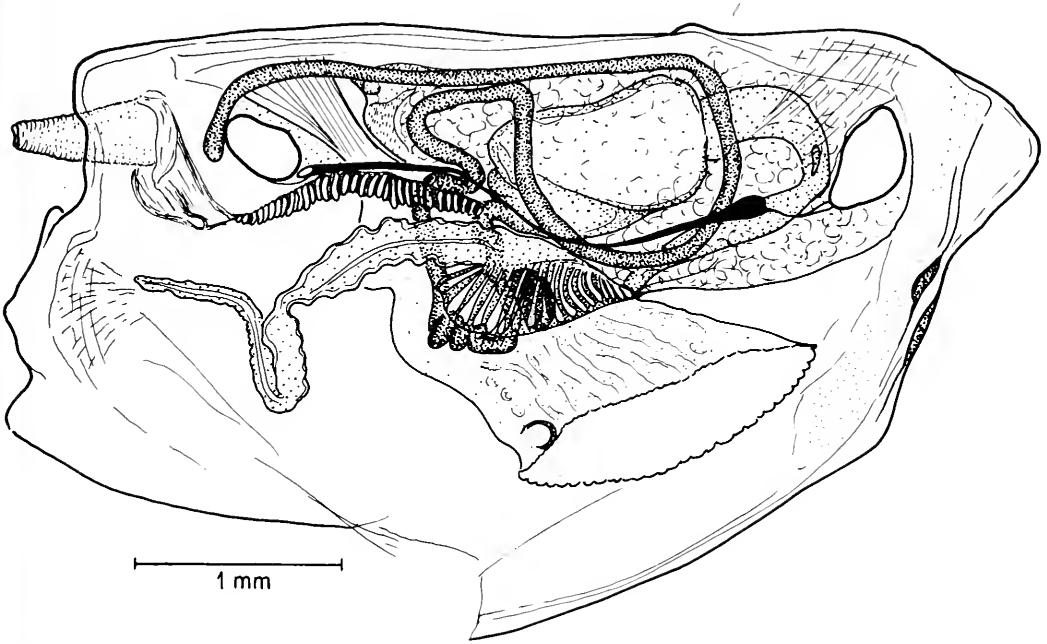

Figure 26. *Silicula rouchi* Lamy. Right lateral, semidiagrammatic view of the body and mantle organs.

of the body space. It has seven or eight broad sorting ridges, and the combined style sac and midgut is relatively short. The hindgut does not penetrate the foot ventral to the pedal ganglion; however, there is one U-bend posterior to the style sac and before the single loop to the right side of the body. The loop does *not* extend as far as the anterior adductor. The pedal ganglion is very large and the visceral ganglia are elongate and cylindrical, while the cerebral ganglia are set forward of the mouth close to the oesophagus between the mouth and the anterior adductor muscle (Fig. 26).

Family LAMETILIDAE new family

Nuculanacid protobranchs with smooth, somewhat tumid shells and rounded in outline; hinge weak, always with elongate teeth which are never more than two in number on either the anterior or the posterior hinge plate, taxodont teeth present or absent; umbo low and relatively elongate; lunule and escutcheon absent; ligament internal, oblong, and amphidetic; inhalent siphon present but not fused on the ventral side; gill filaments broad and leaf-like; hindgut complex, with loops to the right and left sides of the stomach that connect both dorsally and ventrally behind stomach and ventrally in front of stomach; foot relatively square in outline with a small, triangular, posteriorly directed heel.

Genus *Lametila* new genus

Type species: *Lametila abyssorum* Allen and Sanders new species

Teeth exclusively of elongate type; adductor muscles equal in size; viscera occupy only the dorsal half of the shell cavity; hindgut with two loops on the right hand side of body, posterior edge of the foot square. Characters that differentiate the genus *Lametila* from the other genus of the family (*Prelametila*) are given on p. 296.

Lametila abyssorum new species

Figures 28–35

Type locality: ATLANTIS II, Cruise 12, Station 24, in 2891 m. Holotype: MCZ 271978. Depth range = 2496–3834 m. **Records:** Table V.

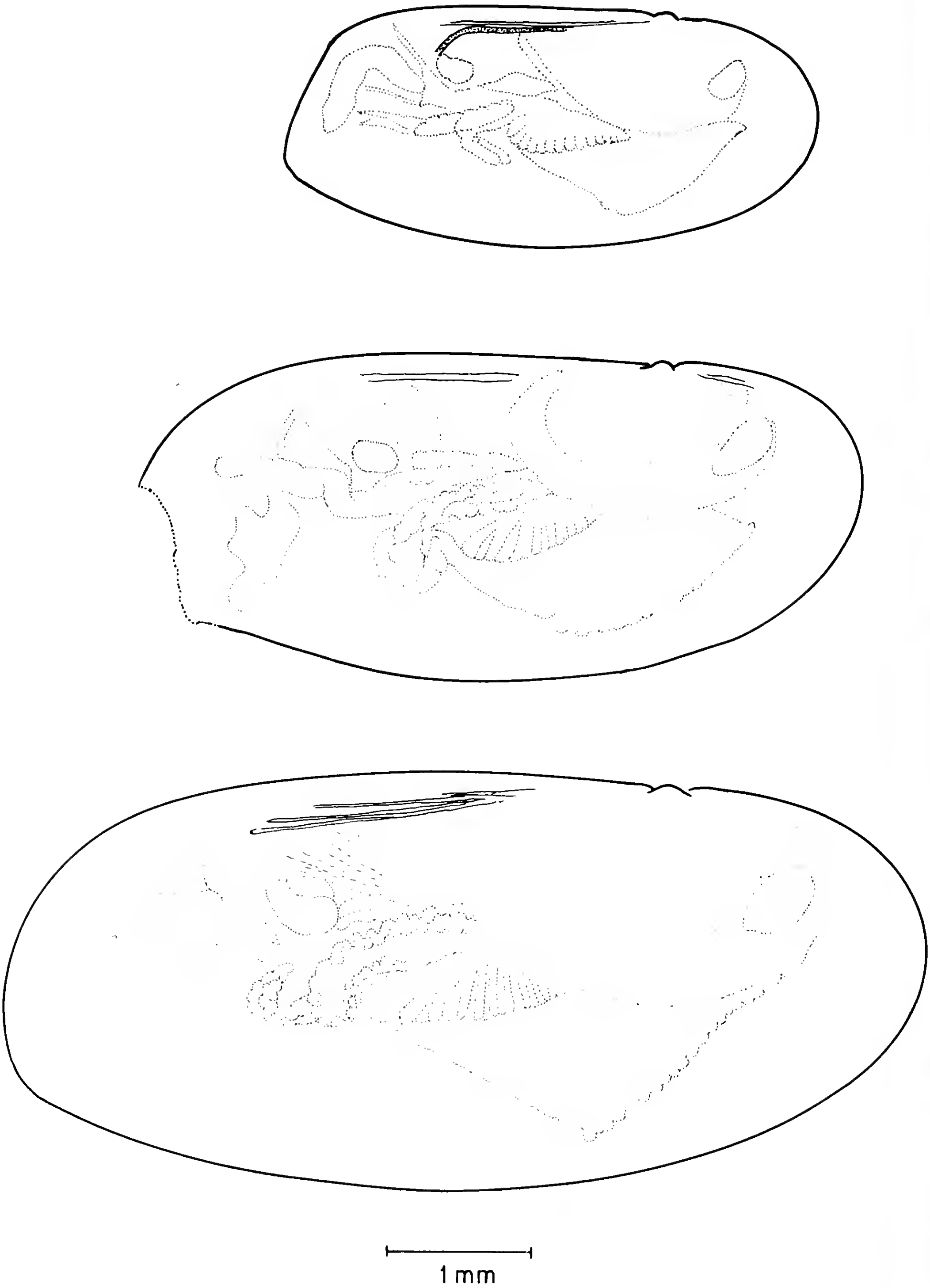

Figure 27. Lateral views of three specimens of *S. rouchi* to show changes in shape with increasing size.

TABLE V. RECORDS FOR *Lametila abyssorum* NEW SPECIES.

Cruise	No.	Sta.	Depth (m)	Speci-mens	Latitude	Longitude	Gear	Date
				NORTH AMERICA BASIN				
Atlantis II	12	62	2496	2	39°26.0′N	70°53.0′W	ES	21.8.64
Atlantis II	12	72	2864	18	38°16.0′N	71°47.0′W	ES	24.8.64
Atlantis II	12	64	2891	60	38°46.0′N	70°06.0′W	ES	21.8.64
Atlantis II	24	126	3806	6	39°37.0′N– 39°37.5′N	66°47.0′W– 66°44.0′W	ES	24.8.66
Chain	50	85	3834	60	37°59.2′N	69°26.2′W	ES	5.4.65
				BRAZIL BASIN				
Atlantis II	31	156	3459	46	00°46.0′S– 00°46.5′S	29°28.0′W– 29°24.0′W	ES	14.2.67
Atlantis II	31	155	3730– 3783	3	00°63.0′S	27°48.0′W	ES	13.2.67

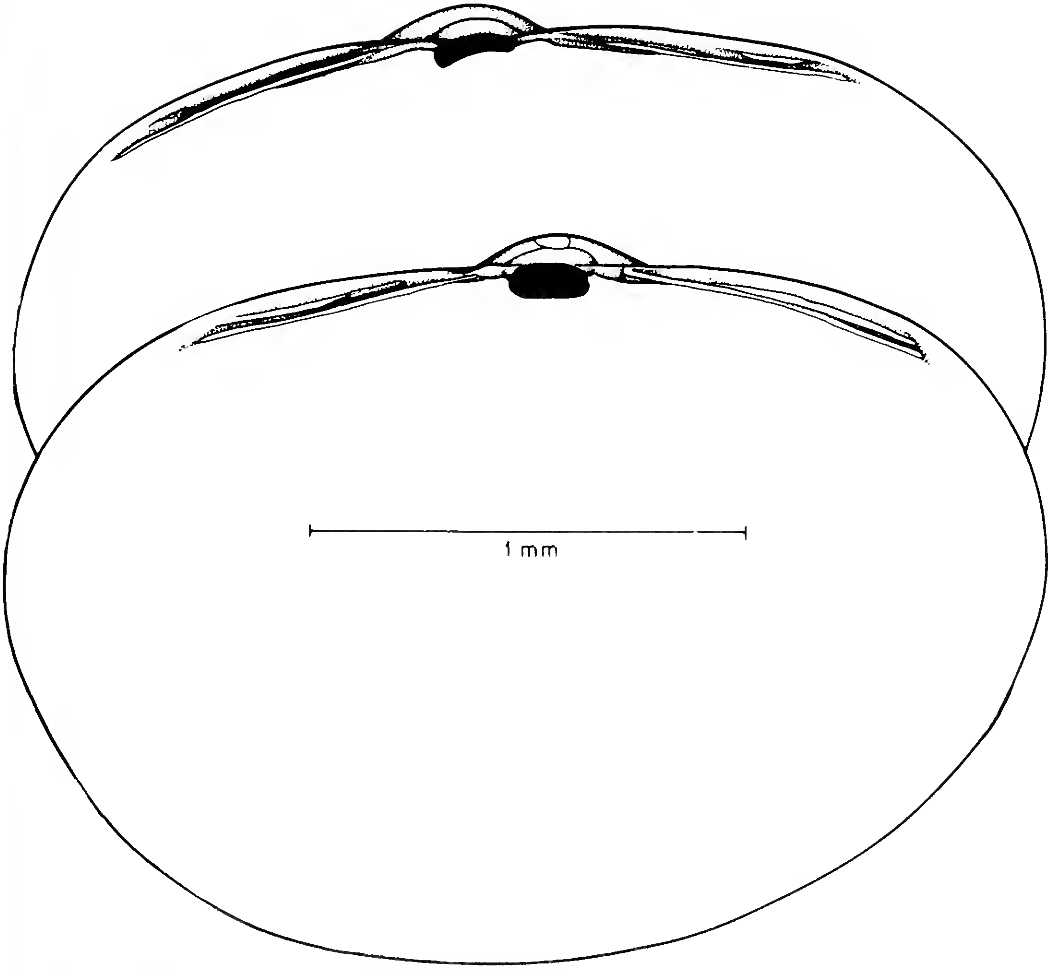

Figure 28. *Lametila abyssorum* Allen and Sanders. Lateral views of the inside of left and right valves.

Shell small, less than 3.5 mm in length; smooth, almost transparent, fragile and with fine concentric striae; height measurement about 0.4 times length (Fig. 34); oblong and rounded in outline; dorsal margin of intermediate length, gently rounded, curving gradually ventrally from the umbonal region and forming raised crests both behind and before the umbo; posterior crest longer than the anterior; posterior margin broad and smoothly rounded with the ventroposterior margin longer than the dorsoposterior; anterior margin narrow and sharply, though evenly, rounded; ventral edge smoothly rounded; umbos small, low, relatively elongate, medially directed with, characteristically, a more opaque medial and ventral region (Fig. 28); umbos central (50%) of the distance along dorsal margin in smaller specimens, but more anterior (45%) in larger individuals (Figs. 29, 34); shell with small gape at the posterior end of dorsal margin (Fig. 31).

Hinge plate long, narrow, weak, with a short section under the umbo straight and parallel to the dorsal margin; anterior and posterior to the umbo the hinge line slopes slightly ventrally; ligament internal, large, amphidetic, at least twice as deep dorsoventrally as long, somewhat bean-shaped in

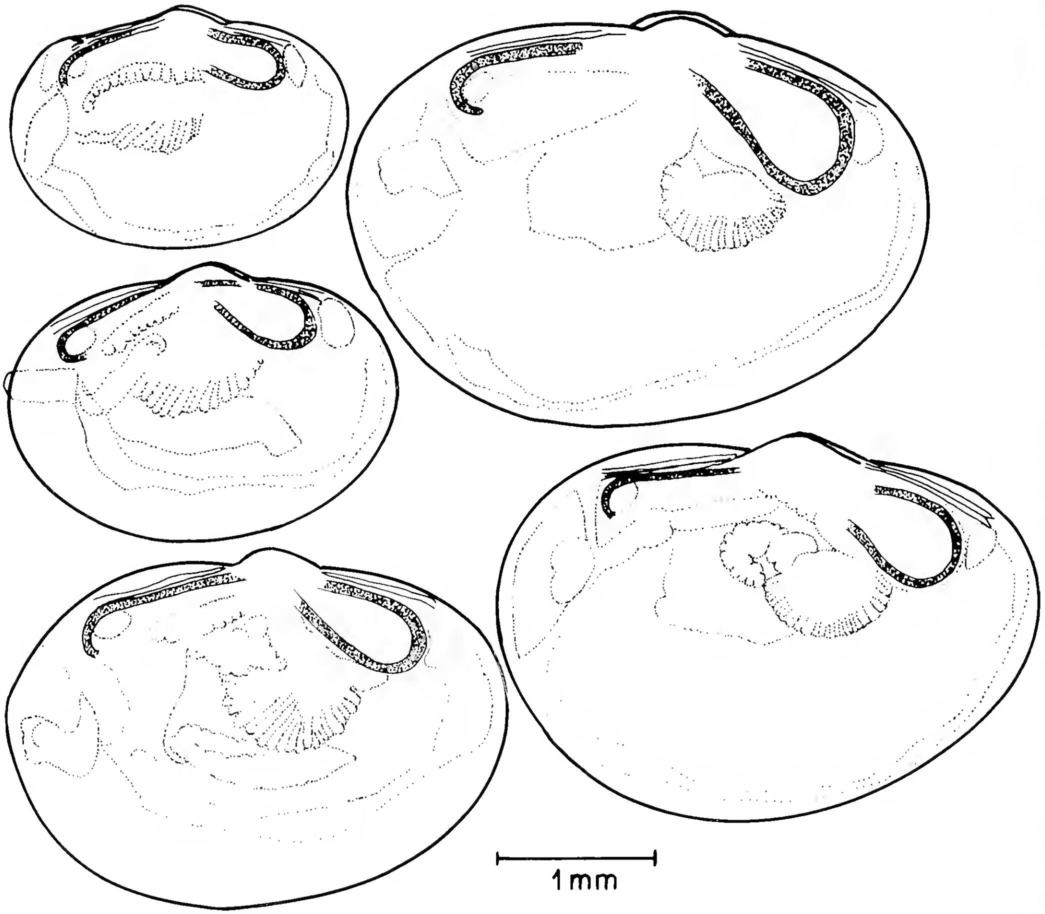

Figure 29. Lateral views of a series of specimens of *Lametila abyssorum* to show changes in shape with increasing size.

outline but wedge-shaped in cross section; two elongate teeth on both the anterior and the posterior hinge plate parallel to or confluent with hinge line; ventral tooth very long, inserted on the thickened medial portion of the hinge plate and angled distally across proximal plate to form the distal 2/3 to 3/4 of the hinge line, terminating above the adductor muscles; dorsal teeth of left and right valves shorter than the ventral teeth; dorsal tooth of left valve relatively elongate and paralleling the distal 70 to 75 percent of the ventral tooth; dorsal tooth on the posterior hinge plate diverges distally from the ventral tooth, the terminal end converging again and forming a crescent-shaped cavity between the teeth; distal divergence of the dorsal tooth on anterior hinge plate less marked and more continuous; dorsal teeth of right valve much smaller; the larger, on posterior hinge plate, about 1/4 the length of the ventral tooth and just medial and parallel to the distal end of the ventral tooth; the smaller dorsal tooth on the anterior hinge plate a thin low ridge, only 1/8 the length of ventral tooth and 1/8 the distance medially from its distal tip.

Combined exhalent and inhalent siphons formed in part from the fusion dorsally and medially of the inner muscular lobes of the posterior mantle edge; inhalent siphon not fused ventrally and the siphonal channel is completed by the adhesion of the ventral edges; although the siphon can be contracted into a very shallow siphonal embayment, there is no obvious development of siphonal retractor muscles from the base of the siphons extending anteriorly within the mantle; retraction appears to be entirely the concern of the internal siphonal musculature. Posteroventrally there is further development of the inner muscular layer into two rather broadly curving pads; these are almost certainly opposed in life and delimit a "feeding aperture" through which the palp proboscides and the tentacle extend. Tentacle large, single, inserted on the right side of the mantle ventral to the base of the siphons (Fig. 30). Anterior mantle sense organs small, but well defined. Very few gland cells are present except above the muscular pads. A well-defined ciliated tract is present between the pad and the gland cells, and probably corresponds to the site of formation of pseudofeces. Adductor muscles are equal in size, elongate and very small, and inserted close to the dorsal anterior and posterior limits of the mantle/shell; long axis of the posterior adductor muscle anteroposterior and that of the anterior muscle dorsoventral.

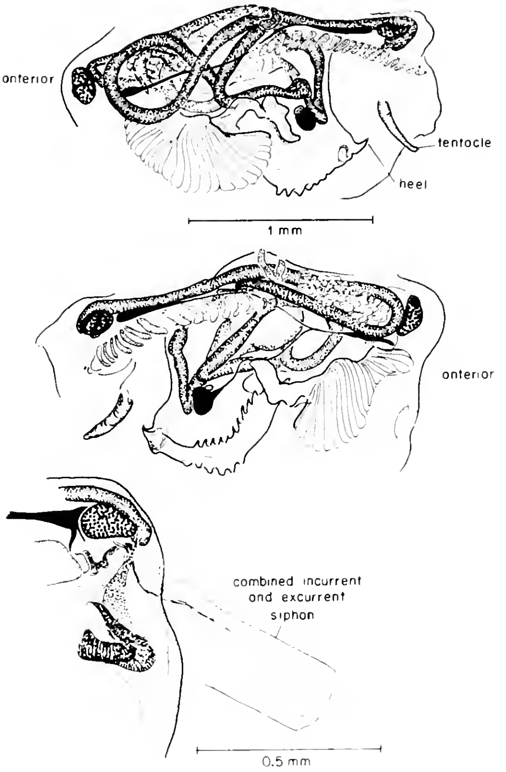

Figure 30. *Lametila abyssorum* Allen and Sanders. Right and left lateral, semidiagrammatic views of the body and mantle organs, with enlarged detail of the siphonal region.

Gills horizontal to the anteroposterior body axis, both inner and outer gill filaments are broad, deep, and equal in size; posteriorly the axes join the septum dividing the exhalent from the inhalent siphon. Hypobranchial gland cells line the posterior part of the cavity laterally and overlie the posterior adductor muscle close to the base of the exhalent siphon. Gills without dense and long frontal cilia as in *Silicula* but are similar to those described for *Lembulus* (Yonge, 1939), having between 17 and 22 filaments on either side of each axis, depending on the size of the animal.

Palps relatively small, placed far anterior; mouth, although not abutting the anterior adductor muscle, is close to its ventroposterior edge. Palps, with 21–26 ridges, do not extend as far posteriorly as the junction of the foot-body, with the result that the palp proboscides are relatively long and narrow. Foot short, somewhat square in outline, its junction with the body far posterior and, in preserved specimens, lying clearly posterior to the palps with the heel frequently close to the aperture through which the palp proboscides are extended; sole of foot short with relatively few (14–16) fringing papillae. As in all protobranchs, the foot is divided. However, in preserved specimens, the two halves of the sole are open and form a flat ventral surface. There is a series of mucus glands at the edge of the foot, just medial to the papillae. "Byssal" gland well developed and just anterior to the short, pointed, posteriorly directed heel.

Oesophagus relatively short, it does not follow an anterior course towards the anterior adductor, but curves dorsally and posteriorly to the large stomach and combined style sac and midgut. Stomach simple with a shallow dorsal hood and nonridged sorting area; three broad ducts lead to the digestive diverticula. The course of the hindgut has no parallel within the protobranches; it extends from the midgut to the anus passing from one side of the body to the other, several times, in front, behind, below and above the stomach. Essentially there are two loops on each side of the body (Fig. 31). From the junction with the midgut, the hindgut passes dorsally, forming a shallow U-bend behind the stomach before passing to the left side of the body. There it makes a short loop and then crosses to the right side of the body below the stomach to make a second loop that curves dorsally forward as far as the oesophagus before turning ventrally and returning to the left side below the stomach but anterior to the first cross, over from left to right. A third loop (the second on the left) is formed and extends forward as far as the anterior adductor muscle before turning back and

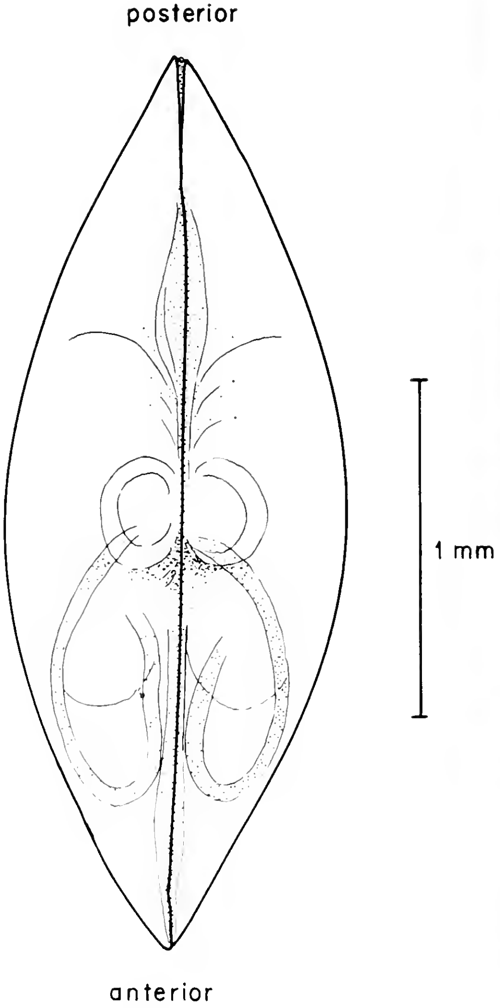

Figure 31. Dorsal view of a specimen of *Lametila abyssorum,* showing the limits of the prodissoconch and anterior loops of the hindgut.

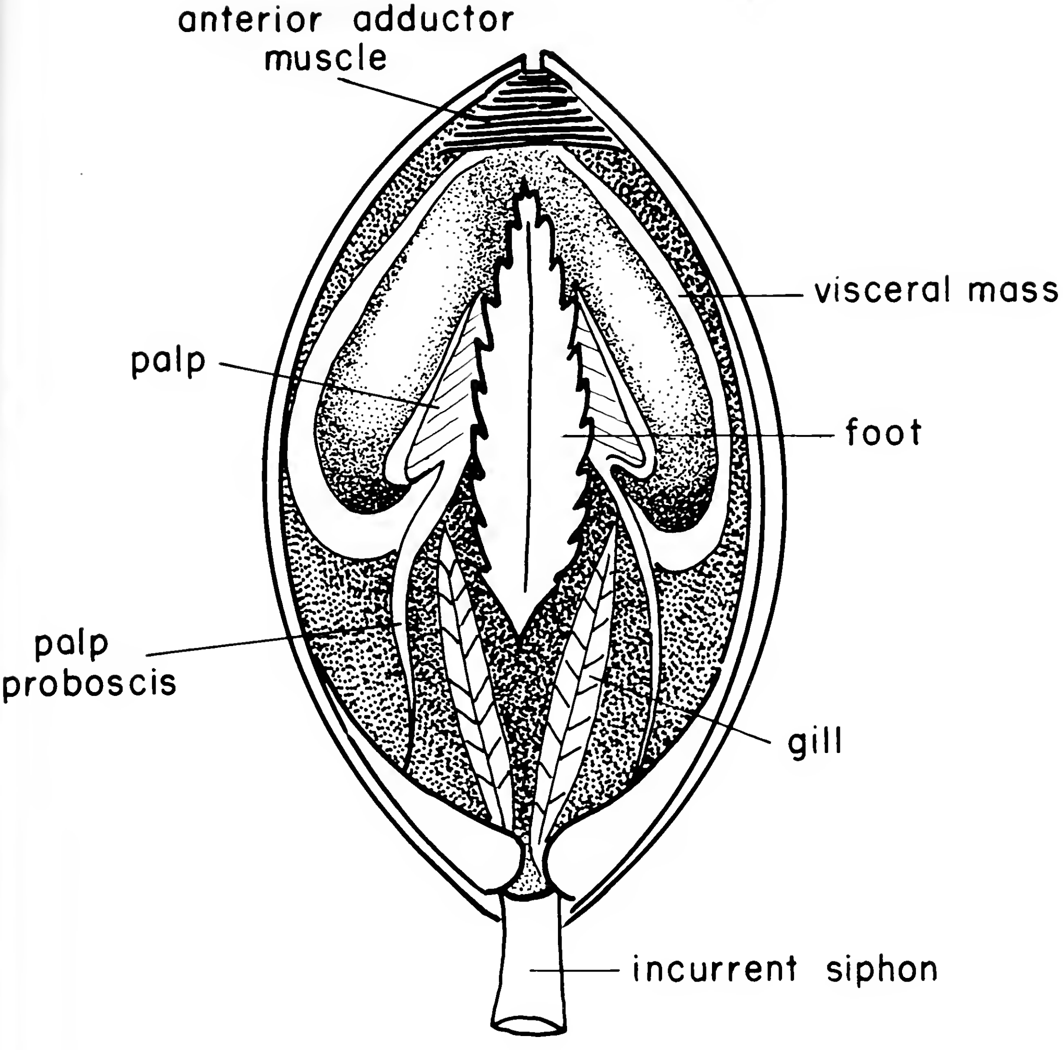

Figure 32. Diagrammatic ventral view of body and mantle organs of *Lametila abyssorum*.

taking a diagonal course from the ventral to the dorsal side of the body. The hindgut crosses again to the right side of the body where it forms the fourth (the second on the right) and last loop, which also passes forwards as far as the anterior adductor muscle before turning dorsally and medially to the anus (Fig. 33). The displacement of the mouth a short distance posterior to the anterior adductor muscle is no doubt a result of the two hindgut loops passing adjacent to the muscle. The globular stomach and the lateral loops of the gut which have a relatively wide-diameter lumen (0.08 mm in a specimen 2.80 mm long) is reflected in the lateral extensions of the body and in the totally different body proportions as compared to *Silicula* (Fig. 32).

Nervous system characterized by elongate and cylindrical cerebral and visceral ganglia; large pedal ganglion positioned high in foot and has an associated pair of statocysts. Sexes separate; gonads lateral and peripheral within body.

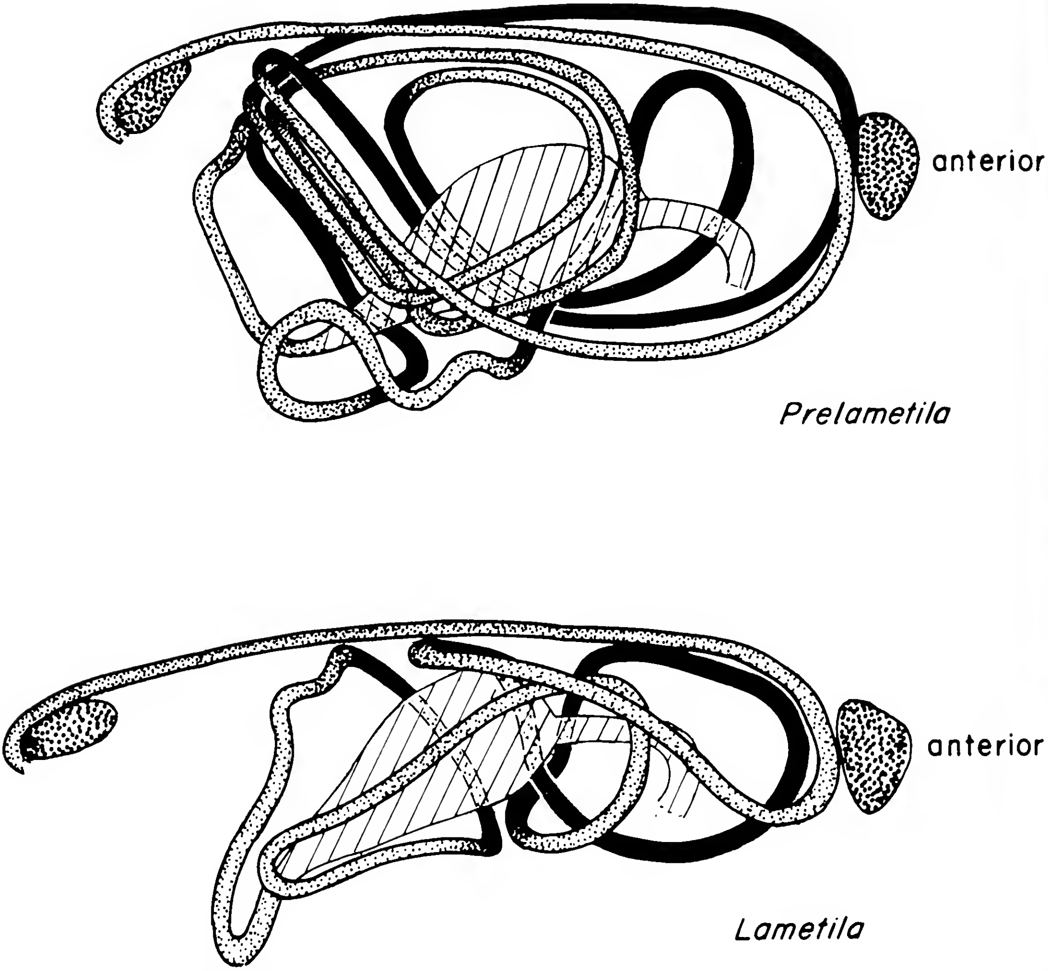

Figure 33. Comparison of the guts of *Lametila abyssorum* and *Prelametila clarkei.* Stippled section on right, and black sections on left of the stomach.

The 38 intact specimens of *Lametila* from Station 64 varied in length from 1.70 mm to 3.25 mm. Within this length range, there is no obvious height/length ratio change with increasing size and most values fall between 0.67 and 0.72 (Fig. 34). However, there is an obvious relationship between the position of the umbo along the dorsal shell margin and the shell length (Fig. 29). Measuring from the anterior end, among the smaller specimens, the umbo is slightly more than halfway to the posterior edge. With increasing size, the position of the umbo becomes progressively more anterior so that, in the largest specimens, it is positioned less than halfway to the posterior margin. This is probably the result of a tangential component of shell growth (Owen, 1952) and thus, although the height/length proportion remains relatively constant with increasing size, differential growth is reflected in the progressively more anterior positioning of the umbo on the dorsal shell margin.

The valves of *L. abyssorum* usually are sufficiently transparent to sex the specimens and approximate their state of maturity. Sexes are separate. Three groupings (the

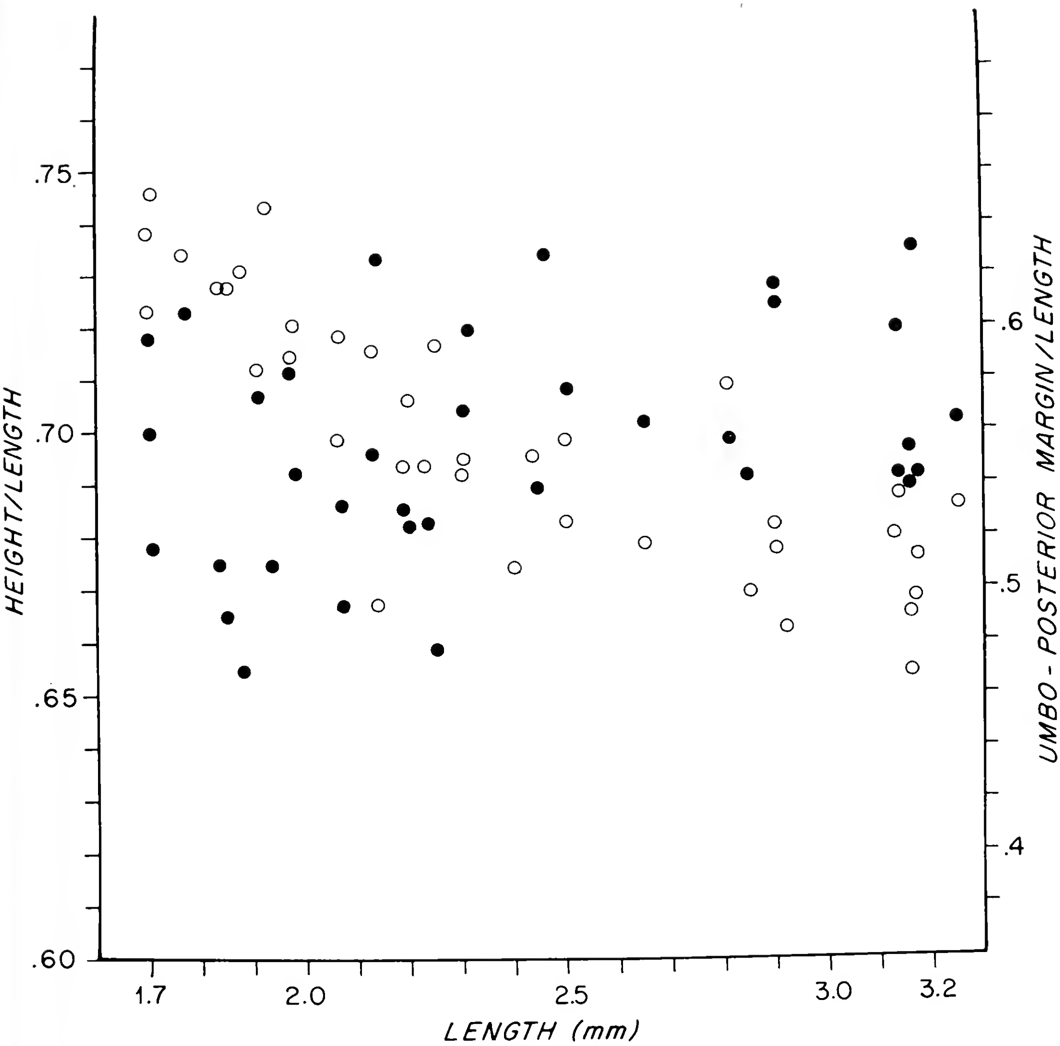

Figure 34. *Lametila abyssorum* Allen and Sanders. Graph showing height/total length (●) and umbo to posterior margin/total length (○) plotted against total length.

immature and incipiently matures, the females, and the males) can be separated with relatively little overlap (Fig. 35). The immature-incipiently mature category (10 individuals) are mostly less than 2.0 mm in length. The females form the numerically most abundant group, 20 individuals, with but three specimens smaller than 2.0 mm and two specimens greater than 3.0 mm. There are only six males in our sample, yet they are among the largest representatives; four specimens exceed 3.0 mm while two

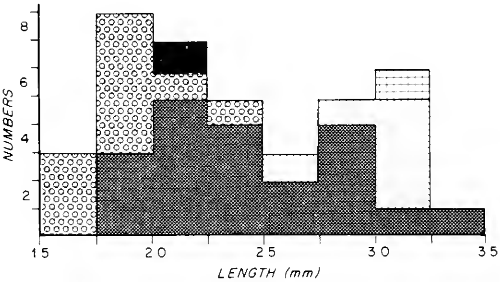

Figure 35. Size frequency distribution of specimens of *Lametila abyssorum* sorted according to sex and gonadial development.

are smaller. Two specimens cannot be categorized, a single larger spent individual (3.13 mm) whose sex is indeterminate and a specimen (2.07 mm) whose shell is too opaque to discern the soft parts within.

Genus *Prelametila* new genus

Type species: *Prelametila clarkei* Allen and Sanders new species

Hinge teeth composed of both elongate and taxodont types; adductor muscles unequal in size; body occupying much of the mantle cavity; hindgut forming 4 loops on the right side of the body; the posterior end of the foot rounded. This genus differs from *Lametila* in the possession of taxodont teeth, more than two hindgut loops on the right side of the body, and by its heteromyarian condition.

Prelametila clarkei new species
Figures 36–38

Type locality: ATLANTIS II, Cruise 60, Station 247, in 5209–5227 m. Holotype: MCZ 271975. Depth range = 4382–4405 m to 5209–5227 m. **Records:** Table VI.

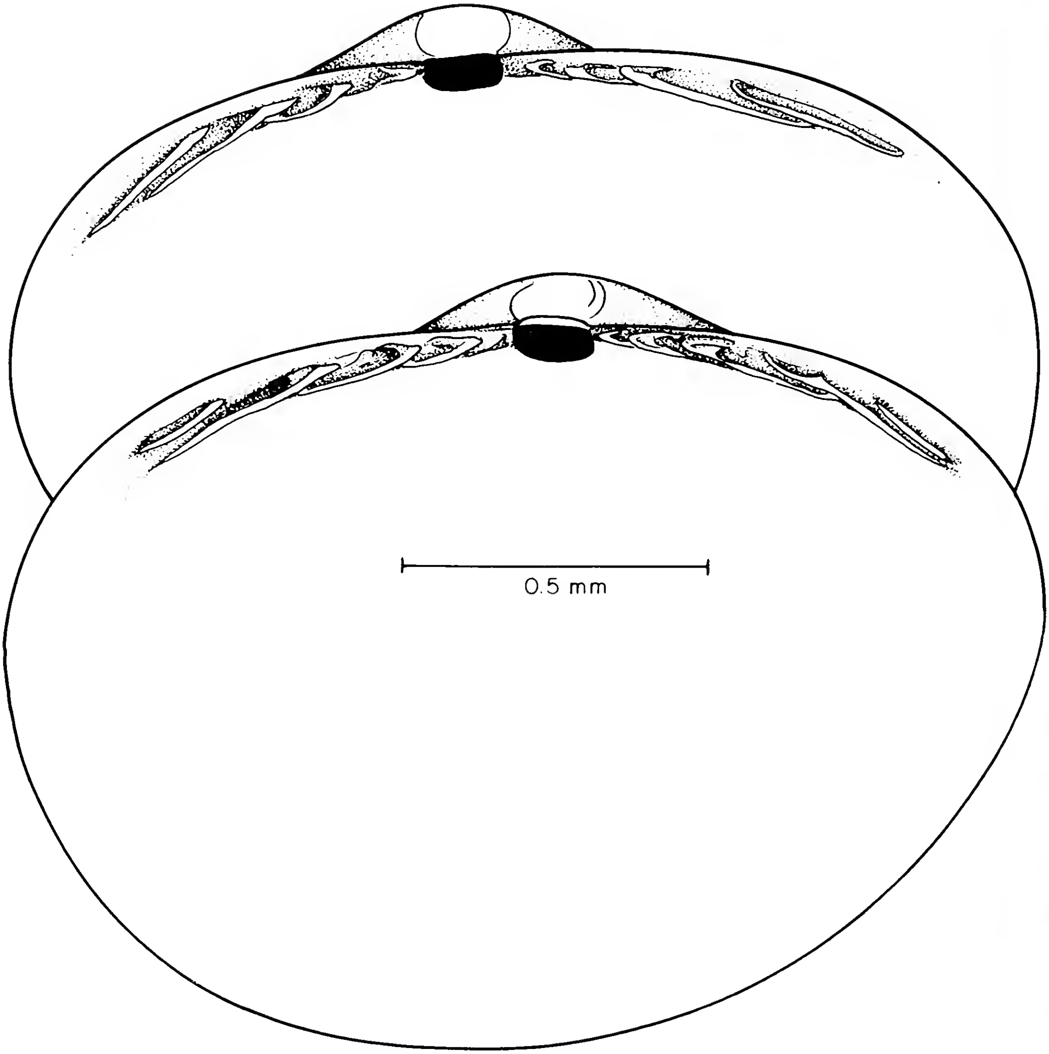

Figure 36. *Prelametila clarkei* Allen and Sanders. Internal views of left and right valves.

TABLE VI. RECORDS FOR *Prelametila clarkei* NEW SPECIES.

Cruise	No.	Sta.	Depth (m)	Specimens	Latitude	Longitude	Gear	Date
ARGENTINE BASIN								
Atlantis II	60	247	5209–5227	239	43°34.6′S–43°33.0′S	48°58.0′W–48°51.1′W	ES	17.3.71
Atlantis II	60	242	4382–4405	29	38°16.9′S	51°56.1′W	ES	13.3.71

Shell small, less than 2.5 mm in length, smooth, semitransparent, not markedly fragile and with fine concentric striae; height about 0.43 times length (Figs. 36, 37); subovate and smoothly rounded in outline; the proportionately short dorsal margin gently rounded behind and more strongly curved in front of the umbo and forming raised crests along both the anterior and the posterior dorsal midline, posterior crest longest; posterior margin broad and smoothly rounded with the ventroposterior margin longer than the dorsoposterior; anterior shell margin is narrow and strongly curved, ventro-anterior margin longer than the dorso-anterior; ventral margin not long, but strongly curved; umbo moderately large, elongate with a flattened medially directed beak; umbo just anterior of the midline being between 47 to 49 percent of the length distance from the anterior edge of the valves; shell gape not visible from the dorsal margin; shell height greatest immediately behind umbo.

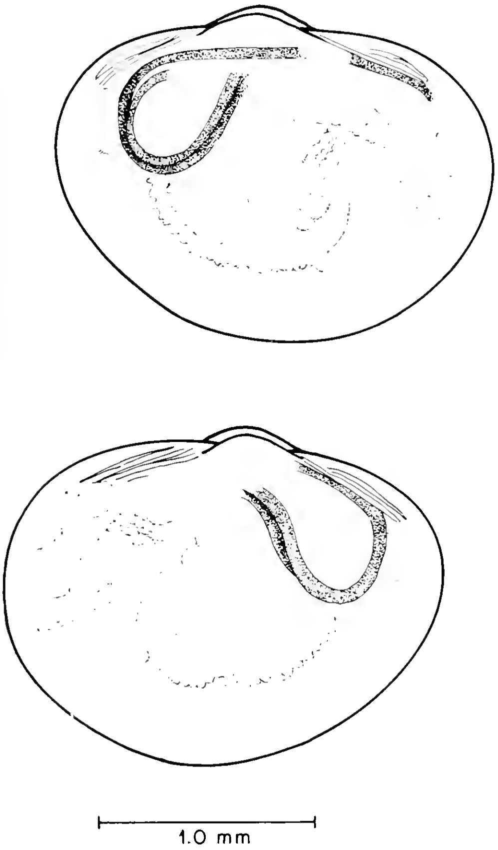

Figure 37. *Prelametila clarkei* Allen and Sanders. Right and left lateral view of an intact specimen.

Hinge plate long and moderately thick; posterior hinge line curving gently downwards, that of the anterior hinge plate more precipitous; ligament internal, amphidetic, oblong and large, but proportionately smaller than in *L. abyssorum*. Hinge teeth of both elongate lateral and taxodont types with gradation between the 2 forms; most proximal 2 teeth typically taxodont, proportionately small and with the dorsal arm nearly as long as the ventral; next most distal tooth the longest, its dorsal arm much reduced, the ventral arm elongate and extending laterally to occupy the entire hinge line below the terminal tooth on the left valve and half the hinge line under the terminal tooth of the right valve; distal tooth elongate, lacking a dorsal arm, and obliquely parallel to the hinge line; distal tooth on the right valve about 1.6 times longer than that on the left.

The four specimens of *P. clarkei* that were picked from the sample aboard ship vary from 1.96 mm to 2.09 mm in total length. The height/length ratio is 0.72–0.74 and the width/length ratio, 0.43; the position of the umbo is between 46.8 to 48.8 percent of the total length measurement from the anterior edge.

Inhalent and exhalent siphon combined and can be retracted into a shallow siphonal embayment, similar to *Lametila;* inhalent siphon not fused ventrally. Ventral and posterior paired extensions of inner muscular layer separate a posterior feeding aperture through which the palp proboscides and tentacle extend. Tentacle placed to the right and more slender and pointed than that of *Lametila.* Small but well-defined anterior mantle sense organs present. Adductor muscles somewhat larger than those of *Lametila;* they differ in size, the anterior being approximately twice as large as the posterior. Gills similar in position and extent to those of *Lametila* but with only 10 filaments on each side of the axis. Palps fan shaped, relatively broad, lying somewhat further back in the mantle cavity than in *Lametila,* because the mouth itself is further from the anterior adductor muscle; 15 palp ridges present in each of the four specimens comprising our collection (Fig. 38).

Course of gut similar to that of *Lametila;* however, it differs in having two additional loops formed by the hindgut on the right-hand side of the body, giving a configuration that is the most complex so far encountered in the protobranchs. The characteristic first section of the hindgut passes dorsally behind the stomach forming a single U-bend; the hindgut then returns to the ventral side of the style sac via the right side of the body, making a single posterior loop before passing to the left-hand side of the body ventral to and in front of the stomach. The posterior loop is not as large as that in *Lametila* but the basic course is, nevertheless, the same. The two additional loops that are present on the right-hand side in *Prelametila* are penultimate to the final loop on the *left* side which extends forward to the anterior adductor muscle. The two additional loops to the right encircle the stomach but do not pass close to the adductor (Fig. 33). As in *Lametila,* the last loop of the hindgut is on the right-hand side of the body and extends forward to the posterior edge of the anterior adductor.

Nervous system similar to *Lametila.* Foot, which has a very small, posteriorly pointing triangular heel, carried more anterior than in *Lametila* and somewhat extended posteriorly as in, but not to the same extent as, *Silicula.* "Byssal" gland moderately small.

There are too few specimens to determine sex ratios, gametogenesis, egg size, and egg numbers.

This species is named in honor of Dr. Arthur H. Clarke, Jr., of the National Museum of Canada, student of the deep-sea Mollusca, for his contributions to this field.

On the basis of shell morphology (*e.g.,* amphidetic ligament, rounded subovate shape and elongate, oblique, lateral teeth [Fig. 2]), *Phaseolus ovatus* might best be included as a separate genus within the Lametilidae. However, in the absence of any knowledge of the soft parts, we prefer to defer making a decision (see p. 266).

FUNCTIONAL MORPHOLOGY OF THE SOFT PARTS OF THE SILICULIDAE AND LAMETILIDAE

From consideration of the form of the soft parts of *Silicula,* and deductions about its habits, it is clear that the following morphological features are of great functional significance: 1) the elongate and extremely slender shape, 2) the tubular exhalent siphon, 3) the inhalent aperture formed by the apposition of the somewhat extended inner muscular lobe, 4) the extremely elongate palp proboscides which, in many preserved specimens, extend out of the *inhalent* aperture, 5) the elongate and deeply cleft foot with extremely well-developed retractor muscles, 6) the curvature of the body/foot axis anteriorly through 90°, 7) the posterior extension of the foot and body, 8) the displacement of the mouth posteriorly, 9) the anterior position of the posterior adductor muscle, 10) the heavy ciliation of the frontal surface of the gill, and 11) the posi-

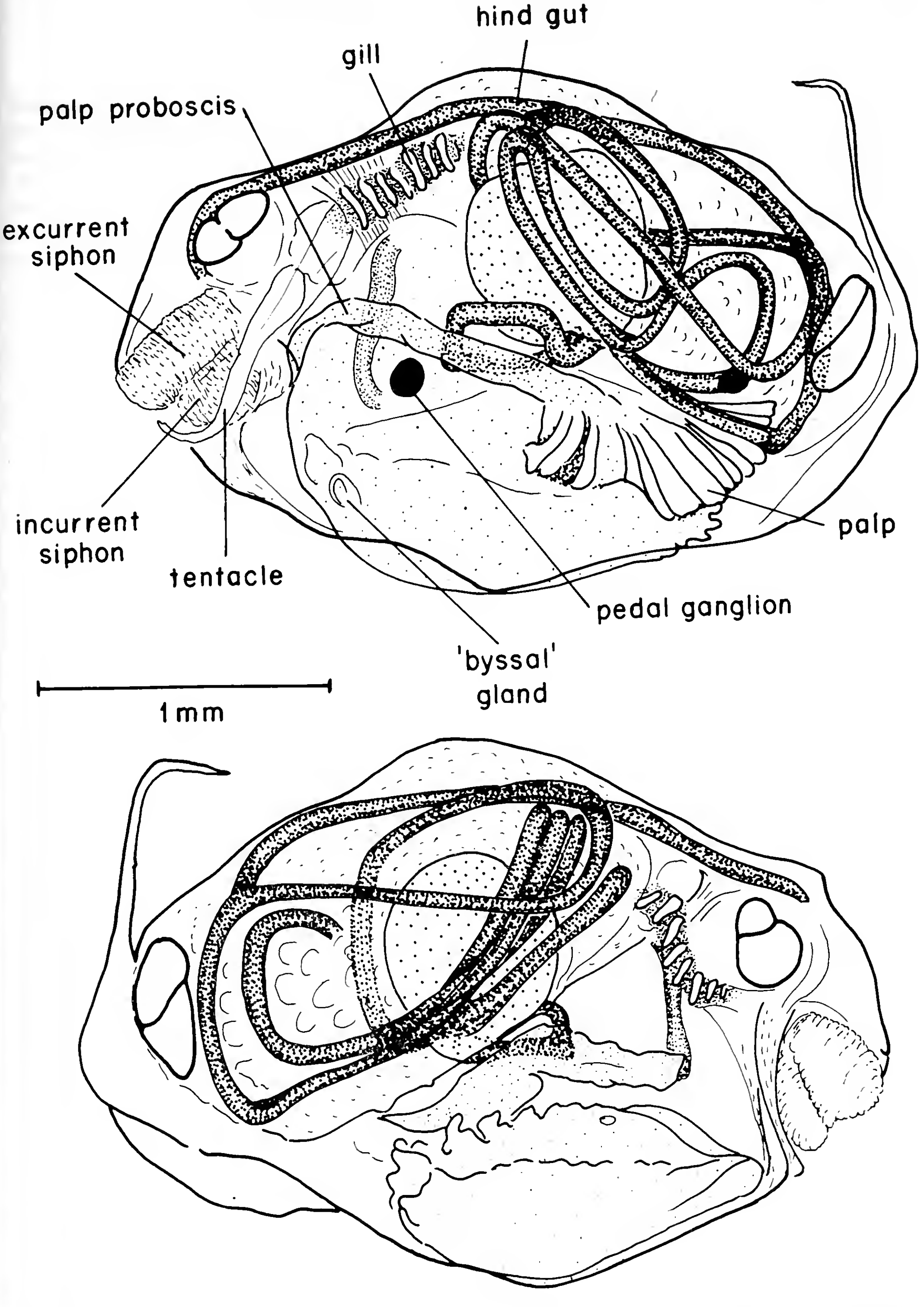

Figure 38. *Prelametila clarkei* Allen and Sanders. Right ventrolateral and left dorsolateral, semidiagrammatic views of the body and mantle organs.

tion of the stomach. Conclusions to be drawn from this array are that *Silicula* can burrow rapidly; that they orientate within the sediment so that the anteroposterior axis is vertical; that, when feeding, the posterior rim of the extended inhalent aperture is level with the sediment surface and the palp proboscides pass through the aperture; and, that the exhalent siphon can be extended at least as far as the limits of extension of the palp proboscides—there is no evidence of coprophagy so the fecal rods probably are deposited beyond the range of the palp proboscides (Fig. 39).

By correlating form and habit and comparing the morphology of the *Silicula* species, it is possible to draw some conclusions as to evolution in the genus. Progressive, posterior elongation of the body has occurred, the extremes being *S. filatovae* on the one hand and *S. mcalesteri* on the other. The more elongate the species the better defined is the exhalent siphonal embayment. We believe that the animal takes up a vertical position* in the sediment, and that this relates to the form and disposition of the foot. Elongation of the foot and the interior turn of its axis through 90° tends to limit the amount of body space available for the gut, digestive diverticula, and the gonads. This limitation compensates the posterior extension of the body/foot. In addition, lateral compression of the body itself limits the available space for body organs. The very shortened gill filaments (the outer

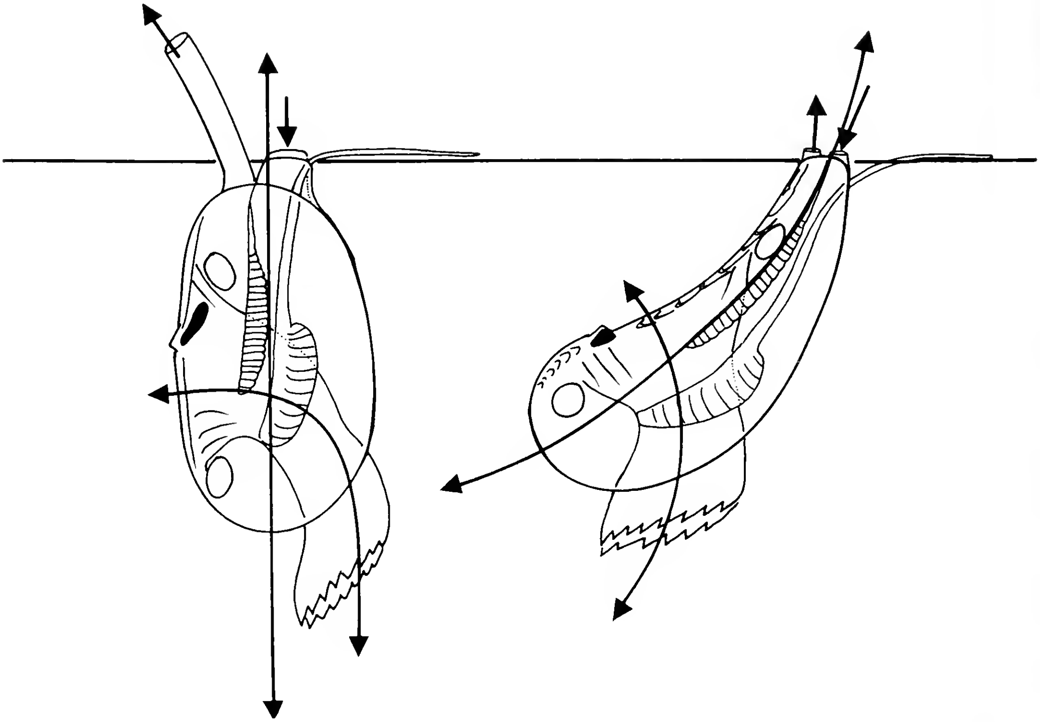

Figure 39. Comparison of hypothetical attitude in life of *Silicula* and *Propeleda*. Arrows indicate anteroposterior and body axes.

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* Note that the hinge line is straight. In other elongate genera, *e.g., Poroleda* and *Propeleda,* with a concave posterior dorsal margin, the anteroposterior axis of the shell may well be diagonal to the sediment surface (Fig. 39).

filaments being half the size of the inner) are modifications to the thinness of the body. The foot, when retracted, lies in the anterior part of the mantle cavity and this may be related to the posterior position of the mouth. However, there is functional reason in the mouth being posterior in position in an elongate animal in which the food arrives posteriorly. In this context the densely ciliated gills should be mentioned, for although a protobranch, it is likely that these convey food material towards the mouth. It is also significant that, although abyssal, these species appear to be selective feeders and, in most animals examined, the stomach and the digestive diverticula are packed with whole diatom frustules of a similar size. The morphology of *Silicula*, in fact, parallels other dimyarian bivalves that are elongate and very active burrowers within soft sediments, *e.g.*, *Pharella* (Owen, 1959), *Pharus* (Yonge, 1959), and *Siliqua* (Yonge, 1952).

It has been shown in the genus *Abra* (Allen and Sanders, 1966), of which there is a series of species showing vertical zonation, that those species from deep water have much longer hindguts than those in shallow water. In general *Silicula* is similar, thus *S. rouchi* and *S. mcalesteri* have much shorter hindguts than *S. fragilis* and *S. filatovae*. It might be expected that *S. fragilis* with its twice-looped gut would occur in water deeper than that in which *S. filatovae*, with one loop, occurs. However, the reverse appears to be the case. It may be that size also has to be taken into account, that small species have relatively larger hindguts than larger species of the same genus at the same depth range. It is true that tiny abyssal protobranchs have exceptionally long hindguts—*vide Pristigloma* and *Microgloma* (Sanders and Allen, 1973), and that the relatively longer hindgut of *S. fragilis*, as compared with *S. filatovae*, is but a reflection of size difference.

The exhalent siphon and inhalent aperture are extended by hydrostatic pressure, and retracted by longitudinal musculature. The siphon is constructed as two cylinders of circular collagen fibers with a lumen between divided into compartments by transverse fibers, thus forming elongate channels approximately rectangular in cross section. Within the channels run longitudinal muscle fibers on the inner peripheral faces. No major nerves pass up the siphon; innervation presumably is brought about by fine fibers close to the walls of the channels. It appears that the palp proboscides are extended and contracted in a similar way, for there is a similar system of muscles, collagen fibers and spaces; however, here there is a very large nerve passing medially along the length of each palp proboscis (Fig. 22).

On morphological grounds it seems likely that the habits of *Lametila* are very different from those of *Silicula*. 1) In *Lametila* and *Prelametila* the respiratory and feeding activities appear to be completely separate, whereas in *Silicula* they are combined. 2) *Silicula* is laterally compressed, elongate, and designed for rapid vertical burrowing, yet it can remain in contact with the surface through the use of the extended inner muscular folds of the posterior inhalent aperture. However, *Lametila*, being more globose, is not especially designed for rapid burrowing and, because it has an inhalent siphon, need not necessarily maintain a vertical position. There is no evidence that the mantle edge of the feeding aperture can be extended, even though it can open separately to the pedal gape and thus allow the palps and tentacle to be extended into the substratum. 3) In the Lametilidae the palps are far anterior and there is no evidence that the gills are associated with the palp proboscides in any way. 4) The foot in *Lametila* and *Prelametila* is totally different in shape, position, and attitude to that in *Silicula*. It is broad, posteriorly situated, and the two halves of the sole are separated to form a flat sole. The body axis is vertical and the foot is, no doubt, extended ventrally and is designed for horizontal progression.

FUNCTIONAL MORPHOLOGY OF THE HARD-PART ANATOMY OF THE SILICULIDAE AND LAMETILIDAE

a) Siliculidae

The light-shelled, razor-thin, elongate form of the Siliculidae together with its large, powerful foot are indicative of an actively burrowing mode of life. The extensive gape along the dorsal shell margin, a feature unique among the protobranchs, permits greater flexibility in the opening and closing of the valves. Such opening and closing phases, when repeated rhythmically, form a pumping activity. Because the water volume between the valves is small in these markedly flattened forms, it is readily expelled as the valves come together during the excurrent phase. On the alternate separating or incurrent phase, water is drawn in by the resulting vacuum, which additionally creates considerable suction that greatly enhances burrowing activity.* The dorsal gape itself is made possible by the characteristic siliculid elongate teeth paralleling the hinge plate rather than by the more typical series of smaller taxodont teeth relatively perpendicular to the dorsal shell margin of most protobranchs. The proportionately anterior position of the posterior adductor muscle is another requisite for the pronounced dorsal gape. With contraction and expansion of the adductors, the elongate teeth roll against one another like the hinges of a door. There is one potential weakness in the system. The tooth configuration on the weak hinge plate is such that it might be displaced as a result of strong pumping activities and cause shearing of the two valves. We believe that the stability imposed by a large internal ligament is an effective countermeasure. The elongate shape of the siliculid ligament and its opisthodetic form are logical responses to the greatly inequilateral shape of the valve (*i.e.*, most of the animal is posterior to the umbo) brought about by the extension of the shell posteriorly.

b) Lametilidae

The relatively equilateral shell, the more inflated form, and small foot cumulatively demonstrate that the Lametilidae, unlike Siliculidae, are not active burrowers. Rather, they are relatively sedentary forms possibly lying in a horizontal or near horizontal position close to the sediment surface. The posterior adductor muscle, as compared to *Silicula*, is close to the posterior margin of the shell with the result that the dorsal gape is very small in *Lametila* and restricted to the most posterior part of the dorsal margin. There is no gape in *Prelametila*. The small adductor muscles, as in *Pristigloma alba* (Sanders and Allen, 1973), can be related to the combination of a fragile shell, more tumid form, weak hinge plate, and lamellar, or elongate, teeth. Despite the similarly fragile shell, the proportionately larger adductor muscles in *Silicula* are possible because the flattened shell and reduced lateral mantle space are structurally stronger than the inflated one. Furthermore, since pumping activities are probably more critical in *Silicula*, its adductor muscles must be larger.

Unlike *Silicula*, the tooth configuration in *Lametila* differs in the two valves. The dorsal tooth on both the anterior and the posterior hinge plate of the left valve is very small and is situated distally. The same tooth on the right valve is considerably longer, arising about one-third the distance from the medial point of the hinge plate and extending distally. Unlike that in *Silicula*, it lies flush against the ventral tooth except at the distal hinge margin where it diverges, slightly on the anterior hinge plate and somewhat more extensively on the posterior hinge plate, to accommodate the dorsal tooth of the opposite valve. Thus only the ventral teeth are capable of

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* Such pumping activity could also assist in feeding. However, we have no evidence for this.

rolling against each other, while the dorsal teeth tend to lock the valves together.

With a weak hinge plate and shallow, elongate teeth (as well as weak taxodont teeth in *Prelametila* which are confined medially on the hinge plate), there is a tendency of the valves to shear. Rigidity and prevention of possible shear is achieved through the elaboration of a large ligament. The shell of *Lametila* is equilateral, and the ligament is internal and amphidetic. The ligament is bean-shaped in outline and wedge-shaped in cross section, being correlated with the more tumid form of the shell. Because of the relatively massive ligament size, the short, medial portion of the hinge plate supporting it is appreciably thickened.

Only the distal teeth of *Prelametila* approximate the *Lametila* tooth configuration. The gradual transition from medial taxodont to distal elongate teeth imposes a somewhat different set of relationships among the components comprising the hard-part morphology. The proximal chevron-shaped taxodont teeth lock the two valves together (Fig. 36) and the small dorsal gape that persists in *Lametila* is absent in *Prelametila*—only the distal elongate teeth are able to roll against one another. The tendency of the valves to shear is thus reduced. In relation to this, the oblong, amphidetic internal ligament, although relatively large in *Prelametila*, is proportionately smaller than in *Lametila*. Similarly, the larger adductor muscles may be a direct response to the less fragile and heavier shell of *Prelametila*.

DISTRIBUTION PATTERNS

The two deep-water siliculids in our collections are either predominantly or exclusively abyssal. On the well-collected Gayhead-Bermuda transect in the North America Basin, *Silicula fragilis* has been taken at three stations, two from depths between 3800 and 3900 meters and one (single specimen) at nearly 2900 meters. Elsewhere in the Atlantic we have collected this species at a depth of 1922 m in the West Europe Basin and in the Argentine Basin at 3305–3317 m. Earlier records for *S. fragilis* are from two further stations in the West Europe Basin (Jeffreys, 1879) at 1493 and 2223 m. Thus *S. fragilis* appears to be an Atlantic species of the deeper slope and abyssal rise depths.

A single large specimen of a siliculid that corresponds closely to *S. fragilis* was taken from a depth of between 4469–4476 m in the Argentine Basin. This was picked from the Epibenthic Sled soon after it came aboard. The samples from the cruise are yet to be processed and we choose for now tentatively to exclude this specimen from the species *S. fragilis* until additional representatives are available for a careful appraisal. Our equivocation is due to a reluctance either to dissolve the shell to study the soft-part anatomy or, alternatively, destroy the soft parts with sodium hypochlorite to study the inner shell morphology. Further reasons for caution are that the specimen is more than twice as large as any known representative of *S. fragilis*, and that it comes from a depth that is 640 m greater than any known record of the species.

Silicula filatovae is a deeper-dwelling species than *S. fragilis*. On the Gayhead-Bermuda transect, its shallowest record is from 3826 m. *S. filatovae* was present in 9 of the 17 stations from that depth to 5042 m and overlaps *S. fragilis* at the shallow end of its range. Both species were taken at Station 85 at a depth of 3834 m. Other than the Gayhead-Bermuda transect, our records for *S. filatovae* are from a single station in the Cape Verde Basin at 3861 m, and three stations in the Angola Basin at 4559–4566 m to 4612–4630 m. These records suggest that *S. filatovae* is broadly distributed throughout the abyssal depths of the Atlantic.

At no station where the quantitative assessment has been completed does *S. filatovae* or *S. fragilis* form a significant percentage of the protobranch fauna. *S. filatovae* contributes almost 4 percent to the protobranch fauna at one station and 1 percent or less at the remaining six. Similarly, at the four stations where it was found, *S. fragilis* comprises 8.5 percent of the protobranchs at one station and 1.0 percent at the other three.

The third representative, *Silicula mcalesteri,* is found at much shallower depths. We have taken it at only one locality in 275–305 m off Uruguay. *S. mcalesteri* is an upper slope and possibly an outer shelf species of the Southwest Atlantic. Despite the fact that the sample from which the present specimens were extracted has yet to be processed, the obvious abundance of *S. mcalesteri* in that sample clearly indicates that it will be an important numerical constituent of the protobranch fauna.

Both representatives of the Family Lametilidae in our collections are totally abyssal. *Lametila abyssorum* has a sharply defined depth range. On the Gayhead-Bermuda transect it is found from approximately 2500–3900 m and is a species constituent at five of the seven stations from that depth interval. The two remaining records for the species are in the eastern Brazil Basin near the mid-Atlantic ridge at depths of 3459 and 3730–3783 m. When *L. abyssorum* is present in a sample, it is often one of the most abundant species. At the seven recorded stations, the bivalve formed 61.33, 31.0, 13.04, 7.76, 1.25, 0.94 and 0.72 percent of the protobranch fauna.

Prelametila clarkei was present at the two deepest stations on the Argentine Basin transect in 4382–4405 m and 5209–5227 m. Thus, *P. clarkei* may be categorized as a lower abyssal species of the Argentine Basin.*

IMPLICATIONS FOR THE FOSSIL RECORD

The protobranchs appeared early in the fossil record during the mid-Cambrian together with another, supposedly nonprotobranch, bivalve group, the Actinodonta. The latter had either radiating cardinal teeth in the region of the umbo or elongate lateral teeth parallel to the hinge line, or both, in various combinations, rather than the chevron-shaped taxodont teeth of the nuculoids. The modern, but enigmatic, family Nucinellidae typically has both cardinal and lateral teeth. Yet, on the basis of soft-part anatomy, they are protobranchs whose nearest known living relatives are the Solemyidae (Allen and Sanders, 1969). We have included them with the Solemyidae within the order Solemyoida of the subclass Protobranchia (Sanders and Allen, 1973). Furthermore, lamellar, elongate, and overlapping rather than taxodont teeth are present in at least one species of nuculacid protobranch, *Pristigloma alba* (Sanders and Allen, 1973). In the present paper, we have shown that within the remaining major protobranch grouping, the superfamily Nuculanacea, two of its constituent families bear elongate, overlapping teeth parallel to the hinge plate rather than exclusively chevron-shaped taxodont teeth. Yet, another form, the Pliocene fossil *Phaseolus ovatus* Seguenza also had elongate and overlapping teeth on both the anterior and posterior hinge plate (Fig. 2). Modern specimens that have been included under this name are clearly not the same species. They lack the elongate teeth and instead have a few taxodont teeth that are very small and rounded or oblong in shape, not unlike the microglomids (see Sanders and Allen, 1973).

On the basis of such accumulating information, it is becoming increasingly evident that the paleontologist must interpret the early bivalve fossil record with considerable caution. Lack of taxodont teeth *per se* can no longer be used as the prime cri-

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* We have recently found a second species of *Prelametila* in three samples from the Argentine Basin that ranged in depth from 3305–3317 to 4382–4405 m. The same species has also been recovered from a sample collected at 4592–4597 m depth in the Angola Basin. A description of this new form will be included in a later paper in the series.

terion for excluding fossil bivalves from the subclass Protobranchia. In fact, there is no way of demonstrating that the early actinodonts could not have been protobranchs.

For example, the Silurian actinodont, *Actinodonta cuneata* (Phillips and Salter, 1848), was strikingly similar to the extant Siliculidae (Fig. 40). Both have the elongate and apparently flattened shell form, a similar small, low umbo, and, to judge from the hinge plate configuration under the umbo, *A. cuneata* must have had a siliculid-like internal ligament that was opisthodetic and elongate.

Pertinent to this discussion are observations of Vogel (1962) that the oldest toothed bivalves, from the base of the mid-Cambrian of Spain, did not have taxodont but instead had elongate teeth parallel to the hinge plate. These were bivalves with an equilateral shell and either one or two elongate teeth on both the anterior and the posterior hinge plates. Vogel (1962) created the actinodont genus *Lamellodonta* to include them. From such forms he derived the remaining actinodonts and, eventually, the other major bivalve taxa. The modern analogue to the *Lamellodonta* is *Lametila abyssorum,* for it has the same transversely oval shell and two elongate teeth on both the anterior and posterior hinge plate that are parallel to the hinge line.

It must be clearly stated, however, that we are not claiming extreme primitiveness for the Lametilidae and Siliculidae. We cannot provide the evidence for a suite of primitive soft-part characteristics that can be associated with the elongate teeth. Instead, the soft-part anatomy shows that both the Siliculidae and Lametilidae are typical nuculanacids.

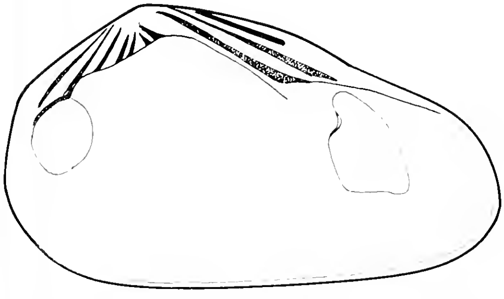

Figure 40. *Actinodonta cuneata* Phillips. Lateral view of inside of left(?) valve. Redrawn from Phillips and Salter (1848).

Yet, even in the distant Cambrian, the protobranchs (and actinodonts) radiated, diverged, and diversified so that they may have been hardly more "primitive" than their modern descendants. In the absence of the later-evolving major bivalve taxa, there were numerous habitats to exploit, a strong impetus for evolutionary change. For example, *Actinodonta cuneata,* with its siliculid morphology, including a probable razor-thin shape and large powerful foot, may well have been an active burrower. Alternatively, the rounded, massive-shelled taxa were relatively immobile surface or near surface forms. A modern analogue is the nonsiphonate *Tindaria.*

Elongate teeth were derived more than once from taxodont teeth or *vice versa.* The presence of the elongate tooth configuration among representatives of both the orders Solemyoida and Nuculoida as well as the two superfamilies composing the Nuculoida provide unequivocal evidence for its multiple and independent origin. Such a tooth pattern might be derived merely by the elongation of one arm of a chevron tooth and the reduction of the other. Alternatively, the elongate tooth can give rise to a taxodont tooth by developing a process and then foreshortening the main axis. The teeth on the posterior hinge plate of *Pristigloma nitens* represent a possible transitional stage (Sanders and Allen, 1973). Of even greater relevance is the documentation in the present paper of the tooth pattern in *Prelametila clarkei* which represents an almost ideal intermediate stage. The medial teeth are taxodont, the distal teeth elongate, and the teeth inbetween have a greatly foreshortened dorsal and a considerably elongated ventral arm.

This constant progression distally from the taxodont to the elongate tooth configuration is even more continual if we consider the teeth on both valves together. Since any given tooth on the right valve inserts more medially than its counterpart on the left valve, *i.e.,* tooth 2 on right (T_2R.V.) as compared to tooth 2 on left valve (T_2L.V.), it is slightly more taxodont in structure. Beginning with the distal elongate tooth on the right valve, the constant trend medially towards the taxodont morphology is as follows: T_4R.V. → T_3L.V. → T_3R.V. → T_2L.V. → T_2R.V. → T_1L.V. (see Fig. 36).

SHELL DIMENSION RELATIONSHIPS

We have observed that the shell shape of many species of deep-sea protobranchs changes as the animal grows, and *Silicula* is no exception. While there is much individual variation, when height/length ratio is plotted against length, there is a continuous shift to lower ratios with increasing length, *i.e.,* the shell elongates as it grows. This is least apparent in *S. filatovae,* and it is significant that this species is the least extended posteriorly with the umbo relatively central in position. *S. fragilis* and *S. mcalesteri* show much greater elongation with increasing size, particularly *S. fragilis* (Fig. 5). In both cases the small umbo is anterior in position and, when the ratio—distance from the anterior shell margin to the umbo/length—is plotted against length, there is a comparable shift to lower ratio values with increasing length, confirming that much of the elongation is due to posterior growth.

Similar measurements taken for *Lametila* show a different picture (Fig. 34). The height/length relationship of this species shows little change with increasing size; if anything there is a slight tendency for the ratio value to increase with increasing length. In contrast the umbo/length to length plot is very similar to that in *Silicula.* We believe that the change in position of the large umbo relative to length is a consequence of a relatively large tangential component of shell growth (Owen, 1952) in association with a large umbo and globular form (a relatively high value for the angle of the logarithmic spiral).

These changes in shape are what might be expected if our conclusions on the functional morphology and habits of these animals are correct.

REPRODUCTION

Unlike the condition found in the Pristiglomidae (Sanders and Allen, 1973), sexes are separate in the Siliculidae and Lametilidae. As many of the shells are transparent we were able to determine the degree of development of the gonad and, from experience, found it convenient to adopt a scale of maturity (0–8), the limits being (0), immature specimens in which no development of the gonads could be seen in lateral view by means of a stereo binocular, and (8), fully ripe animals in which the whole of the body organs were overlain (laterally) with mature gametes. (We have no evidence that the scale of maturity represents an arithmetic progression.) In all species of the Siliculidae and Lametilidae the gonads develop ventrolaterally along a narrow band in the body below the digestive gland and lower sections of the hindgut and also below the heart. With increasing maturity the gonads enlarge and extend dorsally until all available space within the body is occupied (Table II).

In all three species of *Silicula* in which gonads were examined, males and females were in approximately equal numbers. However, it is evident that, although the sizes overlap, males are on an average larger than females and the larger specimens have the more mature gonads. The overall picture of maturity differed according to species. In the shallow-water representative *S. mcalesteri* (Sta. 280, 1971), of 49 specimens examined only one individual showed no sign of gonadal development and in one other it was impossible to sex the animal from external examination (classified as incipient (1)). The 47 remaining specimens were maturing, several

TABLE VII. EGG AND PRODISSOCONCH SIZE AND EGG NUMBER FOR 5 SPECIES OF PROTOBRANCHS.

	Max. Egg Size (μ)	Prod. Size (μ)	Egg Number
S. filatovae	70	290–310	c2000 (4 mm t.l.)
S. fragilis	70	200	c1000 (4 mm t.l.)
S. mcalesteri	90	580	c1000 (8 mm t.l.)
L. abyssorum	70	370	260 (2.5 mm t.l.)
P. clarkei	?	190	? —

being fully ripe; furthermore, the largest specimens were more mature than the smallest.

In the case of S. *fragilis* where specimens from two samples were available, less than half of those from Station 85 showed any trace of gonad development and of those maturing none were more than one-fourth mature. A similar picture was obtained at Station 126, 13 1/2 months later, although here there were a few with more advanced gonad development. The relationship between size and sex is similar both in S. *mcalesteri* and S. *fragilis*, with males being on average larger than the females.

Gonad development of S. *filatovae*, from Station 85, is similar to S. *fragilis* at the same station, though those specimens of S. *filatovae* with developing gonads were in a somewhat more advanced state of maturity.

In all three species there is a wide overlap in the length of the maturing males and females. Although the males are on average longer than the females, there is no evidence of protogyny.

Gonadal development in specimens of *Lametila* from Station 64 is somewhat different from that in *Silicula*. The largest specimens are males and there is little size overlap with the smaller females. The sex ratio is approximately one male to three maturing females. There is a relatively wide range of gonadial stages in the sample. While there is no evidence of sex change in *Silicula*, it would appear, from our limited data, that *Lametila* is protogynous.

That males are larger than females, and that in *Lametila* the female phase precedes the male phase, would appear to have considerable advantage in the deep sea where animal density is low. Larger animals produce more gametes and sperm density is maximized. There is no evidence of brooding in any species discussed in this paper. Egg size is relatively small in all species; however, prodissoconch size varies considerably and, with the exception of *Prelametila*, is relatively large.

In the light of the data presented by Ockelmann (1965) for lamellibranchs, it would seem to be a paradox in that egg size would indicate planktotrophic/lecithotrophic development whereas prodissoconch size would indicate lecithotrophic/direct development (see Table VII).

Ockelmann (1965) does not give information about the Protobranchia and it may well be that their development, involving a "barrel-shaped" larva, does not conform to the general rule applying to the Lamellibranchia.

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Monograph of the Genus *Alcadia* in Cuba (Mollusca: Prosobranchia: Helicinidae)

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MONOGRAPH OF THE GENUS *ALCADIA* IN CUBA (MOLLUSCA: PROSOBRANCHIA: HELICINIDAE)

KENNETH J. BOSS AND MORRIS K. JACOBSON

CONTENTS

Abstract. In this paper, the fifth in a series on the land snails of the prosobranch family Helicinidae in Cuba, the systematics of the genus *Alcadia* is considered, with one new subgenus and one new subspecies introduced. All nominal taxa hitherto proposed on the generic and infrageneric levels were investigated. Fifteen species, two polytypic, are recognized in five distinct subgenera. The zoogeographic distribution of *Alcadia* is contrasted with other Cuban helicinids; *Alcadia* is thought to have invaded Cuba largely by fortuitous transport from Jamaica.

INTRODUCTION

The terrestrial prosobranch family Helicinidae is distributed in two widely separated areas of the world. In the western hemisphere, the family is largely subtropical and richly developed in the Caribbean region. The Philippine Islands and adjacent areas in the eastern hemisphere form the other major concentration of the family. In the Caribbean, the Antillean islands have a highly diversified helicinid fauna, and Cuba, the largest of the Greater Antilles, has an especially rich elaboration of forms with no fewer than four endemic genera.

This paper is the fifth in a series on the Helicinidae of Cuba. Previous studies were devoted to analyses of the highly localized genera *Viana* (Clench and Jacobson, 1968) and *Priotrochatella* (Clench and Jacobson, 1970) as well as the more complex and more widely distributed taxa, the vianine genera, *Ustronia*, *Troschelviana*, *Calidviana*, and *Semitrochatella* (Clench and Jacobson, 1971b) and the endemic helicinine groups, *Emoda* and *Glyptemoda* (Clench and Jacobson, 1971a).

The present study deals with the genus *Alcadia*, a neotropical group occurring on most of the islands in the West Indies as well as on the mainland from southern Mexico to northern South America. Both Jamaica and Cuba support a considerable number of species of the genus, but representatives are also found in Puerto Rico, Hispaniola, and most of the Lesser Antilles south to Trinidad.

This series of papers has, of necessity, been devoted largely to *alpha* taxonomy. No critical revisions of the Cuban helicinids have appeared previously and solution of considerable nomenclatorial problems is basic. Much of the earlier work in Cuba consisted of the description of new species from localized collections, while monographic works, in which the fauna of the entire island was considered, were virtually nonexistent. Recognizing a species' variations and noting the extent of its distribution have proven valuable in attempting to analyse the Cuban helicinid fauna. The number of nominal taxa has been greatly reduced. For example, *Emoda,* of which nearly 30 forms had been described, now consists of 13 species, three of which are polytypic.

The complexities of the taxonomy on a generic level reflect in large part our current ignorance concerning the interrelationship of the various recognizable species-groups of helicinid land snails. Certainly, generic and subgeneric limitations are subject to change in the future as more species are investigated and more information is accumulated on the features that are presently utilized as taxobases. We have been hampered in the lack of properly preserved materials. And the exact value of the structure of the radula in defining generic-level taxa remains to be carefully examined.

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ABBREVIATIONS

ANSP—Academy of Natural Sciences, Philadelphia
BMNH—British Museum (Natural History), London
CBA—Charles B. Adams
IZW—Instytut Zoologiczny Warszawa, Poland
MCZ—Museum of Comparative Zoology, Cambridge, Massachusetts
MP—Museo Poey, Havana, Cuba
USNM—United States National Museum, Washington, D.C.

All localities cited under *Specimens examined* without an acknowledgment to a museum are from the MCZ.

HISTORICAL REVIEW

Alcadia has been widely accepted since 1840, when it was introduced by Gray (Wenz, 1938; Keen, 1960), although some writers (C.B. Adams, 1849–1852; Sowerby, 1866; Reeve, 1874; Arango, 1879) ignored it. Pfeiffer (1852, 1858, 1865, 1876), in the various editions and supplements of his Monographia Pneumonopomorum Viventium, brought together the descriptions of various species, but provided little comparative material. A much more thorough monograph was published by Wagner (1907, 1910), who arranged the species in a system based upon the shell and the operculum. He established several new subgenera and divided the species into *Formenkreise.* Unfortunately he overlooked earlier names (*e.g., Idesa* H. and A. Adams 1856) and separated other subgenera (*e.g., Eualcadia*) on insufficient grounds. But his contribution, as Baker (1922: 29) wrote, is a great advance on all previous work.

Wagner (1907) used the term *Formenkreis* to designate a group of species of infrasubgeneric status. Almost all the *Formenkreise* bear the name of the one of the species in the group. In no case is the *Formenkreis* provided with a description or diagnosis. H. B. Baker (1922) and others accepted some of these *Formenkreis* names as subgenera, with the species name of the *Formenkreis* as the type-species by tautonomy. Keen (1960: 286) suggested that the status of the *Formenkreis* needs clarification. The question was briefly discussed by Mayr *et al.* (1953: 28f) who pointed out that *Formenkreis,* together with Rensch's *Rassenkreis,* though logical, was not widely followed by subsequent writers. In our opinion Wagner's *Formenkreis* names are nothing more than species-group names, designated by the trivial name of a species within the group, and hence should deserve no more taxonomic distinction than, for example, the "group of . . ." names used by Pilsbry in the Manual of Conchology. Although both Baker (1922) and Keen (1960) synonymized some of these nomina, we have not included Wagner's *Formenkreis* names in generic and subgeneric synonymies in order to obviate further taxonomic complications, because we feel these nomina are invalid. The nomina under discussion are the following:

Palliata Wagner 1907, *in* Martini & Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 2, p. 47
Intusplicata Wagner 1907, *ibid.,* p. 60
Sericea Wagner 1907, *ibid.,* p. 62.
Incrustata Wagner 1907, *ibid.,* p. 64
Megastoma Wagner 1907, *ibid.,* p. 66
Nitida Wagner 1907, *ibid.,* p. 68
Mamilla Wagner 1907, *ibid.,* p. 71
Bellula Wagner 1907, *ibid.,* p. 74
Ampliata Wagner 1907, *ibid.,* p. 76
Tamsiana Wagner 1907, *ibid.,* p. 78
Gemma Wagner 1907, *ibid.,* p. 81

The last two names on the list are not *Alcadia.*

New subgenera *Isoltia, Hjalmarsona, Penisoltia* were proposed by Guppy (1895) and Baker (1940, 1954). In the present work the new subgenus *Glyptalcadia* is introduced.

TAXOBASES

Alcadia was established by Gray (1840) on the basis of the basal notch or sinus which separates the peristome from the columella. This characteristic of shell morphology, together with certain features of the operculum, still constitutes the most reliable method of distinguishing members of the genus. Bourne (1911: 798), who investigated the anatomy of *A. palliata* (C. B. Adams) and *A. hollandi* (C. B. Adams) from Jamaica, concluded that in respects other than the two mentioned above, "*Alcadia* is similar to the point of identity to *Helicina.*" Baker (1926) also noted the essential similarity of *Alcadia* with *Helicina* as described by Isenkrahe (1867). Remarks concerning proposed studies of the anatomy of Cuban helicinids were made previously (Clench and Jacobson, 1971a). Earlier, Troschel (1857: 82) expressed surprise that he could find little to distinguish the radula of *Alcadia* from that of *Helicina* in view of the difference in shell morphology. Thus the radulae of *Helicina* and *Alcadia* differ less than their opercula and shells.

The present study shows that *Alcadia s.l.* is recognizable by the presence of a basal notch or sinus, a basal tooth or tubercle which is a downward and outward extension of either the columella or of the umbilical margin of the basal callus, and the wedge-shaped internal lamella and groove on the columellar edge of the operculum (Fig. 2). Additionally the nature of the periostracum—its presence or absence, its relative development and disposition on the shell—was found to be significant in characterizing some species of *Alcadia.*

Radula

The radula in various species of *Alcadia* has been investigated by Troschel (1857), Bourne (1911), and Baker (1922, 1926). We have examined the radulae of *major* Gray, the type-species of the genus *Alcadia* from Jamaica; *hispida* Pfeiffer, the type-species of the subgenus *Penisoltia* H. B. Baker; *rotunda* Orbigny, the type-species of the subgenus *Idesa* H. and A. Adams; *nuda* Arango and *incrustata* Gundlach.

The radula of *Alcadia* (Fig. 1) exhibits the essential features of a helicinid (Troschel, 1857): a single central rachidian tooth (R), flanked by A, B, and C centrals and a lateral complex (LC) consisting of a comb-lateral and an accessory plate and a marginal complex (MC) consisting of numerous teeth or uncini. These structures can be abbreviated in the formula: (MC) (LC) C B A R A B C (LC) (MC).

In the Helicininae, to which the genus *Alcadia* belongs, the marginal teeth all have sharp, acuminate cusps; the comb-lateral has a terminal shank, and the accessory plate on the outer end is highly variable. As described by Baker (1922), the A- and B-centrals have heavy, knob-like, cusp-bearing backs, the A-central having 4 or 5 cusps, the B-central 5; the C-central has 4 cusps, and the R-central is longer than broad (see below). The comb-lateral of the capituliform complex has been described as having variously 4 to 7 large, spatulate cusps, but *A. major* Gray from Jamaica, the type-species of the genus, has a smooth, cuspless cutting edge. The taxonomic significance of this feature is not discussed in the present study. The marginal teeth, of variable number, between 82 and 125, have a laterally increasing number of cusps, the innermost 10 with 3 cusps, the next 5 to 7 with 4, the next 4 with 5 and the last ones with 6. Baker (1923: 119) writes that the trend in the Helicinidae seems to be a reduction of the central field, an increase in specialization of the lateral group, but only a comparatively slow change in the marginal complex.

Text-figure 1. The radula of *Alcadia palliata* (C. B. Adams) from Jamaica (after Baker, 1922), showing the central rachidian tooth (R), the three centrals (A, B, C) the lateral complex with the comb lateral (CL) and accessory plate (AP) and three of the uncini (nos. 1, 5, 15) of the marginal complex.

In the Proserpininae, another important helicinid subfamily, the 14 to 24 inner marginals are unicuspid, the next 2 to 10 are bicuspid, and the rest have 3 large rounded cusps. The A- and B-centrals have 0 to 3 cusps and the C-central 1 to 4. The R-central is triangular-ovoid to broadly elliptical in shape. The T-shaped comb-lateral with a mesially located shank has 0 to 10 cusps, and the accessory plate is reduced in size and has a much reduced lateral wing.

Possessing a terminally placed vertical column of the comb-lateral tooth, *Alcadia* exhibits its affinities to the subfamily Helicininae, especially to *Helicina* itself. Indeed, Troschel (1857), investigating the radula of *A. rotunda* (Orbigny) and *A. palliata* C. B. Adams, noted that the central tooth (the R-central in Baker's terminology) was triangular or diamond-shaped in *Alcadia.* This tooth is usually button-shaped in *Helicina.* However, this distinction cannot hold because the R-central was found to be too variable. For example, *A. rotunda*, the type-species of the subgenus *Idesa*, has a button-shaped tooth.

Baker (1922) has presented the most detailed investigation of the helicinid radula to date. Among species of *Alcadia*, differences occur in the size of the accessory plate of the lateral tooth complex and in the cusps of the paired central teeth. In the Cuban species we studied (*hispida, rotunda, nuda,* and *incrustata*), the comb-lateral was strikingly similar. This structure has a high basal column and a narrow reverted upper margin with 4 to 6 large, triangular cusps. Although Baker (1922: 42) reported 7 cusps in *rotunda,* we could locate no more than 4. In contrast, *A. major* from Jamaica has a smooth edge with no visible cusps (Baker, 1922).

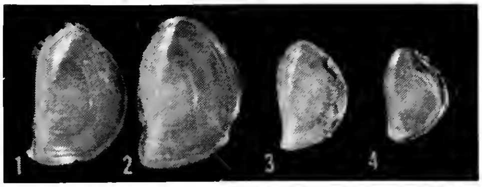
From these very sparse data, it is obvious that the radula cannot presently be used as a diagnostic feature for *Alcadia.* Accordingly, we have placed more emphasis on the features of the shell and periostracum in our investigation.

HABITATS OF *ALCADIA*

Within *Alcadia s.l.,* there are two ecologically different groups: *Idesa,* which is largely arboreal, and those species of *Alcadia s.s.* and *Penisoltia* which are terrestrial, being found under dead leaves, rock, and in moss. Further, in the subgenus *Hjalmarsona,* both arboreal (*neebiana* Pfeiffer) and ground-dwelling forms (*nitida* Pfeiffer) are found. In contrast, other closely related helicinids, such as *Eutrochatella* and other genera of the tribe Vianini in the subfamily Proserpininae, are all strict calciphiles, occurring largely on calcareous rock outcrops (Clench and Jacobson, 1968). Most of the species of *Helicina s.s.* are arboreal, living on the leaves of trees and bushes and quite free of the requirement for a rocky substrate.

In general the terrestrial species of *Alcadia s.l.* are drab and mostly brownish shells frequently incrusted with a dehiscent periostracum.

The operculum, as mentioned previously, has a wedge-shaped internal lamella and groove on its columellar edge (Fig. 2). Although it does not possess the basal extension which Gray (1840) and Fischer (1885) ascribed to it, the operculum is capable of very tight closure in *Alcadia.* Apparently the closure is strengthened by the basal notch or sinus into which the pointed tip of the operculum fits and in which it swivels like a door hinge.



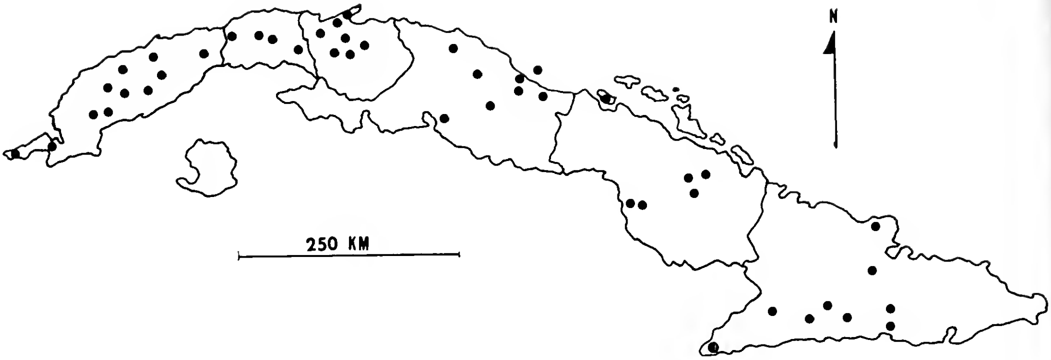
Text-figure 2. Internal view of opercula of *Alcadia* showing internal lamella and groove on the columellar edge (all enlarged). 1) *Alcadia nuda bagaensis* Aguayo (MCZ 128775); 2) *A. nuda nuda* (Pfeiffer) (MCZ 90052); 3) *A. incrustata* (Pfeiffer) (MCZ 74028); 4) *A. spectabilis* (Pfeiffer) (MCZ 74024).

This apparently allows for a strong closure of the operculum, possibly an adaptive feature for species living in the ground mulch or under rocks, for it enables them to resist small predators and dessication. In contrast the rock-dwelling vianine snails, with their calcareous opercula, can find protection by strongly applying the aperture to a hard rock surface.

The arboreal species of *Alcadia,* notably the members of *Idesa* as well as *Hjalmarsona neebiana,* tend to have a smooth, polished periostracum, being rather highly colored and polymorphic like species of *Helicina s.s.* Additionally, the operculum in this group is a less important protective organ and is indeed characterized by a weakened outer calcareous layer and, in general, a decidedly thinner structure.

DISTRIBUTION OF *ALCADIA*

Maps 1–3 show the distribution of the species of *Alcadia* in Cuba. The principal feature that emerges from this zoogeographic pattern is the disjunct nature of the occurrence of most of the species and subgenera. Excepting *Alcadia* (*Penisoltia*) *minima* (Orbigny) (Map 1), which is found in all six of the Cuban provinces (but not on the Isle of Pines) and which is evidently easily dispersed owing to its small size and broad ecological tolerance, the species of *Alcadia* present a more haphazard distributional pattern than any of



Map 1. The distribution of *Alcadia (Penisoltia) minima* in Cuba.

the groups previously considered. Of the vianine helicinids, both *Viana* and *Priotrochatella* are of limited distribution in Cuba in Pinar del Río and the Isle of the Pines respectively (Clench and Jacobson, 1968; 1970). *Ustronia, Troschelviana,* and *Semitrochatella,* also of vianine affinities, exhibit a zoogeographic pattern which indicates that the basic stock of these species entered Cuba via the west from the subtropical mainland of Mexico and Central America and subsequently spread eastward (Clench and Jacobson, 1971b). *Calidviana,* with its single species representing an invasion from the Bahamas (Clench and Jacobson, 1971b), is comparable to the *Alcadia nuda* complex in Oriente (Map 2).

The helicinine genera *Emoda* and *Glyptemoda* reflect a westward movement over the island from Oriente. Species of these genera have a wider ecological tolerance, and though usually confined to mountainous areas, they are not as closely restricted to limestone outcrops as is *Viana* and are sometimes found under leaves, branches, and vines in a ground-dwelling habitat. Like *Alcadia minima,* one species of *Emoda,* namely *E. submarginata,* is eurytopic and has a range embracing the entire island (Clench and Jacobson, 1971a). *Emoda* represents an element coming from the east, most probably Hispaniola, the other Antillean island which has numerous faunal elements in common with Cuba, and which may have been directly connected with it during the Tertiary (Weyl, 1966).

How then may one interpret the distribution of the majority of the species of *Alcadia* in Cuba?

An examination of the Jamaican species shows that many are so close morphologically and analogous ecologically to Cuban species, without any corresponding Hispaniolan forms, that it is difficult to deny the immediate relationship of Jamaican and Cuban species. Following the beautifully reasoned and skillfully presented argument of Darlington (1938), one can accept the assumption that the original stock of *Alcadia* was derived from the mainland of Central America and underwent a primary evolutionary radiation in Jamaica.

Darlington (1938: 295) suggested that the main contact between Jamaica and Cuba, geologically and probably faunistically, was via Hispaniola. He placed the direct connection Jamaica-Cuba in a secondary position, and in all probability a series of archipelagos existed in this area during the late Tertiary (Khudoley and Meyerhoff, 1971). Various authorities were cited by Darlington to indicate direct faunal relationship between Jamaica and Cuba, but the evidence amassed is contradictory.

Both Jamaica and Cuba each have about 18 species and subspecies of *Alcadia,* whereas Hispaniola only has about ten, four of which belong to the subgenus *Analcadia*.[1] Of note is the occurrence of the subgenus *Idesa* in both Cuba and Jamaica and its absence from Hispaniola.

Of the Cuban *Alcadia*, only a minor element was almost certainly not derived from the Jamaican fauna. *Alcadia binneyana* Pfeiffer 1866 from Hispaniola appears to be the ancestor of *A. spectabilis* in Oriente, Cuba. Since *binneyana* is reported only from Haiti and *spectabilis* occurs only in Oriente, the Cuban area closest to the Haitian portion of Hispaniola, *spectabilis* may be assumed to be the result of a more or less isolated invasion.

In many cases the morphological similarities are so close between the Jamaican and Cuban species that the Cuban forms must be assumed to have been comparatively recently introduced. Dispersal of elements from Jamaica to Cuba was probably effected as the result of hurricanes. The paths of these tropical storms are strongly suggestive (Darlington, 1938: fig. 1). Further, among the Helicinidae of Cuba, at least one other example of a probable invasion from Jamaica has been suggested for *Priotrochatella* in which the species of the Isle of Pines appear to have been derived from *P. josephinae* (C. B. Adams) of Jamaica (Henderson, 1916; Clench and Jacobson, 1970).

Table 1 summarizes the data on analogous species from Jamaica and Cuba. An explanation of the conchological and morphological similarities between Jamaican and Cuban forms is beyond the scope of this monograph, but suffice it to say that such factors as size, outline, and color as well as the nature of the basal sinus and tooth show striking resemblances.

This hypothesis suggests that *Alcadia* did not undergo extensive evolutionary radiation in Cuba. Excepting two elements, one from the Bahamas and the other from Hispaniola, the majority of the Cuban forms were introduced from Jamaica and appear to have retained much of their original character with slight modification. Furthermore, it is most likely that they arrived via the mechanism of hurricane winds. Certainly they have remained more or less fixed in the areas where they arrived and found favorable ecological conditions for survival similar to those in Jamaica.

Since *Alcadia* simply does not exhibit a pattern of distribution such as those found in *Emoda* or the vianine genera which reflect their evolutionary history on the island (Clench and Jacobson, 1968; 1970; 1971a and b), this notion explains why, of the 17 specific and subspecific taxa of *Alcadia* which we recognise in the Cuban fauna, no fewer than 13 (and probably 14) occur in only a single province. It will also

Table 1. Comparison of closely related species of the genus *Alcadia* in Jamaica and Cuba. The ecological preferences are taken from H. B. Baker (1934) for Jamaica and Arango (1879) for Cuba

Jamaican species	habitat	Cuban species	habitat
megastoma C. B. A.	fair climber	*rotunda* Orb.	trees
dubiosa C. B. A.	ground	*hispida* Pfr.	under rocks, leaf litter
hollandi C. B. A.	weak climber, mainly ground	*velutina* Poey	on rocks
pusilla C. B. A.	mainly ground	*minima* Orb.	under rocks
major Gray	rock basis	*nuda* Arango	on trees
solitaria C. B. A.	no data	*dissimulans* Poey	on rocks

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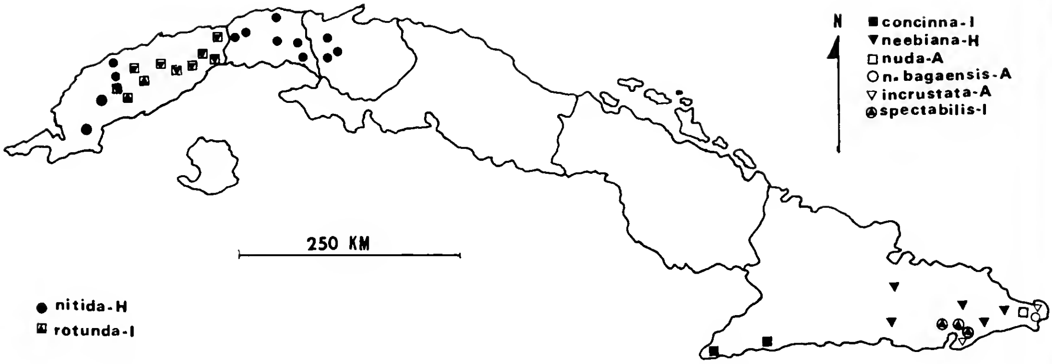
[1] We have not considered the subgenus *Analcadia* Wagner 1907, since it occurs neither in Cuba nor Jamaica.



Map 2. The distribution of the subgenera *Hjalmarsona* (H), *Alcadia* s. s. (A), and *Idesa* (I) in Cuba.

account for the presence of such analogous forms as *A. nitida* in the western part of the island and *A. neebiana* in Oriente.

The distribution of the subgenera also bears out our premise. Either we find species of the same subgenus in widely separated areas (*e.g.*, *Idesa* in Pinar del Río and Oriente, Map 2; *Hjalmarsona* in the west in Pinar del Río, Habana, and Matanzas and in the east in Oriente, with no forms in intervening Las Villas and Camagüey, Map 2) or we find them in a single, more or less restricted area (*e.g.*, *Alcadia s.s.* only in Oriente, Map 2; *Glyptalcadia* in Oriente and Camagüey, Map 3). Only *Penisoltia,* to which the ubiquitous *minima* belongs, is found in all provinces as well as on the Isle of Pines (Maps 1 and 3).

SYSTEMATIC SECTION

GASTROPODA

PROSOBRANCHIA

Family HELICINIDAE Latreille, 1825

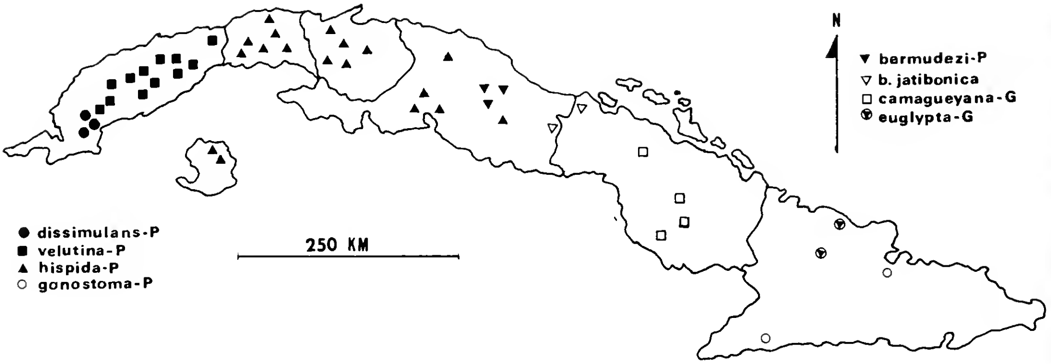
Subfamily HELICININAE Latreille, 1825

Genus **Alcadia** Gray

Alcadia Gray, 1840. Synopsis Contents British Mus., 42nd ed., pp. 134, 153 (or 130, 149) (type-species, *Helicina major* Gray, 1825, subsequent designation, Gray, 1847).

Isoltia Guppy, 1895. Proc. Victoria Inst. Trinidad, Part 2, p. 76 (type-species, *Helicina nuda* "Arango" Pfeiffer, 1866; by monotypy).

Eualcadia Wagner, 1907. *In* Martini and Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 2, p. 47 (type-species, *Helicina major* Gray, 1825, subsequent designation, H. B. Baker, 1922).



Map 3. The distribution of the subgenera *Penisoltia* (P) (except *A. P. minima*) and *Glyptalcadia* in Cuba.

Eucaladia Wagner, 1907. *Ibid.*, p. 46 (spelling error for *Eualcadia*).

Description. Shell moderately large (about 20 mm in width, 15 in height) to quite small (about 5 mm in width, 4 mm in height); depressed turbinate to almost lenticular; moderately strong; surface sculpture generally light, periostracum smooth, pilose or hirsute; peristome simple to moderately flaring; basal sinus small to curved and long. Operculum deeply concave with a variously thin but well-formed outer calcareous layer and an inner, generally horn-colored, thin corneous layer; thickest at the columellar margin; inner surface with a variously shaped, elongate ridge set off by a parallel furrow; outer margin bladelike; nucleus eccentric near the columellar margin.

Remarks. The shell of the members of the genus are distinguished by the presence of a basal notch or sinus, usually accompanied by a variously shaped and sized tooth or tubercle near the columella. The pilose or hirsute periostracum is diagnostic for the subgenera *Alcadia s. s.* and *Penisoltia;* in *Hjalmarsona* and *Idesa* the shell is generally quite glossy.

The operculum differs from that of *Helicina s. l.* in several respects: In *Helicina neritella* Lamarck, the type-species of the genus *Helicina*, the outer calcareous layer is very thin and does not extend to the upper, outer, and lower margins of the strong, dark reddish brown chitinous layer. Here the main structure is the chitinous layer, the calcareous layer appearing as a weak concretion. In addition the operculum is only slightly thicker at the columellar margin, becoming thin rapidly and remaining equally thin for the major portion of the structure. The edges present a frayed appearance probably because in this way they insure complete closure when the animal is retracted. There is no sign of the heavy internal wedge-shaped lamella of *Alcadia*.

In *Alcadia major* the calcareous layer is thick and strong, thinning out only when the outer margins are reached. It is twisted when viewed from the edge whereas in *Helicina* the operculum is almost on a single plane. The inner chitinous layer is very thin, frequently film-like, reaching well beyond the margins of the calcareous layer, even on the columellar edge. Closure here is insured by the extension beyond the margin. Thus in *Alcadia* the calcareous layer is the stronger one, the chitinous appearing only as a thin, internal skin.

KEY TO THE SUBGENERA OF *Alcadia*

1. Shell surface roughly and irregularly sculptured .... GLYPTALCADIA
   Shell surface comparatively smooth 2
2. Shell robust, generally large, palatal lip well developed .... ALCADIA s. s.
   Shell fragile, smaller, lip weakly developed 3
3. Periostracum hirsute or pilose, deciduous .... PENISOLTIA
   Periostracum glossy, persistent 4
4. Spire elevated, frequently colorful ...... IDESA
   Spire more or less depressed, drab .... HJALMARSONA

Subgenus **Alcadia** s. s. Gray

Type-species, *Helicina major* Gray, 1825; subsequent designation, Gray, 1847.

Description. Shell large, strong; periostracum hirsute; operculum strong; basal notch and tubercle weakly developed; palatal lip strong, expanded, occasionally reflected.

Remarks. Our concept of *Alcadia s. s.* differs somewhat from that of Wagner and is here presented provisionally. A proper placement of all species must await more radular and anatomical investigation. However, the characteristics of the shell have always been considered diagnostic for the genus.

KEY TO THE SPECIES OF *Alcadia* S. S.[1]

1. Shell small, up to 9 mm in width .... *incrustata*
   Shell larger, 11 to 15 mm in width 2
2. Shell up to 15 mm in width, lip thickened, strongly reflected .... *nuda nuda*

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[1] These artificial keys to the species of the various subgenera of Cuban *Alcadia* are based on distinctions apparent in large lots rather than individual specimens and are thus more useful in determining populations than single specimens or small lots.

Shell up to 12 mm, lip thickened but not reflected .... *n. bagaensis*

Alcadia (Alcadia) nuda nuda (Pfeiffer)

Plate 2, figures 7–9; Text-fig. 2; Map 2

Helicina nuda "Arango" Pfeiffer, 1866. Malak. Blät., 13: 63 (type-locality, Barigua, [Baracoa, Oriente] type destroyed; specimen here figured, MCZ 90052, T. Bland Collection *ex* Arango). Pfeiffer, 1876, Monographia Pneumonopomorum Viventium, suppl. 3, p. 253. Arango, 1879, Contribución Fauna Malacológica Cubana, p. 50. Crosse, 1890, Jour. de Conchyl., 38: 317, pl. 6, figs. 5, 5a–d.

Helicina nodae Reeve, 1873. Conch. Icon., vol. 19, *Helicina,* pl. 11, fig. 93 [not *Helicina nodae* Arango, 1862].

Alcadia (*Eualcadia*) *nuda* (Arango) Pfeiffer. Wagner, 1907, *in* Martini and Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 2, p. 64, pl. 16, figs. 9–12.

Description. Shell reaching about 11 mm in height, 15 mm in width, depressed conic, smooth, lusterless, solid. Color pale yellow or white, lip and basal callus white. Whorls 5½, slightly convex, increasing rapidly in size. Body whorl about twice as wide as penultimate, obtusely carinate, more rounded and not descending near aperture; base moderately inflated. Aperture broadly triangular, white or yellow within, rounded peripherally, straight basally. Parietal callus white, slightly raised, gleaming, rounded at outer margin, somewhat larger than aperture. Palatal lip thickened, rounded, reflected, narrower at both insertions, not extended above; small, rounded, outwardly directed tooth at columellar angle set off from lip by small, shallow labial sinus. Columella oblique, almost flat above, weakly rounded below. Suture well impressed. Sculpture of irregular, moderately strong, diagonal growth lines; occasional specimens with a few, widely spaced, spiral striae, varying in strength. Axial lineolations within shell substance straight, about twice as wide as their intervals. Protoconch 1½ whorls, white, rounded, microscopically and sparsely punctate, slightly raised above succeeding whorls. Periostracum deciduous, lost in subadult and adult, pilose, reddish brown. Operculum as in genus, outer calcareous layer thin, translucent, minutely granulate; inner chitinous layer pale brown near columellar edge, dark reddish brown at outer margin; inner wedge-shaped lamella well developed.

height in mm	width in mm	
11.5	14.5	Barigua, Baracoa
11.4	14.6	Mesa Grande del Sapote, Baracoa
10.9	15.2	Barigua, Baracoa

Remarks. This species differs from other Cuban *Alcadia* because of its solid texture and thickened, reflected lip. The basal tooth does not emerge from the callus, as in the other species of *Alcadia* but is a clear expansion of the palatal lip. The basal sinus is smaller and the entire structure near the columella is more like *Emoda* than *Alcadia.* However, since it has an unmistakable *Alcadia*-like operculum it seems best to keep it in that genus where it was first placed by Wagner (1907).

The periostracum is very deciduous and in most specimens appears only as a very narrow relic left in the sutures and the crevices between the growth lines. Even in a subadult specimen from Mesa Grande del Sapote with an unformed lip, only a small area of untouched periostracum on an early postnuclear whorl was found.

The species is restricted to a small area around Barigua, Baracoa, Oriente Province. Arango (1879) reported that it lives on trees, but this is unlikely because of its heavy, deciduous periostracum. It probably is a ground-dwelling form occurring under rocks and dead leaves where the related species *A. incrustata* is said to live (Pfeiffer, 1860; Arango, 1879).

The white or pale yellow color and the *Alcadia*-like operculum will separate *nuda* from species of *Emoda,* while the heavy, rounded and reflected lip will distinguish it immediately from the other Cuban *Alcadia.*

Specimens examined. ORIENTE. Barigua, Baracoa; Mesa Grande del Sapote, Baracoa.

Alcadia (Alcadia) nuda bagaensis Aguayo

Plate 1, figures 7–9; Text-fig. 2; Map 2

Alcadia nuda bagaensis Aguayo, 1953. Memorias de la Sociedad Cubana de Historia Natural, 21: 301, pl. 33, figs. 4–5 (type-locality, Bagá, Baracoa, Oriente; holotype MP 17315.)

Description. Shell like that of nominate subspecies but differing in smaller size, thickened but not reflected lip, and in more persistent periostracum.

height in mm	width in mm	
10.2	12.4	El Bagá, Maisí, Oriente
9.2	11.0	El Bagá, Maisí, Oriente

Remarks. This subspecies has the solid, smooth shell of *nuda nuda* with the same coloration, a bit more vivid in some individuals. The periostracum has numerous irregular, narrow, spiral ridges and persists moderately well even in adult shells. It closely resembles *incrustata* Pfeiffer, but it has a relatively more thickened lip and weaker periostracum and is considerably larger.

Bagá lies about 20 km to the southeast of Barigua, the type-locality of the nominate subspecies. The intervening territory is mountainous. This subspecies is thus geographically as well as morphologically justified (Aguayo, 1953).

Specimens examined. ORIENTE. El Bagá, Maisí, Oriente.

Alcadia (Alcadia) incrustata (Pfeiffer)

Plate 2, figures 10–12; Text-fig. 2; Map 2

Helicina incrustata "Gundlach" Pfeiffer, 1859. Malak. Blät., 6: 80 (type-locality, Yateras, Guantánamo, Oriente, type destroyed; specimen here figured MCZ 74028, J. G. Anthony Collection *ex* Poey). Sowerby, 1866, Thes. Conchyl., 3: 280, pl. 2 (267), fig. 50.

Alcadia incrustata Gundlach. Pfeiffer, 1865, Monographia Pneumonopomorum Viventium, suppl. 2, p. 249. Arango, 1879, Contribución Fauna Malacológica Cubana, p. 57.

Alcadia (Eualcadia) incrustata (Gundlach) Pfeiffer. Wagner, 1907, *in* Martini and Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 2, p. 64, pl. 16, figs. 5–8.

Description. Shell reaching about 9 mm in width, 7 mm in height, depressed-globose, solid, smooth, sublustrous under periostracum. Whorls 5, faintly convex, increasing rapidly in width. Body whorl one-half again as wide as penultimate, well rounded, not descending at aperture; base moderately inflated. Color pale yellow, light brown or white, lip and basal callus white; frequently covered by dark brown or black encrusted periostracum. Aperture oblique, semi-lunate, evenly rounded, somewhat flattened dorsally and ventrally. Palatal lip noticeably thickened within, not indented at upper insertion, weakly expanded but not reflected, somewhat narrower above, narrowest below; with small, rounded tubercle near columella; basal sinus wanting or barely perceptible, sublustrous, weakly granulate, indistinctly delimited parietally and with shallow, uneven groove separating it at umbilical area. Columella oblique and slightly convex above, shallowly rounded below. Suture strongly impressed. Sculpture consisting of diagonal, irregular growth lines only. Lineolations within shell substance closely spaced, narrow, white, not sinuous. Protoconch 1½ whorls, rounded, minutely and thickly punctate, raised slightly above succeeding whorls. Periostracum dense, pilose, deciduous, occasionally with higher hairs arranged in wide spiral row. Operculum as in genus, calcareous layer white, somewhat roughened on outer surface; chitinous layer very thin, light brown, darker at palatal margin; inner wedge-shaped lamella moderately developed.

height in mm	width in mm	
7.5	9.4	Yateras
6.4	8.3	Yateras
6.3	8.4	Cayojuín, Baracoa
6.2	7.5	E of Puerto de Baracoa

Remarks. This species is readily recognized by the relatively strong shell, thickened and slightly reflected peristome, small basal tooth with a very small or altogether absent labial sinus. It looks like a miniature *A. nuda bagaensis,* but the shell is strikingly smaller, the lip relatively thinner, the yellow or orange color, when present, more vivid, and the periostracum thicker and more persistent. It ranges from the southern part of the municipio of Baracoa to Yateras, thus lying more to the south than the range of *nuda.*

Pfeiffer (1865) quoted Gundlach's description of the animal: ". . . light brownish, the rugosities on the foot and tail with small gray spots. Head and neck appear darker brown because of the visceral mass showing through. Tentacles gray, darker at the base than at the tip," (translated). He also noted that the species occurs under rotten leaves and Arango (1879) added that it was also found under rocks.

Specimens examined. ORIENTE. *Baracoa:* Maisí (USNM); Jauco; Nibujón; Cayojuín; El Paraiso; E of Puerto de Baracoa; Guantánamo; Yateras; Monte Líbano; near Malabé (USNM).

Subgenus **Idesa** H. and A. Adams

Idesa H. and A. Adams, 1856. Genera of Recent Mollusca, 2: 304; type-species *Helicina rotunda* Orbigny, 1845, subsequent designation, H. B. Baker, 1922.[1]

Schrammia Guppy, 1895. Proc. Victoria Inst. Trinidad, Part 2, p. 75 (type-species *Helicina conuloides* Guppy, 1868, by monotypy).

Leialcadia Wagner, 1907. *In* Martini and Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 2, p. 65; type-species, *Helicina rotunda* Orbigny, 1845, subsequent designation, H. B. Baker, 1922.

Description. Shell small, about 6 to 9 mm in width, 4 to 8 mm in height, subglobose, colorful, often glossy, basal tooth and sinus not conspicuous. Periostracum not hirsute, persistent, occasionally bearing bright colors. Operculum as in genus, rather thin. Arboreal.

Remarks. Two of the three species we place in *Idesa* are among the most brightly colored forms in *Alcadia.* In this respect they can be compared to *Helicina s. s.* with which they share the same leafy habitat. It is noteworthy that these two species are completely allopatric: *rotunda* is found in Pinar del Río in the west and *spectabilis* in Oriente in the east. No forms occur in any of the intervening provinces.

Although *Idesa* exhibits a unique disjunctive distribution, something similar is found in two sympatric species of the helicinid *Proserpina.* Both species of *Proserpina* have disjunct ranges with populations occurring in the west, including Pinar del Río and neighboring Havana, and in Oriente without any intervening.

Wagner (1907) and others placed some of the fragile, rather drably colored, depressed species of *Alcadia* in *Idesa* (*Leialcadia* Wagner), but we think they show affinities with *Hjalmarsona* H. B. Baker.

KEY TO THE SPECIES OF *IDESA*

1\. Shell relatively small, 6 mm wide or less, surface not too glossy; distribution limited to SW corner of Oriente Province ...... *concinna*
Shell larger, 7 to 9 mm wide, surface quite glossy 2

2\. Shell color often uniform throughout or with darker spire, color bands always wanting; distribution limited to Pinar del Río Province and western part of Habana Province .... *rotunda*
Shell generally colorful, frequently ornamented with color bands; distribution limited to southern and east-central Oriente Province .... *spectabilis*

Alcadia (Idesa) rotunda (Orbigny)
Plate 2, figures 4–6; Map 2

Helicina rotunda Orbigny, 1842. Mollusques, *in* Sagra, Histoire Physique, Politique, et Naturelle de l'île de Cuba, 1: 252, pl. 21, figs. 1–3 (type-locality, here restricted, Pan de Guajaibon,[2]

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[1] Fischer (1885: 795) cited *H. rotunda* with *Idesa,* but since he did not clearly indicate that this was a type-selection, it must be regarded as an example and not as a type. For this reason the type-selection must date from Baker, 1922, even though the latter credited it to Fischer.

[2] Orbigny gave only his usual "interieur de l'ile" as the locality. Jaume (1945: 75) found it in abundance at the Pan de Guajaibón.

Pinar del Río, Cuba); type in BMNH. Sowerby, 1842, Thes. Conchyl., 1: 13, pl. 3, fig. 111; 1866, Thes. Conchyl., 3: 280, figs. 51–52. Pfeiffer, 1852, Monographia Pneumonopomorum Viventium, p. 357. Reeve, 1873, Conch. Icon., vol. 19, *Helicina*, pl. 4, fig. 29. Arango, 1879, Contribución Fauna Malacológica Cubana, p. 53. Crosse, 1890, Jour. de Conchyl., 38: 320.

Helicina campanula Pfeiffer, 1849. Proc. Zool. Soc. London, p. 120 (type-locality, Cuba; type destroyed); 1850, *in* Martini and Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 1, p. 41, pl. 9, figs. 12–13; 1852, Monographia Pneumonopomorum Viventium, p. 374. Arango, 1879, Contribución Fauna Malacológica Cubana, p. 53. Crosse, 1890, Jour. de Conchyl., 38: 321.

Helicina retracta Poey, 1852. Memorias Historia Natural Isla de Cuba, 1: 116, pl. 12, figs. 22–26 (type-locality, Cayajabos, Pinar del Río; type, probably in MP). Pfeiffer, 1858, Monographia Pneumonopomorum Viventium, Suppl. 1, p. 194. Sowerby, 1866, Thes. Conchyl., 3: 280, figs. 54–55. Reeve, 1873, Conch. Icon., vol. 19, *Helicina*, pl. 5, fig. 39. Arango, 1879, Contribución Fauna Malacológica Cubana, p. 51. Crosse, 1890, Jour. de Conchyl., 38: 318.

Alcadia (*Leialcadia*) *rotunda* Orbigny. Wagner, 1907, *in* Martini and Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 2, p. 69, pl. 11, fig. 13.

Alcadia (*Leialcadia*) *rotunda campanula* Pfeiffer. Wagner, 1907, *ibid.*, p. 70, pl. 11, figs. 9–12.

Alcadia rotunda (Orbigny). Jaume, 1945, Rev. Soc. Malac. 'Carlos de la Torre,' 3: 75.

Description. Shell reaching about 9 mm in width, 8 mm in height, globose-turbinate, more or less glossy (in some populations exceedingly so), rather solid, smooth. Whorls almost 6, slightly convex, increasing gradually in width. Body whorl about 2½ times wider than the penultimate, evenly rounded, inflated, slightly descending at aperture; base inflated. Color varied: lemon or greenish yellow, pale buff or light flesh colored, spire occasionally darker. Aperture oblique, rounded triangular, somewhat flattened above, angularly rounded at periphery. Palatal lip thin, barely expanded centrally, simple at both terminations, slightly sigmoid above; basal sinus very wide and shallow. Basal callus indistinctly delimited parietally and in umbilical region by rather wide, shallow, curved groove; lustrous, finely granulate, occasionally brownish red or bright yellow. Columella oblique, almost flat above, thickened and weakly concave below, set off from umbilical area by shallow groove and extended outward to merge with low, wide, rounded tubercle near shallow labial sinus. Suture well impressed. Sculpture of fine, irregular growth lines, occasionally with some weak, spiral striae. Axial lineolations within shell substance regular, closely set, weakly sinuous, most noticeable on base. Protoconch 1½ whorls, rounded, minutely and regularly granulate, slightly raised above succeeding whorl. Periostracum thin, persistent, colorless. Operculum as in genus, outer layer thin, glassy, roughly pitted; chitinous layer very thin, light brown; inner wedge-shaped lamella well developed.

height in mm	width in mm	
8.0	9.2	Pan de Azúcar
7.3	7.8	Subido a Rangel
6.7	8.3	Cafetal "La Villa," Candelaria
6.7	7.7	El Mamey, Cayajabos
6.5	8.0	Sierra Viñales
6.3	7.2	El Taco, Rangel

Remarks. This species, confined to Pinar del Río Province, can be recognized by the rather colorful, generally glossy shells, the subglobose outline, and the relatively weak construction of the basal tooth and labial sinus. It is close to *nitida* in size but the latter is more depressed, less glossy and has a rather stronger development of the basal tooth and labial sinus. According to Arango (1879: 53), *rotunda* lives on trees in the entire area of the Sierra de los Organos, whereas *nitida* (*ibid.*: 46) lives in leaf litter and under rocks on the ground, and has a more extensive distribution to Matanzas.

A. rotunda is more elevated, smaller, glossier and more brightly colored than *dissimulans*. In addition the basal sinus is decidedly shallower.

Though the shell of *rotunda* can be easily recognized, some variations do exist. In the Sierra de la Chorrera at San Vicente the colors are frequently more vivid and the aperture and parietal area darker than the rest of the shell. In occasional individuals the spire is darker and more vividly colored than the body whorl. Reddish forms occur at Caiguanabo and Cayajabos, while the population at Pan de Azúcar is largely yellow in color. At El Taco, Rangel, the shells are glossier, thinner, and occasionally a few narrow, indistinct, interrupted and widely spaced spiral bands appear on the body whorl. It is important to note than no large lots from a single locality are uniform in color. Poey's *retracta* from Cayajabos was established on a color-form of *rotunda.*

Pfeiffer (1856: 146) transcribed Gundlach's notes on the animal which we translate as follows: "Animal whitish; a lateral band originating under the eyes as well as the tentacles are dark gray."

Specimens examined. Pinar del Río. La Tenería, Guane; Luis Lazo; Valle de San Carlos, Luis Lazo; Ensenada San Carlos, opposite Sierra Los Acostas, Luis Lazo; Sumidero; Cabezas; Bebedero; Mogote Cerro de Cabras; Kilometer 14 road to Luis Lazo (all USNM). *San Vicente:* La Chorrera; Hoyo Jaruco, La Chorrera (USNM); paredones N side of La Chorrera (USNM); valley E of Baños de San Vicente (USNM); Mogote Pequeño; Mogote Ensenada de San Vicente (USNM); Costanera de San Vicente; Hoyo de Magdaleno, Costanera de San Vicente; Puerta del Ancón (USNM). *Viñales:* Mogote del Refugio; El Queque; Hoyo de Gallardo, El Queque; Mogote Puertecitos; Mogote Capón; Mogote de Justo; Potrero de Miguel Pino, Dos Hermanos; Mogote Mármol (USNM); Laguna de Piedra; Mogote La Jutía, Laguna de Piedra; Valle de Las Delicias; Pan de Azúcar (USNM); Sierra Viñales. *Consolación del Norte (La Palma):* Mogote Palmar, 1 km S of La Palma; La Furnia, Sierra la Güira, San Andrés; Mogote Talavera. *San Diego de los Baños:* Caiguanabo; Los Portales de Caiguanabo. *Rangel:* Subido de Rangel; El Taco; El Retiro; Sierra de Rangel at 1500 ft. (USNM); Río Santa Cruz de los Pinos; Rangel Arriba (USNM); El Guabinacho, Rangel Abajo (USNM); Espiro, Rangel Abajo (USNM); gorge of Río Taco Taco; Bahía Honda; Pan de Guajaibón. Loma del Cuzco, Candelaria (USNM); Peña Blanca, Cuzco (USNM); Cafetal "La Villa," Candelaria (USNM); El Mogote (USNM); El Mamey, Cayajabos; Guanajay; between Guanajay and Artemisa (USNM); km 55 between Artemisa and Havana. Habana. Sierra Anafe.

Alcadia (Idesa) spectabilis (Pfeiffer)
Plate 3, figures 1–3; Plate 6, figures 1–9; Text-fig. 2; Map 2

Helicina spectabilis "Gundlach" Poey, 1858. Memorias Historia Natural Isla de Cuba, 2: 5 [nomen nudum].

Helicina spectabilis "Gundlach" Pfeiffer, 1858. Malak. Blät., 5: 48 (type-locality, here restricted, Buenavista near Bayamo, Oriente; type destroyed; specimen here figured, pl. 6, figs. 1–3, MCZ 74031, J. G. Anthony Collection *ex* Gundlach). Sowerby, 1866, Thes. Conchyl., 3: 287, figs. 246–247. Reeve, 1873, Conch. Icon., vol. 19, *Helicina,* pl. 17, fig. 147. Arango, 1879, Contribución Fauna Malacológica Cubana, p. 52. Crosse, 1890, Jour. de Conchyl., 38: 320.

Helicina bellula "Gundlach" Pfeiffer, 1860. Malak. Blät., 6: 79 (type-locality, Yateras, Guantánamo, Oriente; type destroyed; specimen here figured, pl. 3, figs. 1–3, MCZ 74024, J. G. Anthony Collection *ex* Gundlach). Sowerby, 1866, Thes. Conchyl., 3: 289, pl. 9 (274), figs. 305–308. Reeve, 1873, Conch. Icon., vol. 19, *Helicina,* pl. 10, fig. 83. Arango, 1879, *ibid.,* p. 52. Crosse, 1890, Jour. de Conchyl., 38: 320.

Helicina bellula var. *suturalis* "Gundlach" Pfeiffer, 1860. Malak. Blät., 6: 80 (type-locality, La Cubana, Yateras, Guantánamo; type destroyed; specimen here figured, pl. 6, figs. 7–9, MCZ 74029, J. G. Anthony Collection *ex* Gundlach).

Helicina bellula var. *peripherica* "Gundlach" Pfeiffer, 1860. *Ibid.,* p. 80 (type-locality, Monteverde, Monte Libano, Guantánamo; type destroyed; specimen here figured, pl. 6, figs. 4–6, MCZ 74030, T. Bland Collection *ex* Gundlach).

Helicina spectabilis minor Pfeiffer, 1862. *Ibid.,* 9: 8 (type-locality, Loma del Gato, Cobre, Oriente; type destroyed) [nomen nudum].

Helicina bellula var. *yunquensis* Pfeiffer, 1865. Monographia Pneumonopomorum Viventium, suppl. 2, p. 231 (type-locality, Yunque de Baracoa, type destroyed).

Alcadia (Leialcadia) spectabilis (Gundlach) Poey. Wagner, 1907, *in* Martini and Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 2, p. 75, pl. 13, figs. 13–16.

Alcadia (Leialcadia) spectabilis venusta Wagner, 1907. *Ibid.,* p. 76, pl. 13, figs. 17–18 (type-locality, here restricted, Santiago de Cuba; type, IZW).

Alcadia (*Leialcadia*) *bellula bellissima* Wagner, 1907. *Ibid.*, p. 75, pl. 12, figs. 9–12 (type-locality, Baracoa; type, IZW 8380).

Alcadia (*Leialcadia*) *bellula leptochila* Wagner, 1907. *Ibid.*, p. 75, pl. 12, figs. 13–14 (type-locality, Monte Toro; type, IZW).

Helicina polychroa Reeve, 1873. Conch. Icon., vol. 19, *Helicina*, pl. 17, fig. 153 (type-locality, Cuba; type-specimens, BMNH).

Description. Shell generally about 7.5 mm wide, 6.5 mm high, larger in some populations, moderately strong, subglobose, lustrous. Whorls 5½, moderately rounded, increasing rapidly in width. Body whorl rounded, about 2½ times wider than the penultimate and gradually descending near the aperture; base moderately inflated. Color varied; yellowish white, greenish yellow, light yellowish brown or pale orange, sometimes unicolored, frequently ornamented with a reddish brown sutural or peripheral band of varied width; protoconch occasionally similarly colored. Aperture slightly oblique, subtriangular, rather rounded at periphery. Palatal lip thin, entire, flaring, less so at basal insertion, separated from body whorl by a shallow groove which becomes obsolete at both insertions; a low, rounded tubercle near the columella. Parietal area with a slightly raised, minutely granulate subcircular basal callus, about as large as aperture, with an irregularly curved parietal margin, umbilical margin terminating in palatal tubercle. Columella little convex above, slightly rounded below, merging with the labial tubercle. Suture well impressed, occasionally distorted near the aperture at the terminations of the strong growth lines. Sculpture of rather strong, irregular growth lines only. Axial lineolations within shell substance rather wide, closely spaced, slightly sinuous. Protoconch 1½ whorls, white, pale yellow or bright reddish brown, rounded, minutely granulate, barely raised above succeeding whorls. Periostracum thin, yellow, persistent, and deciduous only in long dead specimens. Operculum as in subgenus, thin, pale brown.

height in mm	width in mm	
6.7	7.3	Monte Líbano, Guantánamo
6.5	7.5	Yateras
6.5	7.2	Cubana, Yateras
8.2	8.4	Pico Turquino, 2,500 ft.
6.5	7.5	Pico Turquino, 2,500 ft.
6.4	6.9	El Yunque de Baracoa

Remarks. This is a highly variable species confined to the southern and east-central parts of Oriente Province where it is to be found on trees and bushes. The shells vary in size, texture, and especially in color. Several variations were given subspecific names but they may safely be rejected. As we shall show later, these morphologic distinctions frequently occur in the same population. Shell morphology sometimes appears to be more stable in single populations; however, this usually is the result of small samples or selective collecting. Even in such cases, some characteristics that predominate in one population are not confined to that population but appear in other populations as well. Wagner (1907: 74) noted the sexually dimorphic characters of shells, *i.e.*, inflatedness of whorls and shape of the apertures from the same population without any intergrades. Many helicinids show such dimorphism.

Wagner (1907) gave the subspecific name *bellissima* to a population of *spectabilis* from Baracoa on the basis of its smaller size, transparent grayish blue or yellow color, and wider palatal lip. But some specimens from the Yunque de Baracoa are only slightly smaller than specimens from La Caridad, Guantánamo, and, in color, strongly resemble samples from populations at Pico Turquino. Thus we are dealing with a population differing slightly from the "typical" and with characteristics found in other populations. The varieties *peripherica* and *suturalis* of Pfeiffer are admittedly found in the same populations with differently colored shells (Pfeiffer, 1860: 80).

The population on the Pico Turquino in Sierra Maestra taken at an altitude of

2,500 feet has the shell more elevated and the lip somewhat wider. The color varies from pale yellow to pale bluff, ornamented with either a reddish brown spot on the protoconch and/or a sutural band on the earlier postnuclear whorls which, in occasional specimens, continues as a peripheral band on the body whorl.

In contrast, the population at La Caridad, Monte Toro, Guantánamo, consists of specimens entirely colored yellow, varying only slightly in the intensity of the color. They are smaller than samples from other populations and the lip may be narrower and less strongly expanded. The subspecific name *venusta* Wagner was given to small, rather fragile forms, but since Wagner cited them from Santiago de Cuba, Bayamo, and Rancho Lucas, he was obviously dealing with ecophenotypic specimens found under less than favorable ecological conditions. The subspecific name *leptochila* was also applied to a form chiefly distinguished by its smaller size.

There is little reason to doubt that in *bellula*, Pfeiffer (1860) was redescribing his *spectabilis* (1858). According to both descriptions, the shells of these two species differ mainly in color, a very variable feature in many arboreal mollusks, pulmonates as well as prosobranchs, and a feature which, in this case, is not of specific significance: the nomina *bellula* and *spectabilis* apply to the same species.

Pfeiffer (1860: 79) quotes Gundlach's notes on the animal, which we translate as follows: "Animal white with ochre-colored sheen; tentacles white at base, gray or blackish in the middle and at the tip. Blackish spots are generally seen on the neck and sides, rarely are these portions completely black. The mantle has a blackish margin. Head with oblique wrinkles. Eyes located on the outer posterior base of the tentacle."

Specimens examined. ORIENTE. Cabo Cruz; Ojo del Toro, Sierra Maestra; Pico Turquino; S side of Pico Turquino; Subido a Pico Turquino; Buenavista, Bayamo; El Jaquey; La Lechuza, Monte Toro, Guantánamo; La Caridad, Monte Toro, Guantánamo; Cafetal "Virginia," Yateras, Guantánamo; Yateras, Guantánamo (USNM); La Cubana, Yateras, Guantánamo; Monte Líbano, Guantánamo; Hoyo de Julian, Rio Guaso, Guantánamo (ANSP); Loma del Gato, Songo; Yunque de Baracoa (MCZ).

Alcadia (Idesa) concinna (Pfeiffer)

Plate 1, figures 10–12; Map 2

Helicina concinna "Gundlach" Pfeiffer, 1857. Malak. Blät., 4: 178 (type-locality, Cabo Cruz, Oriente; specimen here figured, MCZ 86616, Boston Soc. Nat. Hist. Collection *ex* Gundlach). Pfeiffer, 1858, Monographia Pneumonopomorum Viventium, suppl. 1, p. 194. Sowerby, 1866, Thes. Conchyl., 3: 287, pl. 6 (271), figs. 229–230. Arango, 1879, Contribución Fauna Malacológica Cubana, p. 51. Crosse, 1890, Jour. de Conchyl., 38: 318.

Helicina exserta "Gundlach" Pfeiffer, 1858. Malak. Blät., 5: 194 (type-locality, Santiago de Cuba; type destroyed). Pfeiffer, 1865, Monographia Pneumonopomorum Viventium, suppl. 2, p. 288, *non* Martens, 1891. Crosse, 1890, Jour. de Conchyl., 38: 319.

Helicina exerta Gundlach. Arango, 1879, Contribución Fauna Malacológica Cubana, p. 51 (error for *exserta*).

Alcadia (*Leialcadia*) *concinna* (Pfeiffer). Wagner, 1907, *in* Martini and Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 2, p. 72, pl. 12, figs. 15–18.

Description. Shell reaching about 6 mm in width, 5 mm in height, globose-conic, rather solid, lustrous. Whorls 5½, weakly convex, increasing slowly in width. Body whorl about twice as wide as penultimate, moderately inflated, well rounded, descending at aperture; base weakly inflated. Color white, yellowish or very pale reddish, occasionally ornamented with darker reddish sutural band, spire frequently darker than body whorl, basal callus and aperture frequently yellow. Aperture oblique, semilunate, well rounded peripherally and constricted at the peristome. Palatal lip entire, barely expanded, with shallow, very wide, rounded basal sinus; denticle upwardly directed, squarish but rounded at upper portion. Basal callus yellowish or white, finely granulate, weakly delimited parietally, with rather deep, unevenly curved groove at umbilical margin. Columella evenly sigmoid, widely rounded below and terminating in basal tooth. Suture strongly impressed, subcanaliculate at summit of body whorl. Sculpture of rather weak, irregular, diagonal growth lines occasionally with spiral striae on upper whorls. White lineolations within shell substance very narrow, more or less regularly spaced, weakly sinuous. Protoconch 1½ whorls, rounded, minutely granulate, little raised above succeeding whorls. Periostracum deciduous, pale horn colored, very thin. Operculum as in genus, pale horn colored, rather darker at outer margin.

height in mm	width in mm	
5.1	6.0	Cabo Cruz at the Lighthouse
4.2	5.6	Cabo Cruz
4.1	5.0	Cabo Cruz

Remarks. The shell of this species can be recognized by its conic-globose outline, solid substance, sublustrous surface, extremely narrowly expanded lip, and constricted aperture.

The species *H. exserta* Pfeiffer from near Santiago de Cuba is said to differ from *concinna* in its larger size and the presence of spiral lirations on the upper whorls. Since the size of the specimens of *concinna* from near the lighthouse were larger than those from elsewhere on the cape, and since spiral lirations are a variable feature in the Helicinidae, we have decided to consider *exserta* as a junior synonym. The species was probably introduced into Cuba from the neighboring Antilles.

Pfeiffer (1858: 194) transcribed Gundlach's notes on the animal of *exserta*, which we translate as follows: "Animal with black head, neck and tentacles, the latter somewhat lighter near the tip. Foot white with a gray sheen on the rugosities of the surface."

The species lives on trees and bushes and, according to Gundlach, under loose bark among orchid leaves.

Specimens examined. ORIENTE. Four to five km E of Ensenada de Mora (ANSP); Santiago on Shore Road, 10 km E of Ensenada de Mora (ANSP); Punta Icaca (Hicaca) near Cabo Cruz (USNM): Lighthouse at Cabo Cruz; Puerto Portillo, Cabo Cruz; Hill W of Toro River near Cabo Cruz (ANSP); Mouth of Río Puerco near Cabo Cruz (ANSP); Río Ojo del Toro (ANSP).

Subgenus **Hjalmarsona** H. B. Baker

Hjalmarsona H. B. Baker, 1940. Nautilus, 54: 70; type-species, *Alcadia* (*Idesa*) *hjalmarsona* (Pfeiffer) 1856 [from Puerto Rico], original designation.

Description. "Shell smooth and shining with rapid whorl-increase and large aperture; peristome scarcely reflected and only weakly thickened internally, columella weakly convex and scarcely thickened. Calcareous plate of operculum thin but well developed, granulate externally; columellar margin sigmoid." (H. B. Baker)

Remarks. Hjalmarsona is a subgenus which embraces the smaller, fragile, comparatively drably colored, depressed globose forms of *Alcadia s.l.* which have a rather weak development of the basal sinus and tubercle and lack a hirsute or pilose periostracum. Previous authors put these species in *Idesa* from which they differ by being more fragile, less elevated and more drab. They differ from *Penisoltia* which they resemble in color, fragility of the shell, and occasionally in habitat, by the possession of a glossy, persistent periostracum instead of a hirsute, deciduous one. They live either on bushes (Arango, 1879) or under rocks and dead leaves.

KEY TO SUBGENUS *Hjalmarsona*

1. Shell generally 9–11 mm wide, basal tooth and sinus barely visible; distribution limited to eastern Oriente Province .... *neebiana*
   Shell rarely reaching 10 mm, most often smaller, basal sinus wide, shallow, basal tooth small but distinct; distribution from Pinar del Rio to Matanzas .... *nitida*

Alcadia (Hjalmarsona) neebiana (Pfeiffer)

Plate 2, figures 1–3; Map 2

Helicina neebiana Pfeiffer, 1862. Malak. Blät., 9: 8 (type-locality, Cayo del Rey, Mayarí, Oriente [Wright leg.]; type destroyed; specimen here figured, MCZ 90056, T. Bland Collection). Pfeiffer, 1865, Monographia Pneumonopomorum Viventium, suppl. 2, p. 225. Arango, 1879, Contribución Fauna Malacológica Cubana, p. 51. Crosse, 1890, Jour. de Conchyl., 38: 318.

Alcadia (*Leialcadia*) *neebiana* (Pfeiffer). Wagner, 1907, *in* Martini and Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 2, p. 67, pl. 10, figs. 21–25.

Alcadia (*Hjalmarsona*) *selenipoma* Aguayo and Jaume, 1958. Mem. Soc. Cubana Hist. Nat., 24: 93, pl. 1, fig. 7 (type-locality, La Vega, Canapú, Mayarí, Oriente, Cuba; holotype, MP 17433).

Description. Shell reaching about 10.7 mm in width, 8.2 mm in height, subglobose, smooth, glossy, moderately strong. Whorls 5, moderately convex, slowly increasing in width. Body whorl almost 3 times wider than penultimate, inflated, well-rounded, descending little at aperture; base moderately inflated. Color brownish yellow, spire occasionally pale orange and darker than rest of shell; basal callus and palatal lip white. Aperture moderately oblique, semilunate, evenly rounded, not flattened above. Palatal lip slightly thickened, weakly expanded, barely extended above, straight or slightly bent outward at insertion in body whorl, basal notch exceedingly shallow. Columella oblique, almost straight above, slightly rounded below, separated by narrow groove from the basal callus and terminating in very low, white, rounded tubercle. Basal callus subcircular, lustrous, white, indistinctly delimited, not raised, very finely granulate, contrasting well with axial sculpture of rest of base. Suture moderately impressed, occasionally bounded by narrow white band, becoming obsolete near aperture. Sculpture of barely perceptible growth lines, stronger on base; surface very finely punctate. White lineolations within shell substance narrowly separated, weakly sinuous, occasionally vermiculate. Protoconch almost 2 whorls, translucent, rounded, surface finely and regularly punctate, very slightly raised above succeeding whorls. Periostracum thin, glossy, strong. Operculum as in genus, pale brownish yellow, with dark, reddish brown outer margin. Occasional populations with heavy, white, opaque, wrinkled, semilunate deposit covering upper ⅔ of external surface and reaching from near outer margin to ¾ of way to inner.

height in mm	width in mm	
8.2	10.7	La Cantera de Miranda, Oriente
8.2	9.6	La Vega, Canapú, Mayarí
7.2	10.5	La Cantera de Miranda, Oriente
6.0	7.7	La Vega, Canapú, Mayarí

Remarks. This species can be recognized by the glossy, brownish yellow surface, the subglobose outline, and the very weak development of the basal tubercle and notch. It has been reported only from the municipio of Mayarí in north-central Oriente.

Aguayo and Jaume (1958) gave the name *selenipoma* to a population of smaller shells from Canapú on the basis of the peculiar opaque layer on the exterior of the operculum. However, we found the identical layer in a series of typically sized *neebiana* from Miranda, Mayarí (MCZ 276643). This characteristic seems to be caused by some unknown factor in the environment and deserves more study. The other differences cited for distinguishing *selenipoma* from *neebiana*, such as size, texture, and color, are variable and do not merit specific distinction.

Specimens examined. Oriente: Mayarí: [Cayo del Rey] La Cantera de Miranda; Cayo del Rey, about 20 mi. from Miranda (ANSP); hill N of Mercedes Valley, Miranda (ANSP); upper Mercedes Valley (ANSP); La Vega, Canapú; N of Imias, 3,000 to 4,000 ft.; Cuchillo de Guajimero, 2,000 ft.

Alcadia (Hjalmarsona) nitida (Pfeiffer) Plate 3, figures 7–9; figures 10–12; Map 2

Helicina nitida Pfeiffer, 1839. Arch. Naturg., 5th year, vol. 1, p. 355 (Cuba; type-locality, here selected, El Descanso, Coliseo, Matanzas; type destroyed). Sowerby, 1847, Thes. Conchyl., 1: 13, pl. 3, fig. 116. Pfeiffer, 1850, *in* Martini and Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 1, p. 25, pl. 4, figs. 19–21; 1852, Monographia Pneumonopomorum Viventium, p. 356. Arango, 1879, Contribución Fauna Malacológica Cubana, p. 46. Crosse, 1890, Jour. de Conchyl., 38: 312.

Helicina glabra Gould, 1842. Boston Jour. Nat. Hist., vol. 4, no. 1, on back cover; 1842, Proc. Boston Soc. Nat. Hist., 1: 138 (type-locality, Cuba; lectotype, selected by Johnson, 1964, p. 83, pl. 41, fig. 2, MCZ 169172). Pfeiffer, 1856, Malak. Blät., 3: 145; 1858, Monographia Pneumonopomorum Viventium, Suppl. 1, p. 188. Poey, 1858, Memorias Historia Natural Isla de Cuba, 2: 67, pl. 7, fig. 15. Arango, 1879, Contribución Fauna Malacológica Cubana, p. 46. Crosse, 1890, Jour. de Conchyl., 38: 312.

Helicina nitida var. *elatior* Pfeiffer, 1856. Malak. Blät., 3: 145 (type-locality, here selected, Marianao, Havana, Cuba; type destroyed; specimen here figured, pl. 3, figs. 10–12, MCZ 47511, Marianao, Bermúdez leg).

Alcadia (*Leialcadia*) *nitida* (Pfeiffer). Wagner, 1907, *in* Martini and Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 2, p. 68, pl. 11, figs. 5–8.

Alcadia (*Leialcadia*) *rotunda glabra* (Gould). Wagner, 1907, *in* Martini and Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 2, p. 70, pl. 11, figs. 15–18.

Alcadia elatior (Pfeiffer). Aguayo and Jaume, 1939, Mem. Soc. Cubana Hist. Nat., 13: 238. Aguayo, 1949, Rev. Soc. Mal. 'Carlos de la Torre,' 6: 97.

Alcadia (*Alcadia*) *elatior* Pfeiffer. Aguayo and Jaume, 1953, Mem. Soc. Cubana Hist. Nat., 21: 271, pl. 31 [not 32], fig. 3.

Alcadia (*Idesa*) *nitida* (Pfeiffer). Farfante, 1942, Mem. Soc. Cubana Hist. Nat., 16: 50.

Description. Shell reaching about 10 mm in width, 7 mm in height, depressed globose, sublustrous, rather fragile, smooth. Whorls almost 6, weakly inflated, increasing regularly and rather rapidly in width. Body whorl about twice the width of penultimate, rounded, descending slightly at the aperture, base weakly inflated. Color white or various shades of pale brown, spire occasionally darker. Aperture rounded triangular, moderately oblique, internally same color as shell. Palatal lip thin, very weakly flaring, not reflected, slightly depressed and sigmoid above, curved at upper insertion in body whorl with distinct, V-shaped, rather deep notch; rounded sinus at base of columellar process. Basal callus white or very pale brown, minutely granulate, weakly delimited parietally, and by shallow, unevenly semicircular groove in umbilical region. Columella weakly concave, terminating in short, variously rounded peduncle and raised below, forming low, vertical wall above umbilical groove. Suture weakly impressed. Sculpture of weak, irregular growth lines only; white, axial lineolations within shell substance quite narrow, weakly sinuous, separated by rather wide, regular intervals. Protoconch 1½ whorls, rounded, densely granulate, very slightly raised above succeeding whorls. Periostracum wanting. Operculum as in genus, horn colored.

height in mm	width in mm	
7.4	10.2	La Majagua, Luis Lazo, Pinar del Río
7.1	9.6	Hoyo de los Cidros, El Queque, Viñales, Pinar del Río
6.8	9.5	El Descanso, Coliseo, Matanzas
6.6	8.9	Camoa, Habana
5.4	7.5	El Palenque, Matanzas
5.3	8.0	Mogote La Curva, Madruga, Habana

Remarks. The shells of this species resemble those of *A. rotunda* but differ in their more depressed outline, in their more subdued color, and in the somewhat stronger basal tooth and sinus. They differ from *dissimulans* in their smaller size, the shallower basal sinus, and in the straight instead of curved upper labial insertion in the body whorl.

The species is found in humid earth and under rocks (Farfante, 1942: 50) and lives in calcareous areas in the lowlands as well as on hills. It ranges from the eastern half of Pinar del Río through Habana to the central portions of Matanzas. The range overlaps that of *rotunda* only in Pinar del Río. Since their ecological requirements differ—*rotunda* being arboreal—they are found in the same localities, *i.e.,* at El Queque in Viñales and probably elsewhere. In Habana and Matanzas the range overlaps that of *A. hispida,* which, however, continues into Las Villas, where *nitida* does not occur.

Pilsbry collected a series of three imperfect, dead specimens near Florencia in Camagüey (ANSP 148592) and a similar series from Mota in Oriente (ANSP 148669), which seem to be referable to *nitida.* However, both these lots lie far to the east of the range of *nitida* as we are led to understand it on the basis of most specimens available for our examination. Whether *nitida* does indeed range as far to the east as these two series seem to indicate remains to be decided by further collecting in the two easternmost provinces of the island.

The shells vary somewhat in size, the population from San Antonio de los Baños in Habana Province being small, while those around Luis Lazo are larger. However, there is no clinal variation, since shells almost as large are also found in Coliseo, Matanzas.

Pfeiffer (1856: 144) transcribed Gundlach's notes on the animal which we translate as follows: "Animal whitish, with gray dots above. Tentacles blackish, lighter at tip. The animal in the shell, which is always clean, sometimes of one color, sometimes spotted."

The nomen *elatior* Pfeiffer has had a unique history, well related in its entirety by Aguayo (1949). Pfeiffer (1856) described it briefly in a note about *Helicina glabra* Gould but did make two essential points, namely that the peristome (Mundsaum) was not "bogig" or curved above and hence did not form an acute angle at the upper insertion, and that the peristome projected below. As Aguayo pointed out (1949), this may be an insufficient description for taxonomic purposes. Moreover, it can be seen that Pfeiffer did not consider this to be a formal indication, since he omitted it from all the editions of his *Monographia Pneumonopomorum Viventium* (1858, 1865, 1876). Yet the fact remains that Pfeiffer's indication was so clear as to enable Aguayo and Jaume to recognize the taxon in 1939. It was more fully described in 1939, but a full, formal description was given by Aguayo in 1949. Aguayo and Jaume (1953) recorded it from Loma Cantera Blanca in the region of Baracoa. However, we found the characteristics mentioned by Aguayo and Jaume in specimens in other populations of *nitida* and do not accord it a separate status.

Specimens examined. PINAR DEL RÍO. Mendoza; Hoyo de la Cueva, La Majagua, Luis Lazo; Ensenada de Fuentes, Valle de San Carlos, Luis Lazo; El Queque; Hoyo de los Cidros, El Queque; Mogote de la Dinamita, Viñales; Mogote José Mariá García, Palmarito, Viñales; Palmarito; Costanera de San Vicente; Los Paredones, Ceiba del Agua. HABANA. San Antonio de los Baños; Santiago de las Vegas; 1 km from Bejucal; Sitio Perdido, Jaruco (USNM); Camoa near Jamaica; Somorrostro near Jamaica; Marianao. *Madruga:* Mogote Finca Almeida, Pipián; Lafut, Pipián; E end of Sierra El Grillo; E of Zanabria; Mogote la Curva. Cojímar; Loma de Coco; Central Merceditas. MATANZAS. Abra del Yumurí; Mena, Yumurí; Riscos Calderón, 5 km W of Ceiba Mocha; Mogote de Ceiba Mocha; Ceiba Mocha (USNM); Pan de Matanzas (USNM); paredones E of pass, Coliseo (USNM); El Descanso, Coliseo; paredones N of San Miguel de los Baños (USNM); mogote opposite side of road from Mogote Caoba, between Coliseo and San Miguel de los Baños; Loma Odiseo between Coliseo and San Miguel de los Baños (USNM); Vista Alegre (USNM); paredones 2 km S of Limonar; Palenque de Matanzas (USNM); El Palenque; Finca el Pan, Pan de Palenque (USNM); right bank below ferry, Canímar R., El Fundador (USNM); right side of river, El Fundador (USNM).

Subgenus **Penisoltia** H. B. Baker

Hispida Wagner, 1907. *In* Martini and Chemnitz, Conchyl.-Cab., 2 (1): sect. 18, pt. 2, p. 54 (type-species, *Helicina hispida* Pfeiffer, 1839, by tautonymy, see H. B. Baker, 1922, p. 46, *non* Bate 1868 [Porifera]).

Penisoltia Baker, 1954. Nautilus, 67: 139, new name for *Hispida* Wagner, 1907, *non* Bate, 1868.

Description. Shell medium sized (11 × 7 mm) to small (5 × 4 mm), generally depressed globose, brown or faint reddish brown or white, generally fragile. Operculum usually thin, calcareous layer thin, chitinous layer filmy. Periostracum pilose or hirsute, hairs at times arranged in spiral rows, deciduous. The basal sinus and tubercle are generally well developed.

Remarks. The species of this subgenus differ from *Alcadia s. s.* in being generally smaller and more depressed. The shell is more fragile and the development of the basal sinus and tubercle is stronger. We are placing in this subgenus all the smaller, ground-dwelling, fragile, and generally colorless forms having a highly deciduous periostracum.

Penisoltia (and *Hispida* Wagner, 1907) really have never been described (see p. 313). We believe the subgenus should be separated from *Alcadia* for the reasons given above.

KEY TO THE SPECIES OF *Penisoltia*

1. Shell small, 4.5 to 7 mm in width 2
   Shell larger, 7 to 11 mm in width 3
2. Shell 5 to 7 mm wide, basal sinus narrow, deep, outline depressed; distribution from Habana to Las Villas Province and Isle of Pines .... *hispida*
   Shell 4 to 5 mm wide, basal sinus shallow, U-shaped; distribution island-wide except Isle of Pines .... *minima*
3. Periostracum generally covering entire shell 4
   Periostracum generally arranged in spiral ridges 5
4. Periostracal hairs deciduous, reflected on surface by minute pits arranged in spiral rows; distribution in eastern Cuba in Las Villas and Oriente .... *gonostoma*
   Periostracal hairs not reflected by pits; distribution in western Pinar del Río Province only .... *dissimulans*
5. Basal channel pronounced, basal tooth narrow; distribution limited to Las Villas Province and border of Camagüey .... *bermudezi*
   Basal channel weaker, basal tooth wide; distribution limited to Pinar del Río Province .... *velutina*

Alcadia (Penisoltia) hispida (Pfeiffer)
Plate 4, figures 13–15; Map 3

Helicina hispida Pfeiffer, 1839. Arch Naturg., 5th year, 1: 355 (Cuba, type-locality, subsequently designated by A. Torre, 1952, Cafetal Fundador de Canimar, Matanzas; type destroyed); 1850, *in* Martini and Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 1, p. 30, pl. 3, figs. 19–22. Sowerby, 1842, Thes. Conchyl., 1: 4, pl. 3, figs. 112–113; 1866, Thes. Conchyl., 3: 279, pl. 1 (266), figs. 33–34. Gould, 1843, Boston Jour. Nat. Hist., 4: 493.

Helicina dentigera Orbigny, 1842. Mollusques, *in* Sagra, Histoire Physique, Politique et Naturelle de l'Ile de Cuba, 1: 252, pl. 21, figs. 4–6 ("interieur de Cuba"; type in BMNH). Sowerby, 1842, Thes. Conchyl., 1: 4, pl. 3, figs. 107–108. Pfeiffer, 1850, *in* Martini and Chemnitz, Conchyl.-Cab. (2) 1: sect. 18, pt. 1, p. 30 (in synonymy of *hispida*).

Alcadia hispida (Pfeiffer). Pfeiffer, 1852, Monographia Pneumonopomorum Viventium, p. 412; 1856, Malak. Blät., 3: 150. Arango, 1879, Contribución Fauna Malacológica Cubana, p. 57. Crosse, 1890, Jour. de Conchyl., 38: 325. A. Torre, 1952, Rev. Soc. Malac. 'Carlos de la Torre,' 9: 14.

Alcadia (*Eualcadia*) *hispida* Pfeiffer. Wagner, 1907, *in* Martini and Chemnitz, Conchyl.-Cab., 2 (1): sect. 18, pt. 2, p. 55, pl. 8, figs. 8–12.

Alcadia (*Alcadia*) *hispida* (Pfeiffer). Farfante, 1942, Mem. Soc. Cubana Hist. Nat., 16: 50.

Description. Shell reaching about 7 mm in width and 5 mm in height, globose-depressed, fragile, moderately lustrous under pilose periostracum. Whorls about 5½, moderately convex, increasing regularly in width. Body whorl 1½ times wider than the penultimate, well rounded peripherally, descending slightly at aperture. Color under periostracum varied: pale yellow, pale reddish brown, buff, or bluish white; lip and basal callus generally lighter than rest of shell. Aperture semilunate, evenly rounded centrally, straight and flattened above, rounded below. Palatal lip thin, gently expanded except at terminations, flattened and weakly sigmoid above, not curved at insertion into body whorl; basal sinus deep, narrow, rounded below. Basal callus slightly inflated, glassy, surface minutely granulate, indistinctly delimited parietally, set off in umbilical area by well-impressed, curved, rather wide groove. Umbilical margin of base of body whorl with low, curved lamella terminating in high, curved, rounded tooth with raised, drop-shaped thickening on distal inner margin. Columella oblique and weakly convex above, slightly curved and directed forward below, terminating in tooth. Suture well impressed, subcanaliculate near aperture. Sculpture of irregular, weakly developed, diagonal growth lines, stronger on base, crossed by very finely impressed, closely set, occasionally interrupted spiral furrows, forming irregularly decussated surface. Lineolations inside shell substance threadlike, weakly sinuous. Protoconch 1½ whorls, glassy, transparent, rounded, finely punctate, slightly raised above succeeding whorls. Periostracum strong, deciduous, closely pilose, brown or reddish brown, covering entire shell except protoconch and region of basal callus. Operculum as in genus, calcareous layer glassy, finely granulate; chitinous layer white but pale brown at outer margin, strongly extended beyond calcareous layer, especially so at columellar edge; internal wedge-shaped lamellae at columellar edge well developed.

height in mm	width in mm	
4.7	6.9	Mogote at Km 70, Sierra Grillo, Madruga, Habana
4.7	6.5	Guabaira, Soledad, Cienfuegos, Las Villas
4.5	6.8	Sierra de San Juan de La Mar, Isle of Pines
3.3	5.7	Bridge over Canímara River near Matanzas, Matanzas

Remarks. The shell of this species somewhat resembles that of *Alcadia minima* Orbigny, but besides its consistently larger size, *A. hispida* also differs in the stronger expansion of the palatal lip, the relatively deeper and narrower basal sinus, the stronger development of the curved basal groove, the presence of spiral sculpture and the relatively more depressed outline. Even where the two approach each other in size—though *hispida* will always be the larger—the higher outline of *minima* sets it off immediately. Superficially, Orbigny (1842) seems to be right when he wrote of *minima,* "Cette coquille nous représente en petit la forme de *dentiger* [= *hispida*]." Both are found under similar ecological conditions. The rather heavy brown periostracum probably serves to disguise *hispida,* which is found under rocks (Arango, 1879) and under leaves in forests and on limestone knobs, preferring calcareous soil (Gould, 1844). Pfeiffer (1856: 150) reported it in foliage and moss. He also transcribed Gundlach's notes on the animal, which we translate as follows: "Animal whitish. Fine, blackish dots make the head appear gray. Tentacles blackish."

The range of *hispida* is much more restricted than that of its smaller congener, extending only from Pinar del Río to Las Villas, but also occurring on the Isle of Pines, whereas *minima* is found everywhere on the island, except on the Isle of Pines.

Specimens examined. PINAR DEL RÍO. Mogote de La Jagua, Viñales; Mogote Kilometer 14; E of Mogote Trujillo, Viñales; Mogote de Rojero between Cayos de San Felipe and Loma de Isabel María. HABANA. San Antonio de los Baños (USNM); Sitio Bonillo, Jaruco (USNM); Sitio Perdido, Jaruco. *Madruga:* Mogote La Curva; Abra del Café, Sierra El Grillo; E end of Sierra El Grillo; mogote at km 70, Sierra El Grillo; Paredones Entronque, Sierra El Grillo. Camoa near Jamaica; Central Merceditas; 1 km from Bejucal; Cojímar; Managua. MATANZAS. Stone fence at top of road leading to Bellamar Caves (USNM); Playa Bellamar; 10 km from Matanzas on road to Cárdenas; 6 km W of Ceiba Mocha; El Fundador, Canímar; E bank of Río Canímar, NW of Fundador (USNM); Bridge over Río Canímar on Matanzas–Limonar road; Finca Castillito, Río Canímar; paredones E of the pass, Coliseo (USNM); stone fence between Coliseo and Matanzas (USNM); Abra Yumurí; Finca Montecristo, SE of Limonar; sierra S of Martí or Hato Nueva. *Las Villas:* paredones at Finca Santa Theodora, E of Coralillo (USNM); top of mogote W of Coralillo (USNM); Hornos de Cal, Sancti Spiritus; Loma El Ternero, San Juan de los Yeras; mogotes at Jumagua, near Sagua La Grande; Central Ramona, S side of reservoir (USNM). *Soledad, Cienfuegos:* Vilches Potrero; Seboruco near Guaos, 2 miles N of Soledad; Guabairo; Limones Seboruco 1 mi. SE of Soledad; Harvard House; Limones; Palm Grove, 1½ mi. SE of Soledad. ISLE OF PINES. Sierra de Casas; Sierra de Bibijagua; Mina Carlota, Sierra de San Juan; Sierra de San Juan de la Mar.

Alcadia (Penisoltia) bermudezi bermudezi Aguayo and Jaume

Plate 4, figures 10–12; Map 3

Alcadia bermudezi Aguayo and Jaume, 1957. Mem. Soc. Cubana Hist. Nat., 23: 121, pl. 1, figs. 1–3 (type-locality, "La Sierra" Vega Alta, Provincia de Las Villas, Cuba; holotype, MP 17391; paratypes, MCZ 128665).

Description. Shell reaching about 11 mm in width, 6.5 mm in height, strongly depressed, roundly carinate, sublustrous under thin periostracum, rather fragile, translucent. Whorls 5¾, upper ones almost flat, body whorl convex; whorls increase rapidly in width. Body whorl about 2½ times wider than penultimate, convex above, roundly carinate, descending slightly at aperture, base moderately inflated. Color pale lemon or brownish yellow, basal callus and peristome white. Aperture quite oblique, widely semilunate, well rounded peripherally, somewhat depressed and straight above. Palatal lip thin, well expanded except at both terminations, slightly sigmoid near upper insertion, with deep, roundly V-shaped, somewhat forward directed basal sinus above basal tooth. Basal callus glassy, granulate, indistinctly delimited parietally, bordered in umbilical region by curved, rapidly widening, rounded groove. Strong, pointed, forward directed tubercle rising from low, marginal lamella on umbilical edge of basal callus. Columella oblique, sigmoid above, sharply but regularly rounded, terminating in basal tooth. Suture well impressed, subcanaliculate on approach to aperture. Sculpture of rather strong, irregular, curved diagonal growth lines, weakly decussated by numerous shallow spiral striae, most noticeable on penultimate whorl, obsolete on body whorl; lineolations within shell substance white, narrowly separated, weakly sinuous. Protoconch 1.0 whorl, rounded, minutely punctate and with series of weak, irregular, rounded axial cords. Periostracum weak, deciduous, with long, pointed hairs thickly arranged in 4 spiral bands on base and generally one on periphery. Operculum as in genus, yellowish brown, dark reddish brown at outer margin; internal wedge-shaped lamella weakly developed.

height in mm	width in mm	
6.4	11.0	La Sierra, Vega Alta, Las Villas
6.3	10.6	El Purio, Calabazar de Sagua
5.7	9.9	La Sierra, Vega Alta, Las Villas
5.4	9.2	El Purio, Calabazar de Sagua

Remarks. This species is readily recognized by its depressed outline, comparatively large size, strongly expanded peristome, forward directed, rounded basal tooth and, in life, by the presence of narrow, thick, hirsute, brownish spiral periostracal ridges. These hairs are very brittle and easily broken off. This species appears to be closest to *A. velutina* from which it differs in color, in the nature of the periostracum, and in the fact that in *velutina* the basal tooth is noticeably longer and wider.

The species is limited to a restricted area in the north-central part of Las Villas Province in the vicinity of Calabazar de Sagua.

Specimens examined. LAS VILLAS. La Sierra, Vega Alta (MCZ); mogote near Lomo Chicharrón near Vega Alta; second mogote of La Sierra, near Vega Alta; paredones of Finca el Mirador near Calabazar; mogote Mirador near Calabazar; paredones of Mogote Cueva Galana near Calabazar; Loma Batey, Ingenio Santa Clara, 6 km NW of Calabazar; Cueva Galana, Calabazar; El Purio, Calabazar; Loma del Purio, W side of Central Purio; loma W of Loma del Purio, W side of Central Purio; Loma Santa Clararita, S end of Central Purio (all USNM).

Alcadia (Penisoltia) bermudezi jatibonica Boss and Jacobson new subspecies

Plate 5, figures 4–6; Map 3

Holotype, MCZ 128669, Boquerón de Jatibonico, Las Villas. Paratypes, MCZ 276631, same locality; MCZ 128671, Loma Espinosa, Chambas, Camagüey; MCZ 128670, La Vigía, Mayajigua, Las Villas.

Description. The shells of this subspecies resemble those of the nominate subspecies in the depressed, roundly carinate outline and in the structure of the basal sinus and tooth. However, it is consistently smaller, the color is white rather than yellow or pale reddish brown, and the palatal lip proportionately less widely expanded. The periostracum is stronger and more pilose and the spiral hirsute bands less conspicuous and fewer in number. Operculum as in nominate subspecies.

height in mm	width in mm	
5.5	8.2	Holotype, Boquerón de Jatibonico, Las Villas
5.3	8.3	Paratype, Loma Espinosa, Chambas, Camagüey
4.9	8.3	Paratype, La Vigía, Mayajigua, Las Villas

Remarks. The differences between the new subspecies and the nominate subspecies serve to separate them. The range of *bermudezi bermudezi* is centered about Calabazar de Sagua in the north central region of Las Villas Province, whereas *b. jatibonica* occurs between Mayajigua, Las Villas and Chambas, Camagüey, from the northeast corner of Las Villas to the adjacent northwest corner of Camagüey.

Specimens examined. Holotype and paratypes.

Alcadia (Penisoltia) dissimulans (Poey)

Plate 4, figures 7–9; Map 3

Helicina dissimulans Poey, 1857. Memorias Historia Natural Isla de Cuba, 2: 35, pl. 4, figs. 8–10 (not 8–9 only as in text) (type-locality, Guane, Pinar del Río; type probably in MP). Sowerby, 1866, Thes. Conchyl., 3: 279, pl. 1 (266), figs. 28–29.

Alcadia dissimulans Poey. Pfeiffer, 1858, Malak. Blät., 5: 5; 1858, Monographia Pneumonopomorum Viventium, suppl. 1, 223. Arango, 1879, Contribución Fauna Malacológica Cubana, p. 56. Crosse, 1890, Jour. de Conchyl., 38: 325.

Alcadia (*Eualcadia*) *dissimulans* Poey. Wagner, 1907, *in* Martini and Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 2, p. 55, pl. 8, figs. 4–7, 24.

Alcadia dissimularis "Poey" Richards, 1933. Proc. Pennsylvania Acad. Sci., 7: 168 (error for *dissimulans*).

Description. Shell reaching about 11 mm in width, about 8 mm in height, strongly depressed, globose, rather fragile, sublustrous under pilose periostracum, subcarinate. Whorls about 5½, earlier whorls quite flat, later ones weakly rounded, increasing regularly in width. Body whorl 1½ times width of penultimate, weakly carinate, barely descending at aperture; base moderately inflated. Color various, pale reddish brown, pale buff, yellowish white, white or gray under the periostracum; basal callus and lip generally lighter in color than rest of shell. Aperture oblique, roundly triangular, almost straight below, noticeably depressed and flattened above. Palatal lip narrow, thin, weakly expanded centrally, depressed and weakly sigmoid above, somewhat raised below, with shallow, V-shaped sinus before basal tooth. Basal callus glossy, very weakly granulate, indistinctly limited parietally, set off in umbilical region by very shallow, slightly curved groove. Low, rounded and curved lamella near insertion in columellar termination. Columella strongly sloping and weakly inflated above, almost straight, directed outward below, and terminating in low, blunt outwardly directed tooth. Suture moderately impressed. Sculpture of irregular, moderately strong, shallowly curved, diagonal growth lines. Lineolations within shell substance very fine, closely spaced, weakly sinuous, most noticeable on base. Protoconch 1½ whorls, glassy, rounded, minutely punctate, same color as rest of shell, slightly raised above succeeding whorls. Periostracum pilose, deciduous, thin, hairs not arranged in any pattern, absent from area of basal callus and protoconch. Operculum as in genus, thin, pale yellowish brown with outer margin darker orange-brown. Internal wedge-shaped lamellae on columellar edge moderately well developed.

height in mm	width in mm	
7.8	10.6	El Queque, Viñales
7.3	10.4	Isabél María
6.7	10.3	Cabezas
6.6	9.3	El Queque, Viñales
6.4	11.3	Cabezas
6.3	8.3	Isabél María

Remarks. The shells of this species superficially resemble those of *velutina* but differ in having a less strongly developed basal peduncle, notch, and callus groove. The palatal lip is more widely expanded and more strongly depressed above. *A. dissimulans* is distinguished from *nitida* by having the upper lip straight at the insertion into the body whorl; in *nitida* this is curved and forms a shallow notch. In addition *dissimulans* is larger than *nitida* and differs in the nature of the basal tooth, which is narrower in *nitida* and is preceded by a much shallower palatal sinus.

In the MCZ collection we were able to examine some 37 lots of *dissimulans.* All of the more recently collected and more exactly localized series come from an area reaching from Cabezas and Isabél María to Viñales, about 45 kilometers from Guane, which was given by Poey as the type-locality. Guane is also the type-locality of *velutina* and the possibility cannot be overlooked that Poey erred as far as localizing *dissimulans* is concerned. The older published records all give Guane as the type-locality, but this undoubtedly is the result of copying from Poey. One lot in MCZ (72463, H. G. Richards leg.) from the "Sierra de Mendoza" (probably Sierra Guane or Sierra Paso Real) bore the label *dissimulans* but upon examination it proved to be typical *velutina.* We believe that the true type-locality of *dissimulans* is further to the northeast around Isabél María, Viñales.

Specimens examined. PINAR DEL RÍO. *Guane:* Sierra Paso Real; north base of Sierra de Guane (USNM); caves in mogote south side of road opposite Sierra Guane; Sierra Guane; Los Portales (USNM); La Muralla (USNM); Luis Lazo; El Potrero, Luis Lazo; ensenada in Sierra San Carlos opposite south end of Sierra de Los Acostas, Luis Lazo (USNM); Sumidero (USNM); Isabél María; Cabezas. *San Vicente:* Costanera del Abra (USNM); La Chorrera; north part of Sierra La Chorrera; Ensenada de los Baños (USNM); Mogote Ensenada de San Vicente; Ancón; Mogote Pequeño, Costanera de San Vicente. *Viñales:* Puerta del Ancón; Hoyo del Majagual, Sierra del Ancón; Sierra de Viñales; Sitio del Infierno; Hoyo de Los Cimarrones, peak of Sierra del Infierno; Sierra del Infierno; Rinconada de la Sierra Serrucho; Cafetal de la Penitencia; Pan de Azúcar; La Guasasa; Ensenada Miranda, Palmarito; Mogote Palmarito; Hoyo de Junes, Palmarito; Mogote Millo, Ensenada de la Grilla; Mogote Capón; Las Puntas; El Guamá; Las Delicias; El Queque; El Descanso; Mogote del Rojero; between Cayos de San Felipe and Loma de Isabél María; mogotes at Kilometer 14; Santo Tomás; Mogote Dinamita (USNM); Los Hermanos (USNM); Mogote de la Vega (USNM); Mogote de la Mina (USNM); Mogote Martín Miranda; Mogote San Felipe (USNM); Guajamí (USNM). Sitio de la Sierra, San Andrés; Sierra de San Andrés; Pan de Guajaibón (USNM); Mogote La Finca, San Diego de los Baños; La Güira, San Diego de los Baños; Río Dominica, 10 mi. W of Mariel,

Alcadia (Penisoltia) gonostoma (Poey)

Plate 5, figures 1–3; Map 3

Helicina gonostoma "Gundlach" Poey, 1858. Memorias Historia Natural Isla de Cuba, 2: 87 (type-locality, San Juan de Letrán, Trinidad, Las Villas, Cuba; types probably in MP).

Alcadia gonostoma Gundlach. Pfeiffer, 1858, Malak. Blät., 5: 194; 1865, Monographia Pneumonopomorum Viventium, suppl. 2, p. 248. Arango, 1879, Contribución Fauna Malacológica Cubana, p. 56. Crosse, 1890, Jour. de Conchyl., 38: 325.

Helicina goniostoma Poey. Sowerby, 1866, Thes. Conchyl., 3: 297, 299, error for *gonostoma.*

Alcadia (*Alcadia*) *gonostoma* (Gundlach) Poey. Wagner, 1907, *in* Martini and Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 2, p. 53, pl. 8, figs. 16–19 [not 5–8].

Description. Shell reaching about 8 mm in width, 5.5 mm in height, depressed-globose, smooth, fragile, moderately lustrous. Whorls almost 6, rounded, rapidly increasing in width. Body whorl about 1½ times width of penultimate, subcarinate but becoming more rounded near aperture, not descending at aperture; base moderately inflated. Color light yellow or orange yellow underneath periostracum, basal callus and lip white. Aperture oblique, semilunate, well rounded peripherally, not flattened or depressed above. Palatal lip thin, narrowly expanded, except at both terminations, not extended above, not curved at upper insertion. Basal callus white, glossy, surface roughened by minute granules arranged in wrinklelike formations, very indistinctly delimited parietally by a shallow, curved groove in umbilical region. Columellar edge of callus merging into short, white, rounded, somewhat thickened, upward directed, substyloid denticle with short, somewhat irregularly, slightly curved channel submedially situated near its outer margin. Columella weakly sigmoid, shallowly and irregularly concave below, with low ridge connecting it to basal denticle. Suture well impressed, most strongly along body whorl. Sculpture of irregular, curved, diagonal growth lines, crossed by threadlike, shallow, closely spaced, interrupted spiral striae. Axial lineolations inside shell substance white, wider than their intervals, very slightly sinuous. Protoconch 1.0 whorl, rounded, minutely and densely punctate. Periostracum thin, pilose, deciduous, with minute hairs arranged in reticulate pattern, reflected in shell as spiral striae. Operculum as in genus, calcareous layer pale yellow, finely granulate, chitinous layer very thin, brownish yellow, with darker, very narrow palatal border, extending beyond edge of calcareous layer, particularly at columellar edge; internal wedge-shaped columellar lamellae well developed.

height in mm	width in mm	
5.3	7.8	La Vigía, E of Mora, Oriente
5.2	7.5	La Vigía, E of Mora, Oriente

Remarks. This is a poorly known and rarely collected species. Poey did not illustrate it and the only previously published figures are the ones in Wagner (1907) which have an unnatural appearance and are misleading in the nature of the basal callus. It was not mentioned by Reeve (1874), and Sowerby (1866), referring to it as *goniostoma* [*sic*], was unable to identify it. Although the shells we examined came from Oriente Province, whereas Poey's type-locality is in Las Villas, they agree well with the original description. This extension of the range should be verified by more collecting.

Poey compared *gonostoma* with *nitida* Pfeiffer and *dissimulans* Poey, but it is closer to *velutina* Poey and may well be the eastern cognate of that western species. It differs from *velutina* in the stronger basal tooth, the wider and shallower labial sinus, and in the fact that the channel near the umbilical margin of the basal callus is much less strongly developed. Moreover, the tooth of *velutina* is directed forward, whereas in *gonostoma* it stands straight up. Finally, the periostracum of *gonostoma* is less dense and generally covers the entire shell.

Poey gives Gundlach's notes on the color of the animal as follows: "Animal brownish.

the surface rugosities somewhat darker gray. Brow and neck (as well as head) blackish; tentacles black with a somewhat lighter distal end." (translated).

Specimens examined. ORIENTE. La Vigía, E of Mora; Piloto del Medio, Sierra de Nipe (IZW).

Alcadia (Penisoltia) velutina (Poey)

Plate 3, figures 4–6; Map 3

Helicina velutina Poey, 1857. Memorias Historia Natural Isla de Cuba, 2: 35, pl. 4, figs. 5–7 (not only 6–7) (type-locality [Sierra de] Guane); types (probably in MP). Reeve, 1873, Conch. Icon., vol. 19, *Helicina,* pl. 3, fig. 16. Sowerby, 1866, Thes. Conchyl., 3: 279, pl. 1 (266), fig. 32. Crosse, 1890, Jour. de Conchyl., 38: 324.

Alcadia velutina Poey. Pfeiffer, 1858, Malak. Blät., 5: 5; 1858, Monographia Pneumonopomorum Viventium, suppl. 1, p. 223. Arango, 1879, Contribución Fauna Malacológica Cubana, p. 56.

Alcadia (*Eualcadia*) *velutina* Poey. Wagner, 1907, *in* Martini and Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 2, p. 54, pl. 8, figs. 1–3.

Description. Shell reaching about 10 mm in width, 7 mm in height, depressed-globose, weakly lustrous under pilose periostracum, fragile, subcarinate. Whorls about 5, almost flat, slowly increasing in width. Body whorl about twice the width of penultimate, rounded carinate, descending slowly at aperture; base moderately flattened. Color varied: pale reddish brown, dirty white or gray, lip and band in umbilical area white. Aperture roundly triangular, flattened below, moderately depressed above. Palatal lip thin, expanded, widest centrally, less so at both terminations, sigmoid above and with a narrow, long, U-shaped sinus before the basal tubercle. Basal callus lustrous, unevenly and microscopically granulate, lighter than rest of shell, weakly delimited parietally, and set off by a deep, curved groove umbilically. Umbilical margin of callus with gradually thickening lamella, terminating in strong, rounded, outward directed, substyloid tubercle; inner margin of tubercle with rounded, raised lamella; outer margin with shallow groove. Columella lightly sigmoid above, strongly curved and directed outward below and terminating in basal tubercle. Suture well impressed. Sculpture of strong, irregular, slightly curved growth lines. Protoconch 1½ whorls, glassy, lustrous, rounded, minutely and regularly punctate, slightly raised above succeeding whorls. Periostracum thick, deciduous, pilose, almost scaly at outer callus margin, arranged in closely set, narrow spiral bands; bands occasionally gathered in more regular and wider spiral structures. Operculum as in genus, calcareous layer very thin, granulate, slightly thickened and yellowish near columellar margin; chitinous layer bright reddish brown, somewhat darker at outer margin; wedge-shaped internal lamella well developed.

height in mm	width in mm	
6.8	10.5	Sierra de Guane
6.4	9.7	Sierra de Guane
5.3	7.8	Cueva el Catre, Paso Real

Remarks. The shells of this species can be readily recognized by their large size, strongly depressed outline, and thick, occasionally banded periostracum. The long basal sinus and the strong, forwardly directed basal tooth are also characteristic.

According to Arango (1879: 56), *A. velutina* lives on rocks. It has been reported only from the area of Guane in western Cuba where the Sierra de Guane and Sierra Paso Real are its only habitats. This restricted range can probably be explained by the habit of living only on rocks and not in leaf mould. It is larger and more depressed than *dissimulans,* has a thicker periostracum and noticeably more strongly developed basal sinus and tubercle. This last feature also serves to distinguish it most easily from the somewhat similar *nitida* and *rotunda.*

Sowerby (1866) did not succeed in distinguishing *velutina* (pl. 1, fig. 32) from *dissimulans* (pl. 1, fig. 28) since in his drawings the basal sinus of both species is practically alike.

Specimens examined. PINAR DEL RÍO. Pedrera de Mendoza; Cueva el Catre, Sierra Paso Real; Sierra de Guane; W part of Sierra de Guane.

Alcadia (Penisoltia) minima (Orbigny) Plate 1, figures 1–6; Plate 5, figures 7–9; Plate 6, figures 10–15; Map 1

Helicina minima Orbigny, 1842. Mollusques, *in* Sagra, Histoire Physique, Politique, et Naturelle de l'Ile de Cuba, 1: 253, pl. 21, figs. 7–9 ("interieur de l'Ile de Cuba"; type-locality, here restricted, Peña Blanca, Sierra Anafe, Habana; type BMNH. Sowerby, 1842, Thes. Conchyl., 1: 5, pl. 3, fig. 119; 1866, Thes. Conchyl., 3: 279, pl. 2 (267), figs. 37–38. Pfeiffer, 1850, *in* Martini and Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 1, p. 30, pl. 3, figs. 23–25.

Alcadia minima (Orbigny). Pfeiffer, 1852, Monographia Pneumonopomorum Viventium, p. 412; 1856, Malak. Blät., 3: 150. Arango, 1879, Contribución Fauna Malacológica Cubana, p. 57. Crosse, 1890, Jour. de Conchyl., 38: 326.

Alcadia gundlachi Pfeiffer, 1854. Malak. Blät., 1: 110 (Cuba, type-locality, here restricted, Cabo Cruz, Oriente; type destroyed); 1856, Malak. Blät., 3: 150; 1858, Monographia Pneumonopomorum Viventium, Suppl. 1, p. 224. Sowerby, 1866, Thes. Conchyl., 3: 286, pl. 1 (271), figs. 211–212. Arango, 1879, Contribución Fauna Malacológica Cubana, p. 57. Crosse, 1890, Jour. de Conchyl., 38: 325.

Alcadia capax 'Gundlach' Pfeiffer, 1857. Malak. Blät., 4: 113 (Magua and Letran; type-locality, here restricted, Magua near Trinidad, Las Villas; type destroyed; specimen here figured, pl. 6, figs. 10–12, MCZ 90050, T. Bland Collection); 1858, Monographia Pneumonopomorum Viventium, Suppl. 1, p. 224. Arango, 1879, Contribución Fauna Malacológica Cubana, p. 57.

Helicina proxima 'Gundlach' Poey, 1858. Memorias Historia Natural Isla de Cuba, 2: 6 [*nomen nudum*]. Pfeiffer, 1858, Malak. Blät., 5: 49 (type-locality, Buenavista, Oriente; type destroyed).

Helicina montana 'Wright' Pfeiffer, 1864. Malak. Blät., 11: 160 (type-locality, Luis Lazo, Pinar del Río; type destroyed; specimen here figured, pl. 6, figs. 13–15, MCZ 90055, T. Bland Collection *ex* Poey); 1865, Monographia Pneumonopomorum Viventium, Suppl. 2, p. 220. Arango, 1879, Contribución Fauna Malacológica Cubana, p. 46. Crosse, 1890, Jour. de Conchyl., 38: 312.

Alcadia proxima (Pfeiffer). Pfeiffer, 1865, Monographia Pneumonopomorum Viventium, Suppl. 2, p. 250. Arango, 1879, Contribución Fauna Malacológica Cubana, p. 57. Crosse, 1890, Jour. de Conchyl., 38: 326.

Alcadia (*Eualcadia*) *minima* (Orbigny). Wagner, 1907, *in* Martini and Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 2, p. 57, pl. 8, figs. 20–23.

Alcadia (*Leialcadia*) *gundlachi* (Pfeiffer). Wagner, 1907, *in* Martini and Chemnitz, Conchyl.-Cab., 2 (1): sect. 18, pt. 2, p. 73, pl. 11, figs. 22–25 (San Juan de los Pinos).

Alcadia (*Eualcadia*) *proxima* (Pfeiffer). Wagner, 1907, *in* Martini and Chemnitz, Conchyl.-Cab., 2 (1): sect. 18, pt. 2, p. 58, p. 9, figs. 4–8.

Alcadia (*Leialcadia*) *rotunda montana* (Pfeiffer). Wagner, 1907, *in* Martini and Chemnitz, Conchyl.-Cab., 2 (1): sect. 18, pt. 2, p. 70, pl. 11, figs. 19, 21.

Alcadia (*Alcadia*) *minima* (Orbigny). Farfante, 1942, Mem. Soc. Cubana Hist. Nat., 16: 50.

Alcadia quinonesi Clench and Aguayo, 1950. Rev. Soc. Malac., 'Carlos de la Torre,' 7: 63, pl. 12, figs. 9–11 (type-locality, Los Tambores, between Playa Puerto Rico and Punta de Mulas, Banes, Oriente, Cuba; holotype MP 12913; paratype MCZ 185800).

Alcadia balteata Aguayo and Juame, 1954. Rev. Soc. Malac. 'Carlos de la Torre,' 9: 57, pl. 6, figs. 4–6 (type-locality, "Ballenato Grande," Bahia de Nuevitas, Camagüey; holotype in MP).

Description. Shell reaching about 5.5 mm in width, 4.5 mm in height, depressed-globose, fragile, weakly lustrous under periostracum. Whorls almost 6, slightly convex, slowly increasing in width. Body whorl slightly wider than penultimate, well rounded, descending slightly at aperture; base inflated. Color gray or pale brownish white, occasionally pale reddish, lip and area of basal callus white. Aperture slightly oblique, semilunate, irregularly rounded peripherally, flattened at both terminations. Palatal lip thin, very narrowly expanded except near both terminations, slightly sigmoid above, not curved at upper insertion, with a shallow, widely U-shaped basal sinus. Basal callus white, strongly granulate, raised and well delimited parietally, with a rather strong, curved lamella in the umbilical margin, widening and growing stronger rapidly and terminating distally in a strong, rounded, upward directed tooth which does not project above the height of the basal lip. Columella weakly sigmoid, shortly rounded below and connected to the basal tooth by a low, narrow ridge. Suture moderately impressed. Sculpture of well-defined, irregular, diagonal growth lines only. Axial lineolations inside shell substance rather wide, narrowly separated, weakly sinuous. Periostracum thin, pilose or hirsute with very short hairs, deciduous, light brown. Operculum as in genus, internal chitinous layer light yellow, reddish brown at palatal margin; outer calcareous layer thin, white, finely granulate; inner wedge-shaped lamellae at columellar edge well developed.

height in mm	width in mm	
4.4	5.5	Silla de Gibara, Oriente
3.8	5.0	Valle San Juan, Guanacabibes, Pinar del Río
3.4	4.7	Coliseo, Matanzas
2.9	4.4	Peña Blanca, Sierra Anafe, Havana

Remarks. This species has been reported from all over Cuba, even appearing in some of the satellite keys and in the westernmost peninsula of Guanacabibes, a flat and barren area. It is strangely absent from the Isle of Pines. On the basis of the material available to us it does not appear to live in the same microhabitats as its closest congener, *hispida,* though both appear to favor the same sort of surroundings, since Arango (1879) reports finding *minima* under rocks and leaf litter (hojarasca), where Gould (1844) also found *hispida.*

Alcadia minima is characterized by its small size, fragile and rather colorless shell, pilose periostracum, and the very narrow, slightly expanded lip (see also under *hispida*). It is quite uniform in appearance throughout its large range, varying only slightly in size, color, and in the strength of the basal tooth. One lot (MCZ 90050, T. Bland Collection), probably collected in Matanzas by either Pfeiffer or Gundlach, consists of smaller shells, rather more lustrous and somewhat heavier and bluish gray in color.

An examination of large numbers of specimens from numerous localities over the entire island as well as a comparison of the written descriptions and published figures has convinced us that *minima* has been named many times from many parts of Cuba. All the specimens parading under such names as *gundlachi* Pfeiffer, *capax* Pfeiffer, *montana* Pfeiffer, *quinonesi* Clench and Aguayo, *balteata* Aguayo and Jaume, and probably *proxima* Pfeiffer have the following characteristics in common: 1) the shell is small, generally 5 mm or less in width, fragile and some shade of light brown or dirty white, 2) the periostracum is thinly pilose, 3) the basal sinus is wide, shallow, and U-shaped, 4) the basal denticle is low, narrow, rounded distally, upward and outward directed, and rests at the termination of a low marginal lamella on the basal callus, 5) the operculum is thin and darker at the outer edge. The differences between the "species," real and supposed, are variable or minor. Thus *gundlachi, quinonesi,* and *balteata* are said to have spiral color bands, but these bands admittedly do not appear on all the members of the same population. Moreover, color in the Helicinidae must be regarded as an exceedingly variable characteristic. Other cited differences among the synonyms, such as the relative strength of the basal furrow, degree of carination, depth of suture, relative width of the body whorl, are subjective judgments and not consistent in "species" when large numbers of specimens are examined.

It is also important to realize that few of these species were clearly described or well figured, and, in the cases where comparisons with related species were made, no distinction was drawn with *minima.* Thus Clench and Aguayo contrasted their *quinonesi* with *concinna* Pfeiffer because both forms were thought to have color bands. But *concinna* is quite a different species, easily distinguishable from the whole group of *minima*-related taxa. No comparison was made with *minima,* an obviously very closely related—in our opinion identical—species. When *balteata* was described, a contrast was drawn between it and *quinonesi,* again without the mention of *minima,* which should have been the first species to be contrasted. Even then the differences drawn between *quinonesi* and *balteata* were relative: spiral sculpture weaker, basal furrow deeper.

The species *quinonesi* was established because of the presence of spiral striae, as in some species of *Emoda.* But an inspection of a good-sized paratype lot (MCZ 185800) showed that many individuals had no sign of such sculpture and were identical with *minima* except for an occasional specimen with light-colored spiral bands.

Pfeiffer wrote that *gundlachi,* of which he had only three specimens, had the denticle "retroflexum." It is difficult to know what he meant, unless he was referring to the fact that the denticle is directed outward when the shell is held vertically with the aperture facing the viewer. But all denticles of *Alcadia* have this feature in common. The only difference in direction we were able to detect is that sometimes denticles are directed upward toward the columella (most species) and sometimes directed forward toward the periphery, as in *velutina* Poey, for example. All denticles are, in addition, directed more or less outwards.

The confusion regarding the identity of these shells is reflected in the erratic naming of series in museum collections. To the investigator, it is soon obvious that the persons responsible for the determinations were not able to fix clear separations for the various taxa and distributed names more or less haphazardly.

The species *minima* is distributed all over Cuba and variations appear both in individuals and in populations. But these variations are not persistent or consistent enough to justify taxonomic recognition, even of a subspecific nature.

Pfeiffer (1856: 150) transcribed Gundlach's notes on the animal which we translate as follows: "Animal pale, with gray spots spread over the entire body, especially underneath the eyes. Tentacles somewhat gray."

Specimens examined. Pinar del Río. Cabo San Antonio (USNM); Valle San Juan, Guanacabibes (Guanahacabibes): *Guane:* La Tenería, La Muralla (both USNM); ensenada in Sierra San Carlos, opposite S end of Sierra Los Acostas (MCZ); Cerro de Cabras (USNM); mogote N side of Km 14 between Pinar del Río City and Luis Lazo (MCZ). *Viñales:* Mogote la Mina; Mogote Dinamita; Mogote Cayo San Felipe (all USNM); Cueva de los Santos (MCZ). *San Vicente:* Mogote Ensenada de San Vicente; Costanera de San Vicente; Puerta del Ancón; Cueva del Indio, Mogote Bosque; Mogote Palmarito; Laguna de Piedra; La Chorrera (all USNM); Baños de San Vicente (all MCZ). *Rangel:* El Paco; El Retiro (both MCZ). *San Diego de los Baños:* Mogote Indios; La Güira; Mogote 8; Mogote 9; La Cumbre (all USNM); Mogote la Finca; Tibisi; El Toro, Sierra de Limones; El Mamey, Cayajabos; Peña Blanca, El Cuzco (all MCZ). Habana. El Mudo; Tapaste; Madruga; Sitio Bonilla, Jaruco; Sitio Perdido, Jaruco; mountains near Jamaica; Loma de Camoa; Sierra Anafe, S slope (all USNM); Peña Blanca, Sierra Anafe (MCZ). Matanzas. Fundador; Canímar River above ferry, Fundador (both USNM); El Palenque (MCZ); Finca El Par, Pan de Palenque; Portuondo, Pan de Palenque; Pan de Matanzas; Punta de Sabanilla; paredones W bank of Río Canímar below Carretera Central; W of pass, Coliseo; S of pass, Coliseo; Loma Odiseo between Coliseo and San Miguel de los Baños; Mogote Caoba, between Coliseo and San Miguel de los Baños; (all USNM); Monte Cristo (MCZ); paredones, 2 km S of Limonar; Varadero; Abra de Figueroa, Yumurí (all USNM); Abra de Yumurí; Granja Escuela, Colon (both MCZ). Las Villas. N slope of Sierra Jatibonico; S end of Loma Ramón Martínez; Jumagua near Sagua La Grande (all USNM); Chinchilla, Sagua La Grande; San Miguel, Sagua la Grande; Finca Valdés, Camao, Remedios; La Puntilla, Remedios (all MCZ); SE side of El Palenque near Remedios; Mogote Ramón Martínez, E side of road between Remedios and Zulueta; Mogote Charco, W side of road between Remedios and Zulueta; Loma San Augustín, SE of Central San Augustín (all

USNM); Loma near San Augustín (MCZ). *Vega Alta:* Vereda del Abra (MCZ); Loma Murciélago; 1st mogote at entrance to Las Piedras; 2nd mogote of La Sierra; Mogote Sola; mogote near Loma Chicharrón; Loma La Sinaloa (all USNM). Cayo Lucas, Yaguajay; Finca Cuetoa, Caibarién; La Portuguesa, Soledad (all MCZ); Cienfuegos; La Vigía, Trinidad; Nacimiento del Río, NW of Trinidad (all USNM); Buenos Aires, Trinidad (MCZ). CAMAGÜEY. Punta de San Juan de los Perros (MCZ); Loma de los Perros, 1 km W of Punta Alegre; 3.5 km from N entrance of Paso Tinaja, E side of Cubitas Mts.; on rocks, Sitio Afuera, S end of Paso Escalera, Cubita Mts.; Los Corrales de Cangelones, Cubitas Mts.; El Terreplén, Turiguanó Id. 1 km W of River Mota; La Vigía, Ensenada de Mora (all ANSP); Heliograph Hill, Turiguanó Id. (MCZ). ORIENTE. *Miranda:* hill N of Mercedes Valley; upper Mercedes Valley; Arroyo del Agua (all ANSP); 2 mi. S of Central Ramón; Buena Vista, S of Bayamo, Sierra Maestre; Cayo Duan, Santiago de Cuba; Puerto Portillo; Cabo Cruz (all US NM); Silla de Gibara; Cayo Francés, Palma Soriano; Portales de Camayén; Pico Turquino (all MCZ).

Glyptalcadia Boss and Jacobson new subgenus

Type-species, *Alcadia* (*Alcadia*) *euglypta* Clench and Aguayo, 1950.

Description. Shell small with the basal tooth and notch of *Alcadia s.l.* but differing in the variously formed, somewhat strong surface sculpture.

Remarks. Most species of *Alcadia s.l.* are characterized by the lack of surface sculpture other than generally weak axial growth lines and, very occasionally, weak, punctate spiral striae. The comparatively strong development of surface sculpture in *A. euglypta* and *camagueyana* is remarkable and deserves, in our opinion, superspecific recognition, for which *Glyptalcadia* is suggested. This subgenus is comparable to the helicinine *Glyptemoda* Clench, which has been treated at the generic level by Clench and Jacobson (1971a) and which consists of strongly sculptured forms differing from the closely related weakly sculptured species of *Emoda.* It is noteworthy that both these groups occur sympatrically in the eastern part of Cuba.

KEY TO THE SPECIES OF *Glyptalcadia*

1. Sculpture of flat, irregularly spaced and shaped tubercles; frequently carinate; distribution limited to central Camagüey Province .... *camagueyana*

   Sculpture of elongate, white, interrupted axial ridges, never carinate; distribution in northeastern Oriente Province only .... *euglypta*

Alcadia (Glyptalcadia) euglypta Clench and Aguayo
Plate 4, figures 1–3; Map 3

Alcadia euglypta Clench and Aguayo, 1950. Rev. Soc. Malac. 'Carlos de la Torre,' 7:64, pl. 12, figs. 6–8 (type-locality, Cerro Cariblanco, Holguín, Oriente; holotype, MP 12911; paratypes, MCZ 185797, 185801).

Description. Shell reaching about 5½ mm in width, 3½ mm in height, strongly depressed, rather solid, surface roughly sculptured, lusterless. Whorls 4 to 5, barely convex, increasing regularly in width. Body whorl about 2½ times wider than penultimate, more rounded below with a weak but distinct, narrowly rounded carina near shoulder, descending briefly but strongly at aperture. Color dirty brown or buff, with irregular, elongate, white, interrupted axial ridges under thin, darker brown hirsute periostracum. Aperture oblique, widely semilunate, well rounded peripherally, somewhat flattened below, weakly extended above and slightly curved at insertion into body whorl. Palatal lip thin, expanded weakly except at both terminations and with shallow, rounded, wide notch before basal tubercle. Basal callus indistinctly delimited parietally, sunken at umbilical area and set off by raised base of body whorl. Curved, slowly strengthening lamella along inner margin of body whorl terminating in low, upward directed, rounded and somewhat thickened tubercle. Columella sigmoid, irregularly concave below, connected to basal tubercle by low, narrow, rounded, concave ridge. Suture well impressed, strongest near aperture. Sculpture somewhat strong, consisting of numerous narrow, diagonal axial cords, which cover rather high, lighter colored, unevenly wide axial ridges; intervals between ridges about as wide as ridges themselves. Spiral sculpture consisting of few, irregularly and rather widely spaced, occasionally interrupted cords. Sculpture weakening on the base with axial ridges growing noticeably narrower and becoming shallowly and irregularly sinuous. Protoconch 1½ whorls, glossy, rounded, surface much roughened, closely and unevenly granulate. Periostracum hirsute, hairs long, pointed and sparsely set, more closely juxtaposed in intervals between spiral ridges. Operculum as in genus, light reddish brown near the outer margin, paler near inner margin.

height in mm	width in mm	
3.2	5.1	Loma la Vigía, Gibara
2.8	4.5	Loma la Vigía, Gibara
2.6	4.4	Cerro Cariblanco, Holguín

Remarks. Our description is based upon three paratypes. We were unable to detect the colors mentioned in the original description, although one of the specimens examined was collected alive.

This species has a very distinctive shell, which can easily be recognized by its relatively strongly sculptured surface. The white, high axial ridges can be seen at the periphery with the naked eye. Its depressed shape and sculpture will immediately separate it from other species of *Alcadia* of similar size.

This species has been reported only from around Gibara and Holguín, two areas on the northwest coast of Oriente Province about 35 kilometers apart. Although no ecological details were given, it appears to be, like most *Alcadia,* a ground dweller, probably found in leaf mulch and under rocks.

Specimens examined. ORIENTE. Cerro Cariblanco, Holguín; Loma la Vigía, Gibara.

Alcadia (Glyptalcadia) camagueyana Aguayo and Jaume

Plate 4, figures 4–6; Map 3

Alcadia (*Penisoltia*) *camagueyana* Aguayo and Jaume, 1957. Mem. Soc. Cubana Hist. Nat., 23: 122, pl. 1, fig. 9 (type-locality, La Caridad de Mendoza, Minas, Camagüey; holotype, MP 13264; paratypes, MCZ 128771).

Alcadia (*Penisoltia*) *camagueyana porosa* Aguayo and Jaume, 1957. *Ibid.,* p. 123, pl. 1, fig. 7 (type-locality, "Los Cangilones," Sierra de Cubitas, Camagüey; holotype, MP 13266).

Alcadia (*Penisoltia*) *camagueyana ecarinata* Aguayo and Jaume, 1957. *Ibid.,* p. 124, pl. 1, figs. 11–12 (type-locality, Sierra de Najaza, Camagüey; holotype, MP 13268; paratype, MCZ 47840).

Description. Shell reaching about 6 mm in width, 4 mm in height, depressed, carinate, weakly lustrous, opaque, solid. Whorls 5½, flat, strongly keeled, rapidly increasing in width. Body whorl 1½ times width of penultimate, rounded below, generally with a white, tuberculate keel at shoulder (obsolescent in some specimens) and descending sharply at aperture. Color light chocolate-brown with numerous irregularly formed, opaque, milk-white, irregularly spaced patches, occasionally arranged in spiral bands on the base. Aperture oblique, semilunate, irregularly rounded peripherally, with obtuse angle above and below center. Palatal lip slightly thickened, well expanded, less so at both terminations, narrowly projected above, inserting straight into body whorl; basal sinus exceedingly shallow, wide. Basal callus white, minutely punctate, indistinctly delimited parietally, sunken at umbilical area where set off by subperpendicular, rather high wall of base of body whorl. Upward directed, low, narrow, rounded tooth rising from low, curved lamella on umbilical margin of raised base of body whorl. Columella sigmoid, rounded below and connected to tooth described above by low, rounded ridge. Suture well impressed, sometimes margined by unevenly raised ridge composed of uneven white tubercles. Sculpture rather strong, consisting of variously well-marked, raised, uneven spiral ridges, composed of irregular flat tubercles and crossed by variously strong, diagonal, curved axial cords; sculpture generally weaker on base. Lineolations within shell substance wider than their intervals, slightly sinuous, most noticeable on white portions of the shell. Protoconch 1½ whorls, glassy, rounded, minutely and unevenly punctate, little raised above succeeding whorls. Periostracum usually wanting but occasionally with long filiform hairs. Operculum as in genus, amber colored, transparent.

height in mm	width in mm	
3.9	5.8	El Cacaotal, Najaza
3.2	5.4	La Caridad de Mendoza, Minas
3.4	6.1	Paso de la Tinaja, Cubitas
3.4	5.5	La Caridad de Mendoza, Minas
3.4	5.4	Cangilones, Cubitas Mts.

Remarks. The shell of this species is distinctive because of its depressed outline, the unique and rather strong sculpture, and the carina, which is visible to the naked eye and is formed of white tubercles. Even when the carina is obsolescent, as in the specimens which were described as *ecarinata* by Aguayo and Jaume (1957), the species is readily recognized by the strong sculpture.

Closely related to the consubgeneric *A. euglypta* Clench and Aguayo from the neighboring Oriente Province, *A. camagueyana* may be differentiated by its surface sculpture, which consists of flat, irregularly spaced and irregularly shaped tubercles. Additionally, a carina is frequently present in *A. camagueyana* and the species lacks the numerous axial cords found in *A. euglypta*.

The species, which is highly variable in its shell features, is found only in Camagüey Province where it occurs in mountain ranges of both Cubitas and Najaza as well as in some intervening hilly areas. No consistent or marked differences between samples from Najaza or Cubitas were detectable. Further, in a single large series of specimens from La Caridad de Mendoza, we found many specimens which correspond to the descriptions of *porosa* and *ecarinata*, described by Aguayo and Jaume (1957) from Sierra Cubitas and Sierra Najaza, respectively. This overlap in conchological characters and the lack of geographic isolation indicate that there are no recognizable subspecies of *A. camagueyana*.

Apparently *A. camagueyana* must occur in large numbers and must be comparatively easily collected, since some lots at our disposal were extensive. Like several other species of *Alcadia*, it is probably a ground-dwelling species, found under leaves and on rocks.

Specimens examined. CAMAGÜEY. *Cubitas Mts.:* S of Vereda de los Burros; Los Cangilones; Los Corrales de Cangilones (USNM); La Caridad de Cangilones (USNM); Bainoa, Banoa; Sitio Afuera, S end of Paso Escalera, on rocks (USNM); Finca Pico, north entrance to Paso Escalera (USNM); first descent S of north entrance to Paso Escalera (USNM); E side of the ensenada, Paso Paredones (USNM); 1 km N of south entrance to Paso Paredones (USNM); Paso Paredones; W side of Paso Guanaja, 1 km N of south entrance (USNM); E side of Vereda del Burro, 1.5 km N of Finca "San Clemente" (USNM); N side of Cubitas between Paso Guanaja and Paso Paredones (USNM); Paso de la Tinaja; north entrance to Paso Tinaja; Salta de la Tinaja, 1.5 km from north entrance to the pass (USNM); E of Salta de la Tinaja, 1.5 km from north entrance; 2½ km from N entrance of Paso Tinaja (USNM); E side near south entrance to Paso Tinaja, 1 km from Bainao. El Cacaotal, Najaza; Arroyo Hondo; Loma Santa Cruz, Minas; Guaicanamar near Najaza; La Caridad de Mendoza, Minas; El Zanjón.

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Plate 1

Figs. 1–6. *Alcadia (Penisoltia) minima* (Orbigny).
Figs. 1–3. MCZ 128742, San Juan de los Perros, Camagüey (height = 4.5 mm).
Figs. 4–6. MCZ 128722, Silla de Gibara, Oriente (height = 4.9 mm).
Figs. 7–9. Topotype of *Alcadia (Alcadia) nuda bagaensis* Aguayo, MCZ 128775, El Bagá Maisi, Oriente (height = 9.2 mm).
Figs. 10–12. *Alcadia (Idesa) concinna*, MCZ 86616, ex Gundlach [Cabo Cruz, Oriente] (height = 4.5 mm).

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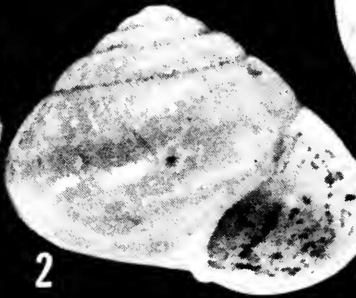

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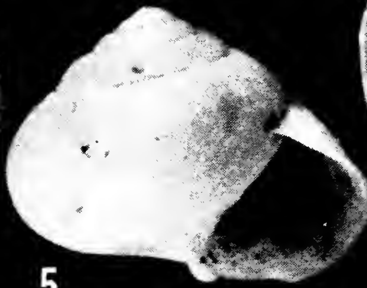

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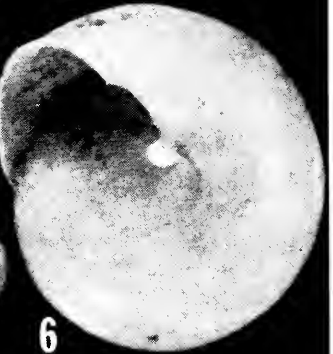

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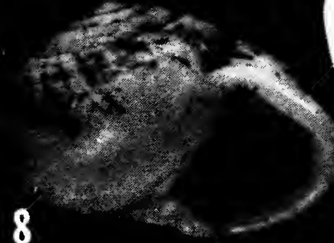

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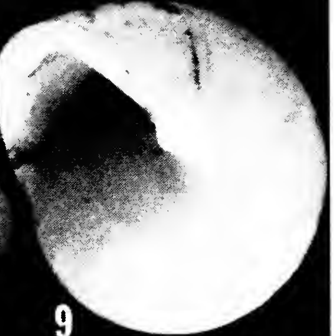

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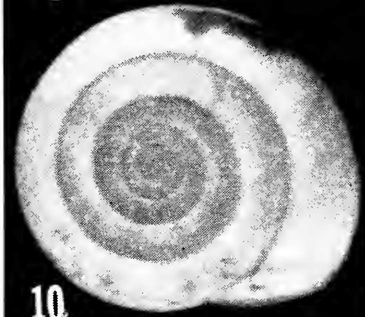

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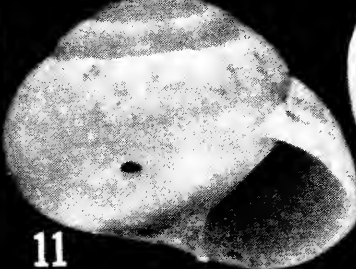

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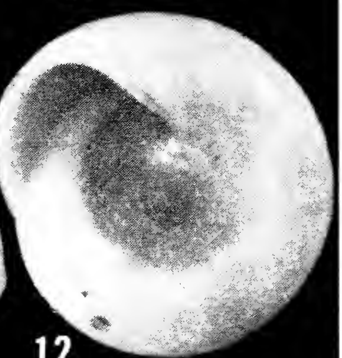

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Plate 2

Figs. 1–3. *Alcadia (Hjalmarsona) neebiana,* MCZ 90056, ex Bland [Cayo del Rey, Mayarí, Oriente] (height = 8.2 mm).

Figs. 4–6. *Alcadia (Idesa) rotunda* (Orbigny), MCZ 279757, Pan de Azúcar, Pinar del Río (height = 8.0).

Figs. 7–9. *Alcadia (Alcadia) nuda nuda,* MCZ 90052, ex Bland [Barigua, Baracoa, Oriente] (height = 11.5 mm).

Figs. 10–12. *Alcadia (Alcadia) incrustata,* MCZ 74028, ex Poey [Yateras, Guantánamo, Oriente] (height = 7.5 mm).


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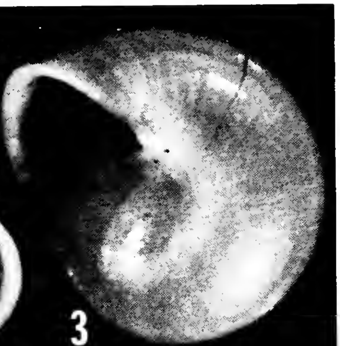
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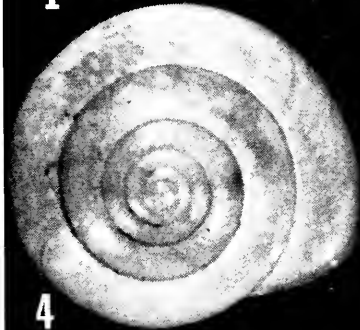
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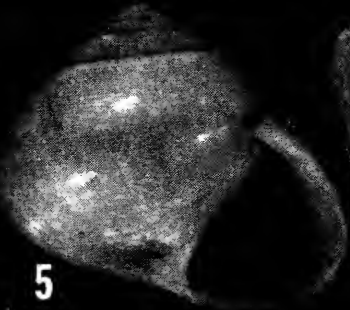
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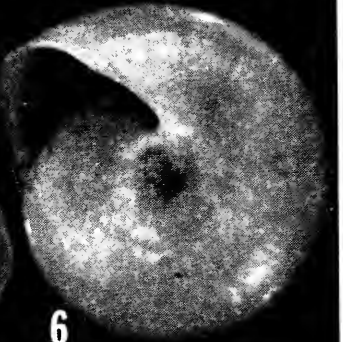
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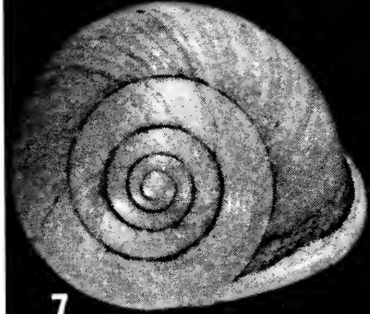
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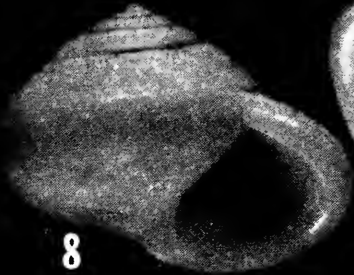
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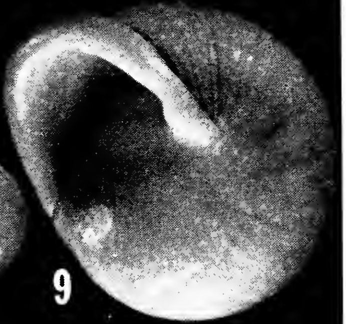
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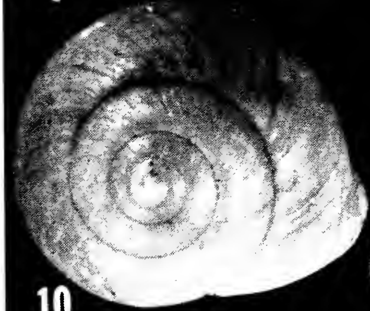
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Plate 3

Figs. 1–3. *Alcadia (Idesa) spectabilis* (Pfeiffer), MCZ 74024, ex Anthony [Yateras, Guantánamo, Oriente] (height = 6.5 mm).

Figs. 4–6. Topotype of *Alcadia (Penisoltia) velutina* (Poey), MCZ 128663, Sierra de Guane, Pinar del Río (height = 6.8 mm).

Figs. 7–9. Topotype of *Alcadia (Hjalmarsona) nitida* (Pfeiffer), MCZ 128693, El Descanso, Coliseo, Matanzas height = 6.8 mm).

Figs. 10–12. *Alcadia (Hjalmarsona) nitida* (Pfeiffer), MCZ 47511, ex Bermudez, Marianao, Havana (height = 5.1 mm).


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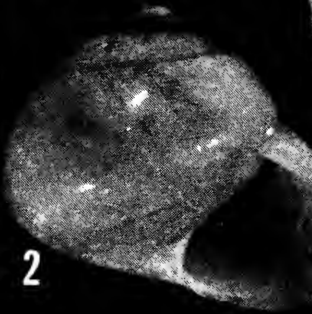
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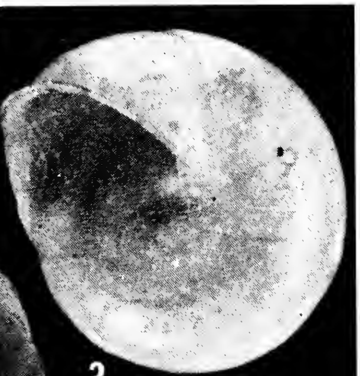
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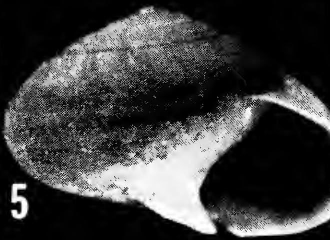
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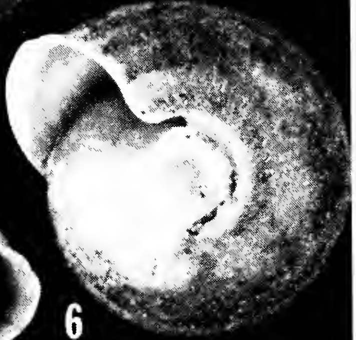
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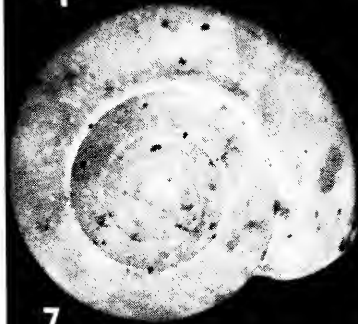
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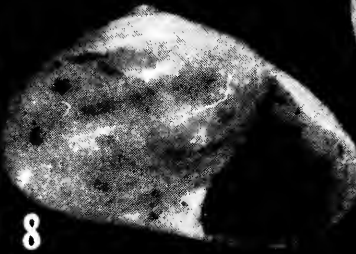
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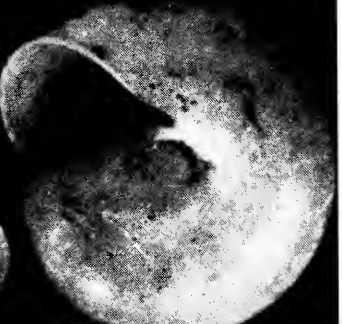
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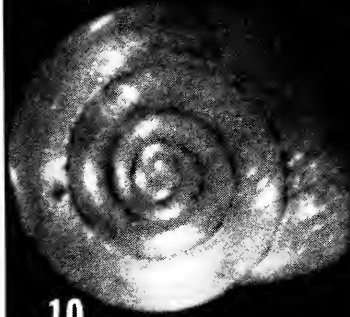
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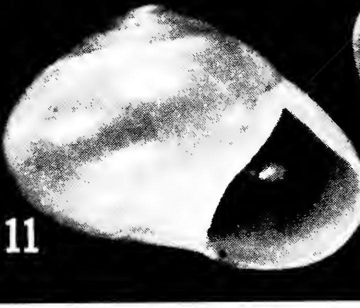
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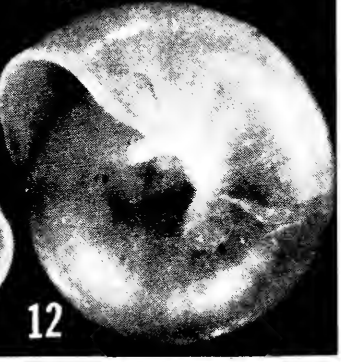
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Plate 4

Figs. 1–3. Paratype of *Alcadia euglypta* Clench and Aguayo [= *Alcadia (Glyptalcadia) euglypta*], MCZ 185797, Cerro Cariblanco, Holguín, Oriente (height = 2.6 mm).

Figs. 4–6. Paratype of *Alcadia (Penisoltia) camagueyana* Aguayo and Jaume [= *Alcadia (Glyptalcadia) camagueyana* Aguayo and Jaume], MCZ 128771, La Caridad de Mendoza, Minas, Camagüey (height = 3.4 mm).

Figs. 7–9. *Alcadia (Penisoltia) dissimulans* (Poey), MCZ 98781, Sierra de la Chorrera, San Vicente, Pinar del Río (height = 6.5 mm).

Figs. 10–12. Paratype of *Alcadia bermudezi* Aguayo and Jaume [= *Alcadia (Penisoltia) bermudezi bermudezi* Aguayo and Jaume], MCZ 128665, "La Sierra," Vega Alta, Las Villas (height = 6.4 mm).

Figs. 13–15. *Alcadia (Penisoltia) hispida* (Pfeiffer), MCZ 80849, Managua, Habana (height = 4.4).

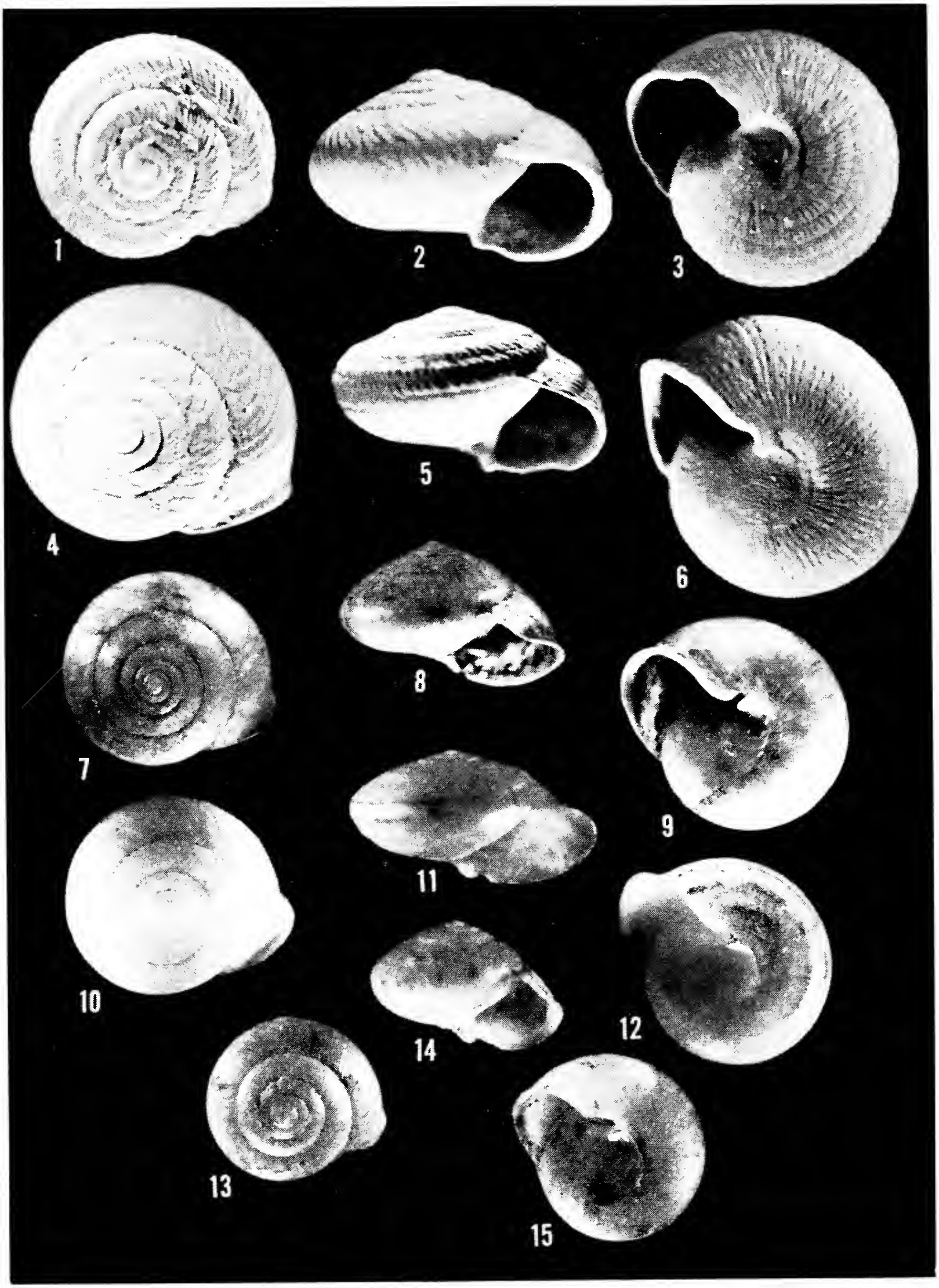
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Plate 5

Figs. 1–3. *Alcadia (Penisoltia) gonostoma* (Poey), MCZ 85595, La Vigía, E of Mora, Oriente (height = 5.2 mm).

Figs. 4–6. Holotype of *Alcadia (Penisoltia) bermudezi jatibonica* Boss and Jacobson, new subspecies MCZ 128669, Boquerón de Jatibonico, Las Villas (height = 5.5 mm).

Figs. 7–9. *Alcadia (Penisoltia) minima* (Orbigny), MCZ 128729, Mogote La Finca, San Diego de los Baños, Pinar del Rio (height = 4.1 mm).

Figs. 10 and 11. *Alcadia (Idesa) spectabilis* (Pfeiffer), MCZ 277250, S side of Pico Turquino, 1500–3800 ft., Sierra Maestra, Oriente (height = 7.5 mm).

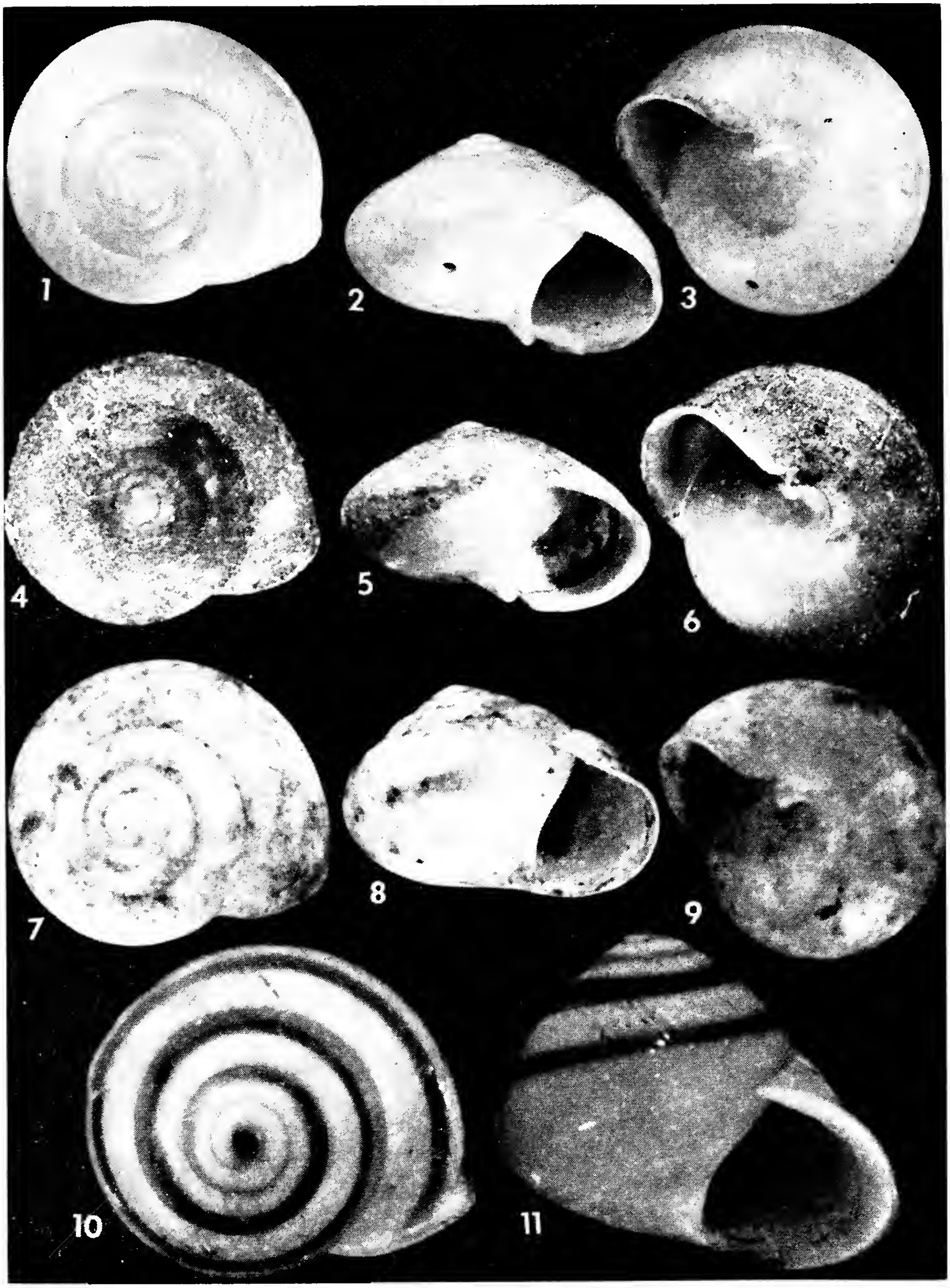
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Plate 6

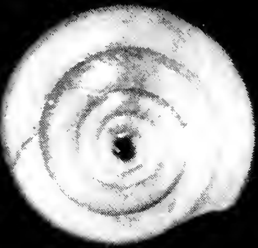
Figs. 1–3. *Alcadia (Idesa) spectabilis,* MCZ 74031, ex Gundlach, Buenavista near Bayamo, Oriente (height = 6.0 mm).

Figs. 4–6. *Alcadia (Idesa) spectabilis,* MCZ 74030, Mante Líbano, Guantánamo, Oriente (height = 6.7 mm).

Figs. 7–9. *Alcadia (Idesa) spectabilis,* MCZ 74029 [La Cubana, Yateras, Guantánamo, Oriente] (height = 6.5 mm).

Figs. 10–12. *Alcadia (Penisoltia) minima,* MCZ 90050, Trinidad, Las Villas (height = 3.3 mm). Specimens sprayed. Ventral view (Fig. 12) with mounting medium.

Figs. 13–15. *Alcadia (Penisoltia) minima,* MCZ 90055 [Luis Lazo, Pinar del Río] (height = 2.5 mm). Specimens sprayed. Ventral view (Fig. 15) with mounting medium.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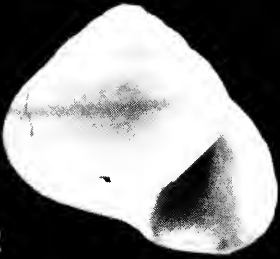
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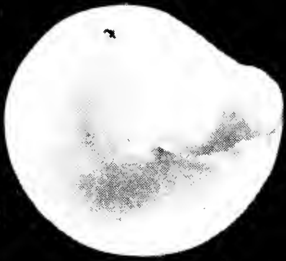
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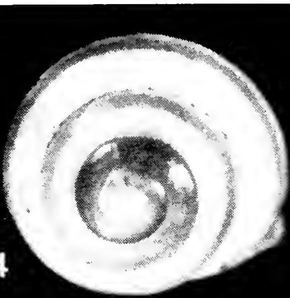
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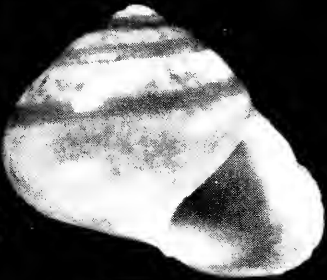
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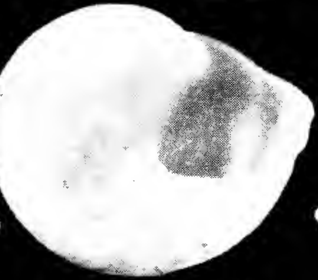
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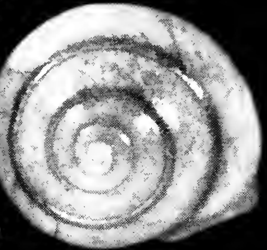
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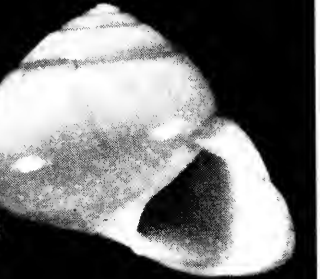
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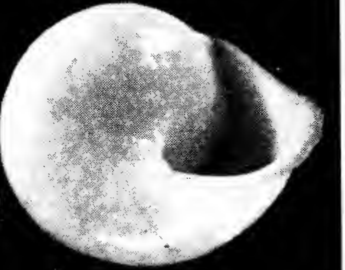
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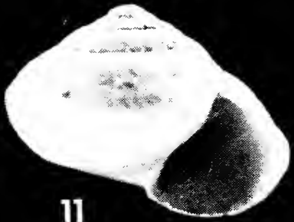
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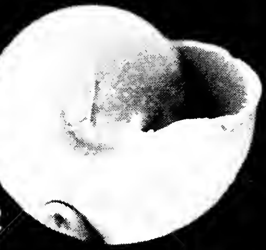
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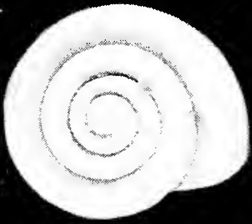
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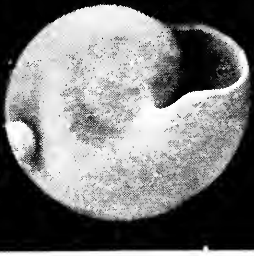
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CURT TEICHERT, BERNHARD KUMMEL, AND WALTER SWEET

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PERMIAN-TRIASSIC STRATA, KUH-E-ALI BASHI, NORTHWESTERN IRAN

CURT TEICHERT,[1] BERNHARD KUMMEL,[2] AND WALTER SWEET[3]

CONTENTS

Abstract. The Permian-Triassic boundary is studied in Kuh-e-Ali Bashi, northwestern Iran, in a locality situated about 8 km southeast of the classical section on the north side of the Aras River, west of Soviet Dzhulfa. Here, strata with a typical Dzhulfian fauna are overlain by a sequence of shale, sandstone, and impure limestone, 16.5 to 20.5 m thick, for which we propose the name Ali Bashi Formation. This is overlain by the Elikah Formation of Early Triassic age. The Ali Bashi Formation embraces Beds 52–61 of the stratigraphic section published by Stepanov, Golshani, and Stöcklin (1969) and is equivalent to Dzhulfian horizon 5 plus Induan horizons 1–4 of Ruzhentsev and Sarycheva (1965) on the Soviet side of the Aras River.

The fauna of the Ali Bashi Formation is described and discussed. Total number of species is about 45. New genera and species are the ammonoids *Iranites* Teichert and Kummel, n. gen., and *Shevyrevites shevyrevi* Teichert and Kummel, n. gen. and n. sp., and the conodont species *Anchignathodus julfensis* Sweet, n. sp. and subspecies *Neogondolella carinata subcarinata* Sweet, n. subsp.

The macrofauna of the Ali Bashi is of predominantly Dzhulfian aspect, but its ammonoid fauna contains distinctive elements of the Changhsingian fauna of southern China. Conodonts indicate that the Ali Bashi and at least 13.5 m of the overlying Elikah Formation belong in the *Anchignathodus typicalis* Zone, the lower boundary of which is herein established at the base of the Ali Bashi Formation, where *Neogondolella orientalis* (Barskov and Koroleva) is replaced by *N. carinata subcarinata* Sweet, n. subsp. The occurrence of *Anchignathodus isarcicus* (Huckriede) in the lower 4.5 m of the Elikah indicates a correlation of those strata with the Early Triassic Kathwai Member of the Mianwali Formation of West Pakistan and with the lower Werfen Formation of the southern Alps. The Ali Bashi does not contain any distinctively Triassic components and we conclude, therefore, that the formation is of latest Permian age, not largely Triassic as suggested by Ruzhentsev and Sarycheva for Soviet Dzhulfa and by Stepanov *et al.* for Kuh-e-Ali Bashi.

INTRODUCTION

Defining the Permian-Triassic boundary and explaining the significant turnover of invertebrate faunas at this stratigraphic level have long been important problems in earth history. There have been countless published contributions centered on discussions of this boundary and its significance in the history of life. In 1958, during an informal discussion of this problem, Teichert and Kummel noted that, whatever data they

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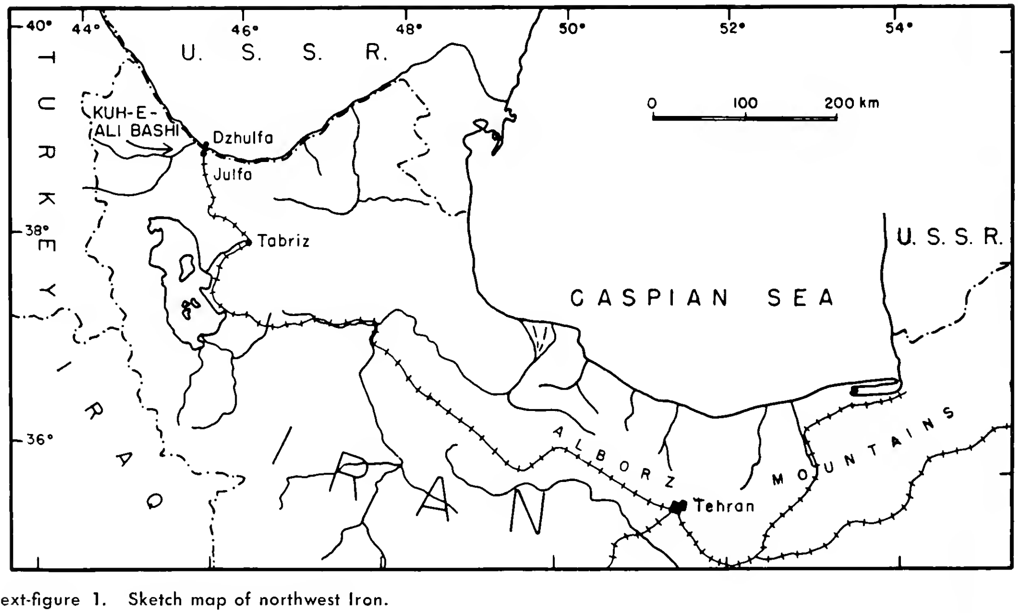
contained, most published reports were based on old, classical, original geologic and stratigraphic studies of areas known to contain marine Late Permian and Early Triassic strata in superposition. These are the Salt Range of West Pakistan, Kashmir, the Dzhulfa region of the USSR, and East Greenland. They then agreed that the time had come to reinvestigate in a fully modern stratigraphic, sedimentologic, and paleontologic sense these so-called classical areas to determine just what were the facts. Since that time they have followed this plan, the first investigated being of the marvelous sections in the Salt Range of West Pakistan. Their final report on this work (Kummel and Teichert, 1970) encompassed the work of several colleagues who are specialists on various invertebrate and plant groups. After their original field work in the Salt Range of West Pakistan, they were privileged to visit the Guryul Ravine in Kashmir (briefly reported on by Teichert, Kummel, and Kapoor, 1970), Kap Stosch in East Greenland (Teichert and Kummel, 1971 and 1973b), and the Julfa region of northwestern Iran, the objective of this report (Text-figs. 1, 2).

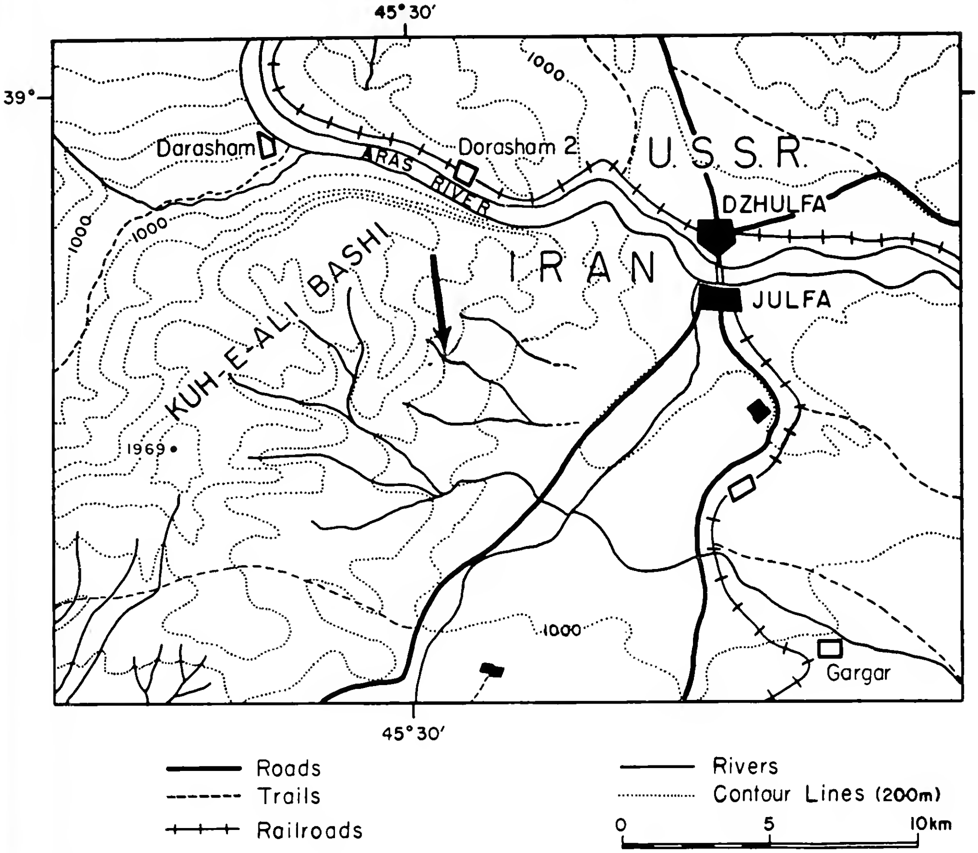
Field studies in the Kuh-e-Ali Bashi area of northwest Iran were carried out by Teichert and Kummel in July of 1968. These two authors are thus responsible for measurement and description of the sections discussed in this report; for collection of the fossils newly described herein; and for collation of reports received from various specialists to whom portions of the collections were submitted for study. Bulk samples collected by Teichert and Kummel proved to contain numerous conodonts, and it has been Sweet's responsibility to prepare these collections, describe them, and assess their stratigraphic significance. Because of this division of responsibility, it is to be understood that all statements pertaining to conodonts, including authorship of several new names, are to be credited to Sweet.

A few notes on the spelling of place names are in order. The river that divides the outcrop area in the USSR from that in Iran, discussed in this report, is the Araxes River of classical times, named after a mythical king of the ancient Greeks. Present spelling is Araks in Russian and Aras in Persian. We are here using the Persian version, Aras River.

Julfa is the name of a border settlement



Text-figure 1. Sketch map of northwest Iran.



Text-figure 2. Sketch map of Julfa region and Kuh-e-Ali Bashi.

on the Iranian side of the Aras, where a road and a railroad cross from Iran into Soviet territory. The Soviet counterpart on the north side of the Aras is a settlement whose name is correctly transliterated as Dzhulfa. It should be understood that wherever we use the name Julfa in the present paper, we refer to the area south of the Aras River in Iran and where we refer to Dzhulfa, we mean the Soviet area north of the river.

It should be noted that the *Dzhulfian Stage* has its type locality on the Soviet side of the river and that its name should therefore be spelled as indicated here. However, the Julfa beds, as used by Stepanov *et al.* (1969) and in this report, derive their name from Iranian Julfa. The Julfa beds are considered to be of Dzhulfian age.

ACKNOWLEDGMENTS

Teichert is indebted to Eng. N. Khan, Director, Geological Survey of Iran, for supplying field support for his first reconnaissance of the area in October, 1966. Teichert and Kummel wish to thank F. Golshani, Geological Survey of Iran, for guidance and assistance during their field work in 1968. They also profited from discussions with J. Stöcklin, D. L. Stepanov, M. Mehrnush, and K. Seyed-Emami, all of the Geological Survey of Iran. Acknowledgments to colleagues who supplied paleontological information are made in appropriate places in the text.

Victoria Kohler, research assistant at the Museum of Comparative Zoology, prepared most of the fossil samples, drafted all the text-figures, prepared most of the plates, and finally, helped immensely in editorial processing of the manuscript. We are all deeply indebted to her for these aids. Teichert and Kummel are indebted to Roger L. Williams and Rex E. Crick, both of the University of Kansas, who assisted in the compilation of some plates; to Dorothy S. Simms, of the same institution, who assisted efficiently in the study of the crinoid stems; and William L. Fisher and Jack D. Keim, also of the University of Kansas, who prepared all coral peels and most coral photographs. Sweet is grateful to Kristine M. Gable, Research Assistant at the Ohio State University, for assistance in processing the samples.

Our investigations were supported by National Science Foundation grant GA-996 (to Teichert) and GB-29037 (to Kummel). Teichert's work also received support from the Wallace E. Pratt Research Fund at the University of Kansas.

HISTORY OF RESEARCH ON THE PERMIAN-TRIASSIC SEQUENCES OF TRANSCAUCASIA AND NORTHWESTERN IRAN

Research on the Permian-Triassic deposits in Transcaucasia began as early as 1878, whereas in Northwestern Iran such investigations were not initiated until 1966. It is therefore advisable to deal separately with the history of research in the area north and south of the Aras River.

Transcaucasia

The history of investigations of the Permian and Triassic deposits of Transcaucasia has been exhaustively described by Shevyrev in Ruzhentsev and Sarycheva (1965). The general part of this book has been made available in English translation by D. A. Brown as Publication No. 117, Geology Department, Australian National University, Canberra, 1968. With the gracious permission of Professor Brown, the following account leans heavily on this translation. Our account is concerned more especially with the stratigraphic succession in the area immediately west of Dzhulfa, where the Aras River flows through a narrow and steep gorge. The stratigraphy and paleontology of the rocks exposed on the northern, Russian side of this gorge have been the object of investigation for nearly a century. The section was first studied by Abich (1878), who recognized the following four stratigraphic units in descending order:

4. Laminated limestones with *Pecten tortilis* Semenov;
3. Dark gray laminated limestones;
2. Limestones with layers of marl, containing numerous brachiopods;
1. Limestones and marls with brachiopods and ammonoids.

From the lowermost two units, Abich obtained a large collection of fossils from which he described 39 species and varieties of brachiopods, 11 species and varieties of corals, gastropods, bryozoans, and crinoids, 17 species of nautiloids, and 6 species of ammonoids. He noted the mixed character of the faunas from these units, which he divided into four groups of species characteristic of different ages.

Abich believed the first group to include brachiopods known from the Carboniferous deposits. Brachiopods of the second group he found to be similar to species from the Zechstein (Upper Permian). In the third group, he recognized several ammonoids resembling *Ceratites* (*Proptychites*) *lawrencianus* de Koninck, then known from Triassic deposits of the Salt Range. Finally, in the fourth group, he included species known only from deposits of the Dzhulfa area. From the predominance of species of the first group in this complex faunal assemblage, Abich considered the fauna that he had described to be Early Carboniferous in age. Moreover, he first noted in these deposits the common occurrence of ammonoids with ceratitic and goniatitic sutures.

In the year following the publication of Abich's work, Möller (1879) reevaluated several of the species of brachiopods and cephalopods described by Abich and, on the basis of his restudies, raised the age of the fauna to Early Permian. This revision was based particularly on presence of the ammonoids identified by Abich as *Goniatites striatus* Martin, which were placed by Möller in a new species, *G. abichianus* (now *Pseudogastrioceras*).

Abich's collections were further studied by Mojsisovics (1879). In one sample, this author found an ammonoid that he believed to be a respresentative of *Tirolites*, a genus widely distributed in the Campilian deposits of the eastern Alps. Mojsisovics further believed that the species described by Abich as *Pecten tortilis* was closely related to *Avicula* (now *Claraia*) *clarae* (Emmrich), a bivalve widely distributed in rocks of Early Triassic age. According to Mojsisovics, these fossils clearly indicated an Early Triassice age. It is now clear that the poorly preserved ammonoid specimen that Mojsisovics identified as *Tirolites* actually belonged to the genus *Paratirolites*, established by Stoyanow in 1910. Thus Mojsisovics was the first to suggest presence of rocks of Permian as well as of Triassic age in the section along the Aras Gorge west of Dzhulfa, although most facts of physical stratigraphy and of the stratigraphic distribution of the known species remain to be described.

Griesbach (1880), in his descriptions of the fossils from the Niti Limestone of the Himalayas, expressed the opinion that the ceratites described by Abich were close to, or identical with, *Otoceras*, a genus that he regarded as characteristic of beds transitional from Permian to Triassic.

Karpinsky (1890), in his monograph on the Artinskian ammonoids, expressed the view that the Dzhulfa beds in all probability were not only younger than the Artinskian beds but also younger than the Upper Productus limestone of the Salt Range. However, in his correlation table (Table D), he placed the Dzhulfa beds at the same level as the Upper Productus limestone, that is, at the top of the Permian system. Waagen (1891) believed that the Dzhulfa beds could be divided into a lower part containing brachiopods and *Gastrioceras*, which was of Late Permian age, and an upper part containing *Otoceras*, which was transitional to the Triassic.

In subsequent years, Mojsisovics and Diener contributed greatly to the problem of correlation of the Dzhulfa beds. Mojsisovics (1892) concurred with Griesbach's view that the Himalayan otoceratid fauna occupies the lowest position in the Triassic system. At the same time, however, he believed that the so-called otoceratid fauna of Dzhulfa was older. He pointed out that the Himalayan forms possess clearly differentiated and well-expressed so-called axial lobes. In the Dzhulfa species of so-called *Otoceras*, on the other hand, he observed that the lobes and saddles near the umbonal region are not differentiated, which he took to indicate a lower degree of evolutionary development and therefore a Late Permian age.

Diener, in several publications, resolutely supported this view on the different ages of the Himalayan and Dzhulfa *"Otoceras."* He also pointed to the coexistence of these forms at Dzhulfa with a rich assemblage of definitely Paleozoic brachiopods and nautiloids. He correlated the Dzhulfa beds with the Upper Productus limestone of the Salt Range, the Productus shales of the Himalayas, and the Bellerophon beds of the eastern Alps. He correlated the higher limestones in the Dzhulfa section containing *Pseudomonotis* sp. cf. *P. clarae* and *?Tirolites* with the Lower Ceratite limestone, the Ceratite marls, and the Ceratite sandstone of the Salt Range, with the *"Otoceras"* and *subrobustus* beds of the Himalayas, and with the Scythian of the eastern Alps.

At the end of the last century, Frech and Arthaber (1900) visited the Dzhulfa Gorge but had very little time to undertake detailed stratigraphic investigations. From the large collection that they made from talus of the Dzhulfa beds, Arthaber (1900) identified and described 46 species. Both authors came to the conclusion that the Paleozoic beds of the Dzhulfa section may be correlated with the lower part of the Upper Productus limestone of the Salt Range and placed them above the Artinskian Stage and the Fusulina beds of Sosio (Frech and Arthaber, 1900: 295). Frech (1901: 568) repeated his view that the Dzhulfa beds contain one of the best known faunas of the early Late Permian in the "pelagic" development.

In the higher part of the Dzhulfa section, Frech and Arthaber could not find any fossils and came to the conclusion that those identified by previous workers as "*Avicula*" or "*Pseudomonotis*" cf. *clarae* and as ?*Tirolites* could not have come from this locality.

Chernyshev (Tschernyshew) (1902: 419), in his well-known monograph on the Late Carboniferous brachiopods of the Urals and the Timan, erroneously correlated the Upper Productus limestone of the Salt Range with the Artinskian Stage of the Urals. Therefore, he also believed the Permian beds in the Dzhulfa area to be of Early Permian age.

Chernyshev, like other authors before him, had called attention to the necessity of obtaining more detailed information on the stratigraphy and the distribution of the fossil faunas in the sequence. Such information was not forthcoming until A. A. Stoyanow went to the area in 1908 and worked out the first detailed stratigraphy and faunal sequence of the section. Because of the considerable importance of Stoyanow's work, his scheme of subdivision of the Dzhulfa section is given here in condensed form (Stoyanow, 1910):

Unit	*Description*	*Thickness (meters)*
15	Gray marls, separated under the name "pelecypod beds," with "*Avicula*" sp. cf. *A. clarae* (Emmrich)	6
14	Alternate white marls and limestones without fossils	56
13	Red marls, in the lower part with indeterminate fossil remains, and in the upper with "*Xenodiscus*" *radians* Waagen, "*X.*" sp. aff. *X. kapila* Diener, "*X.*" sp. cf. *X. rotula* Waagen, "*X.*" (*Paratirolites*?) *mojsisovicsi* Stoyanow, "*Stephanites*" sp., "*S.*" *waageni* Stoyanow, *Paratirolites kittli* Stoyanow, "*Balatonites*"? sp. cf. *B. euryomphalus* Benecke (zone of *Paratirolites kittli*)	30
12	White marls without fossils	1
11	Red marls, forming the zone of "*Popanoceras*" *tschernyschewi* Stoyanow, with "*P.*" *tschernyschewi* and "*Gastrioceras*" *abichianum*	3.5
10	White marls without fossils	10
9	Red marls, divided into two parts: a) lower, with crinoids *Cyathocrinus*? and with "*Gastrioceras*" *abichianum*, and b) upper, with "*G.*" *abichianum*	15
8	Reticularid zone with *Reticularia indica* Waagen, *R. pulcherrima* Gemmellaro, *R. convexiuscula* Gemmellaro, *R. waageni* Loczy, *Spirigera protea*, "*Gastrioceras*" *abichianum*	10
7	Cephalopod zone with "*Otoceras*" *trochoides* Abich, "*Gastrioceras*" *abichianum* Möller, *Orthoceras transversum* Abich, *O. obliqueannulatum* Waagen, *O. cribrosum* Geinitz, *O. bicinctum* Abich, *O. lopingense* Stoyanow, *Nautilus hunicus* Diener, *Spirigera protea*	3
6	Zone of *Spirigera protea* Abich with *Orthotetes eusarcos* (Abich) and *Strophalosia* sp.	1.5
5	Zone of *Productus djulfensis* Stoyanow with *Orthis indica* Waagen and *Marginifera spinosocostata* (Abich)	1
4	Crinoidal reef with *Poteriocrinus*? and *Tschernyschewia typica* Stoyanow	2.5
3	Polyzoan reef with *Polypora fastuosa* de Koninck and *Notothyris djoulfensis* (Abich)	3
2	Zone of *Notothyris djoulfensis* (Abich) with *N. nucleolus* (Kutorga)	1
1	Zone of *Productus intermedius* Abich with *Tschernyschewia scabricula* (Martin), *T. humboldti* (d'Orbigny), *Marginifera helica* (Abich), *Camarophoria* sp. cf. *C. solitaria* Gemmellaro, *Orthotetes armeniacus* Arthaber, *O. peregrinus* (Abich)	2
	Total Thickness	145.5

Stoyanow dated his units 1 to 11 inclusive as Early Permian because he regarded the many species of brachiopods as closely related to the species in the Schwagerina limestone and Artinskian deposits of the Ural Mountains. He believed the upper part of unit 13 to be Triassic because of the occurrence of *Paratirolites* and other Triassic genera. The unfossiliferous unit 12 and the lower unfossiliferous part of the red marls of unit 13 he regarded as Late Permian in age. Thus, Stoyanow regarded the lower, highly fossiliferous part of the Dzhulfa section as Lower Permian, separated from earliest Triassic rocks by a few meters of unfossiliferous marls to which he assigned a Late Permian age.

Much later, Stoyanow (1942) reconsidered several of his conclusions. More particularly, he raised the age of the beds with the Paleozoic fauna to Late Permian. Directly above the zone of *Popanoceras tschernyschewi* in unit 11, he determined the presence of the Triassic zone of *Meekoceras-Hedenstroemia,* and in this way, believed that he had established the existence of a stratigraphic break at the boundary between the Permian and Triassic.

Only two years after Stoyanow had completed his investigations in the Dzhulfa area, two French geologists, P. and N. Bonnet, began to study the stratigraphy of the Paleozoic and Mesozoic deposits of Transcaucasia and described their results in a large number of mostly short reports. It is unnecessary for our purposes to record in detail the many opinions that were put forward by them in these various publications. However, their last monographic work (Bonnet and Bonnet, 1947), issued after the death of N. Bonnet, must be considered in somewhat greater detail because it was in this work that they presumably presented their latest and most mature opinions on the succession in the Dzhulfa Gorge and its age. These writers divided what they believed to be the Permian deposits in the Dzhulfa section in the following way:

Lower Permian. Shales and limestones 7–8 m thick:

- a) beds with corals, crinoids, polyzoans, and brachiopods—*Amplexus abichi* Waagen and Wentzel, *Zaphrentis leptoconica* Abich, *Poteriocrinus* sp., *Polypora fastuosa* de Koninck, *Notothyris djoulfensis* (Abich), *N. nucleolus* (Kutorga);
- b) beds with brachiopods—*Dalmanella indica* Waagen, *Productus hemisphaericum* Kutorga, *Marginifera spinosocostata* (Abich), *M. intermedia helica* (Abich), *Lyttonia nobilis* Waagen, *Richthofenia? sicula* Gemmellaro.

Middle Permian. Limestones and shales, 15 m thick, with brachiopods—*Productus subcostatus* Waagen, *Marginifera intermedia helica, Martinia semiplana* Waagen, *Reticularia waageni, R. indica* Waagen, *R. lineata* Martin, *R. pulcherrima* Gemmellaro, *R. convexiuscula* Gemmellaro, *Spirigera protea* Abich, *S. felina* Arthaber, *S. abichi* Arthaber.

Upper Permian. Limestones and shales 20–25 m thick (lower otoceratid beds) with *Orthoceras annulatum* Sowerby, *O. bicinctum* Abich, *O. transversum* Abich, *Nautilus cornutus* Golovk., *N. parallelus* Abich, *Pleuronautilus pichleri* Hauer, *P.* sp. cf. *P. verae* Arthaber, *Coelonautilus dorsoplicatus* (Abich), *Goniatites abichianus* Möller, *Otoceras djoulfense* (Abich), *O. intermedium* (Abich), *O. tropitum* (Abich), *O. trochoides* (Abich), *Hungarites pessoides* (Abich), and brachiopods of the genera *Marginifera, Reticularia,* and *Spirigera.*

The total Permian section recorded by Bonnet and Bonnet was 42–48 meters thick.

In the same publication, the authors also gave a description of what they believed to be deposits of Triassic age in the same section and described them as follows:

Lower Triassic

- I. Lower Werfenian substage. Marly limestones about 250 m thick.
  - 1. Red limestones with several horizons of gray marl 10 m thick, with crinoids, corals, and rare productids.
  - 2. Red limestones 25–30 m thick with problematical cephalopods.
  - 3. Red laminated limestones 3–4 m thick, which are divided into two parts:
    - a) a lower part with *Xenodiscus* (*Kashmirites*) *dimorphus* Waagen, *X.* (*K.*) *armatus* Waagen, *X.* (*K.*) *acuteplicatus* Waagen, *X. radians* Waagen, *X. himalayanus* Griesbach, *X. kapila* Diener, *X. mojsisovicsi* Stoyanow, *Goniatites abichianus* Möller;
    - b) an upper part with *Paratirolites dieneri* Stoyanow (cf. *Danubites nivalis* Diener), *P. kittli* Stoyanow, *Stephanites? waageni* Stoyanow.
- II. Upper Werfenian substage
  - 4. Gray laminated marly limestones with uneven surface, containing bivalves—*Pseudomonotis* (*Claraia*) sp. cf. *P. clarae, P.* (*C.*) *himaica* Bittner, *P.* (*C.*) *decidens* Bittner and rare undetermined

> ammonoids. These limestones are correlated with the *Hedenstroemia* beds of the Himalaya.

Bonnet and Bonnet continued to insist that species of *Otoceras* similar to the Himalayan representatives of this genus existed in the Dzhulfa section. It remained for Spath (1930, 1934) and for Ruzhentsev (1959, 1962, 1963) to clear up the distinctions between the Permian and the Triassic otoceratids. The Permian forms were divided into a number of genera by Spath and Ruzhentsev and shown to belong to a new family Araxoceratidae Ruzhentsev, the members of which are distinguished from the Otoceratidae by differences in form of shell and less complex sutures. On the basis of an analysis of the various faunas concerned, Spath in 1934 regarded the Dzhulfa beds as younger than the Upper Productus limestone of the Salt Range. The zone of *Paratirolites kittli* Stoyanow (the upper part of unit 13 of Stoyanow, 1910) was placed by Spath (1934) and by Kummel (1957) in the Upper Scythian, and Kummel correlated it with the upper *Owenites* beds or the zone of *Anasibirites.* In the years following the investigations of Stoyanow and the Bonnets, the Upper Paleozoic deposits of Transcaucasia were studied by Yakovlev (1931, 1933, 1934). As a result, in the Dzhulfa section the Permian System was made to include the sequence of limestones, 150 m thick, which previous authors usually considered as Middle and Upper Carboniferous. This was confirmed mainly by the study of Foraminifera, corals, and Bryozoa.

The Late Permian age of the Dzhulfa beds was also confirmed by studies made by Varentsov and Laliev (1939), Paffengolts (1948, 1959), Arakelyan (1951, 1952a, b), Azizbekov and Paffengolts (1952), Sadykov (1954), Azizbekov (1960, 1961), Ilina (1962), Arakelyan *et al.* (1964), and others.

Miller and Furnish (1940) pointed out that there is little in common between the Permian ammonoids of Transcaucasia on the one hand and of the Salt Range and Himalayas on the other. Nevertheless, in their correlation table, they correlated the Dzhulfa beds with the Upper Productus limestone ("Chideru Group") of the Salt Range and the Chitichun I and Kuling beds of the Himalayas.

Schenck *et al.* (1941) were the first to suggest the name Dzhulfian Stage for which the type section was the Permian sequence in Transcaucasia. They also suggested the name Punjabian Stage as typified by the Upper Productus limestone of the Salt Range. However, it must be pointed out that the name Punjabian had already been preoccupied by Noetling (1901) for the Lower Permian deposits of the same locality. When Glenister and Furnish (1961) suggested that the uppermost stage of the standard scale of the Permian system be named the Dzhulfian with its type locality in the Aras Gorge, they considered this stage to be the approximate equivalent of their *Cyclolobus* Zone, despite the fact that this genus had not, at that time, been reported from the Dzhulfa section.

During the 1950's and 1960's, numerous investigations were carried out by many authors in Transcaucasia, especially in the area of the Nakhichevansk ASSR as summarized by Shevyrev in Ruzhentsev and Sarycheva (1965). These contributed much to the more detailed knowledge of Permian and Triassic deposits in this area but had little special bearing on the problem of the Permian-Triassic boundary as such. According to Sadykov (1953), the Lower Triassic in this area begins with reddish argillaceous and sandy limestones, containing *Paratirolites kittli* at the base, which is 2 to 5 m thick, and is thus clearly identical with the upper part of unit 13 of Stoyanow (1910). It is interesting to note that Sadykov also mentions solitary corals and rare brachiopods from this unit. Apart from this, Sadykov must have had a mixed fauna at his disposal because he also mentions *Kashmirites* as occurring together with *Paratirolites.* However, *Kashmirites,* according to Spath (1934) and Kummel (1957), is characteristic of Middle Scythian strata rather than Lower ones.

Rostovtsev (1958), also working in the same area, related that Upper Permian limestones with *Composita protea* are overlain without break by a unit of light gray and pink limestone, 8 m thick, with *Otoceras* sp. aff. *O. woodwardi* corresponding to the *Otoceras* Zone of the Himalayas. In this unit, there are rare *Productus* sp., *Athyris* sp., and *Pseudogastrioceras abichianum* (Möller). Above the beds with *Otoceras,* according to Rostovtsev, the most characteristic Lower Triassic bed of Transcaucasia consists of red marly limestone, from 5 to 20 m thick, and contains a rich assemblage of ammonoids, the composition of which, in all its variety, clearly indicates association with the Indian Province of the Tethys. Characteristic ammonoids of this unit were said to be *Paratirolites kittli, P. mojsisovicsi, P. waageni, Kashmirites stoyanowi, Flemingites* sp., and others. In the opinion of Rostovtsev, this faunal assemblage corresponds to the Scythian and basal Campilian stages of the Lower Triassic, equivalent to the *Ophiceras, Meekoceras,* and basal *Hedenstroemia* zones of the Himalaya.

In the light of present knowledge, these studies must have been based on mixed collections from more than one biostratigraphic zone. Apparently, Rostovtsev perpetuated the error of so many of his predecessors by mistaking one of the genera of the Araxoceratidae of the Upper Permian in the Dzhulfa section for *Otoceras woodwardi* or a closely related form of the lowest Triassic beds of the Himalaya. Up to this point, it seems that Sadykov (1953) was the only geologist to have recorded an occurrence of Triassic ammonoids in the same bed with brachiopods and corals of a Paleozoic type. However, his listing of the stratigraphic conditions and the occurrence of the faunas were far from clear.

Up to this point, as Shevyrev (*in* Ruzhentsev and Sarycheva, 1965) so succinctly summarized, there is

> "quite clear evidence of the great confusion in the ideas of individual investigators on the stratigraphy of the Upper Permian and Triassic deposits of Trans-Caucasis and, primarily, on the boundary between these systems. Some of the authors place the Permian-Triassic boundary at the base of the red limestones with *Paratirolites* (Sadykov, 1953; Stoyanov, 1910), others lower this boundary considerably to the base of the so-called "otoceratid" zone (Rostovtsev, 1958). Especially mobile were the views of Bonnet, who was sometimes ready to agree with Stoyanov's opinion about placing the boundary at the base of the limestones with *Paratirolites,* sometimes to lower it 25 to 30 m to the base of the unfossiliferous calcareous-argillaceous sequence (Bonnet, 1912a, b), and sometimes inclined to place it even lower at the "otoceratid" zone (Bonnet, 1919). So far, there is no single opinion among investigators about the age of the individual faunal horizons of the Dzhul'fa section nor on their correlation with the Permian and Triassic deposits of other regions of the globe."

(Shevyrev *in* Ruzhentsev and Sarycheva, 1965: 19. English translation, Brown, 1968: 15.)

This statement by Shevyrev is probably a fair summation of the state of knowledge in regard to the Permian-Triassic boundary in the Dzhulfa section and other parts of Transcaucasia toward the end of the 1950's. It must have been about this time that a large group of geologists and paleontologists from the Paleontological Institute of the Academy of Sciences of the USSR began to organize a special study of the Paleozoic and Triassic sections in Transcaucasia. These studies were not concentrated on the Dzhulfa section only, but were extended to 20 additional localities in the Nakhichevansk ASSR and in the Armenian SSR. The results of these investigations were published in book form in 1965 as volume 108 of the Transactions of the Paleontological Institute of the Academy of Sciences of the USSR under the editorship of V. E. Ruzhentsev and T. G. Sarycheva. It is in this book that the main features of the Permian-Triassic sequence in the Dzhulfa section and its fossil content were described in detail for the first time.

The Soviet geologists found that in the entire area, Permian deposits rest transgressively with insignificant angular unconformities, or without visible unconformity on Devonian and Lower Carboniferous rocks of various ages. The base of the Permian is marked almost invariably by a thin, basal conglomerate. Apparently, the entire Permian system is represented from the Lower Permian to the top of the Upper Permian, but since the emphasis of the report is on the Upper Permian and Lower Triassic, the Lower Permian deposits are not described. Total thickness of the Permian deposits varies from 400 to 900 m. The Upper Permian Series is subdivided into a lower Guadalupian Stage and an upper Dzhulfian Stage. The rocks of the Guadalupian Stage are subdivided into two "horizons," called Gnishik Horizon and Khachik Horizon (Text-fig. 3). These "horizons" are, at present, best regarded equivalents of four stratigraphic formations in terms of American stratigraphic procedures. The entire sequence is highly fossiliferous, and many of the species are described —or at least illustrated—in the Russian report. However, since we have not studied in detail the equivalents of these rocks on the Iranian side of the Aras River, we do not further consider them here.

The Dzhulfian Stage is subdivided into informally named units called "beds."

Unit	*Description*	*Thickness (meters)*
5	Beds with *Phisonites* and *Comelicania*	4.5
4	Beds with *Vedioceras* and *Haydenella*	0.2–19
3	Beds with *Araxoceras* and *Oldhamina*	8.0
2	Beds with *Araxilevis*	12.0
1	Beds with *Codonofusiella* and *Reichelina*	2.0–5.5

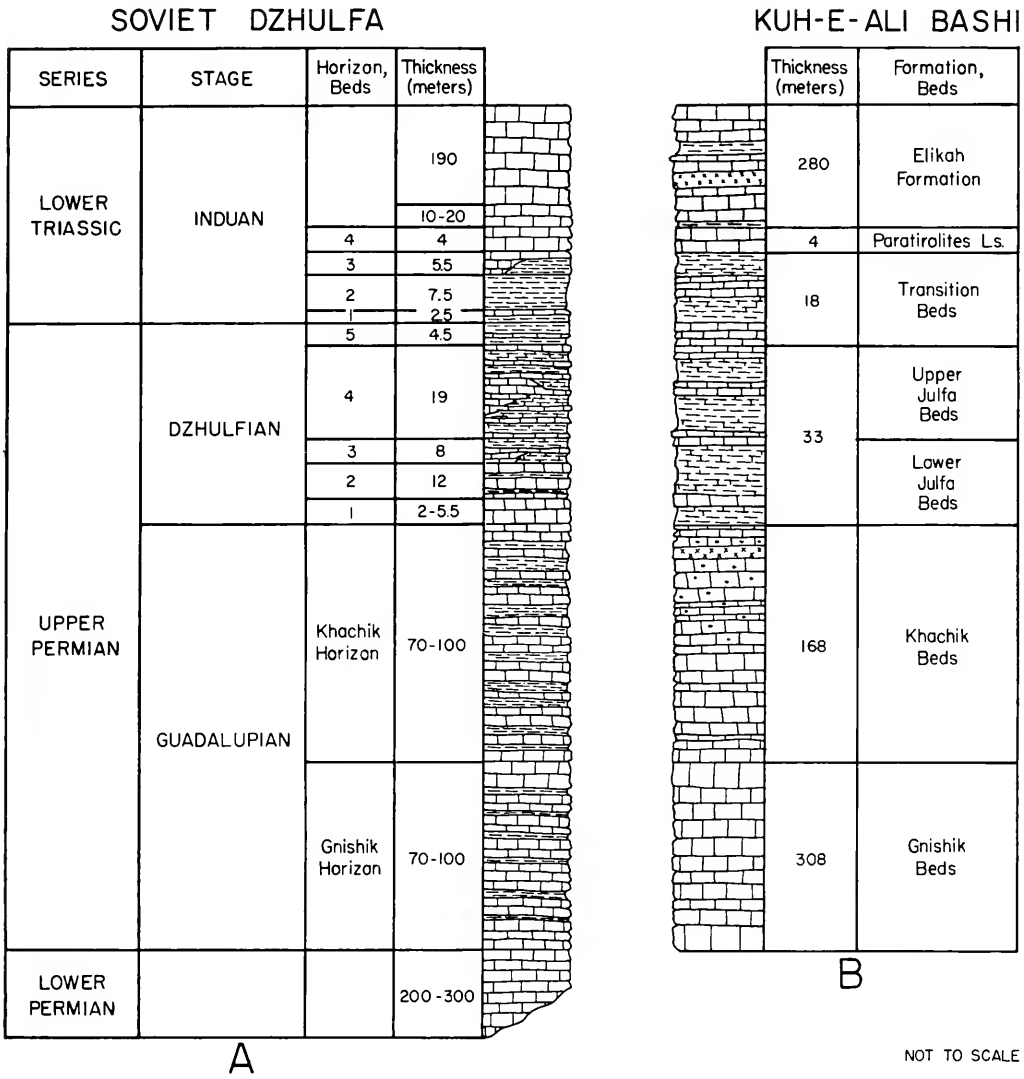
Thus, the entire sequence of rocks representing the Dzhulfian Stage may range from about 27 to about 50 m. It seems that this sequence represents one single formation in the American sense of this term. On the Iranian side we refer to it, with the exception of unit 5, simply as Julfa beds, for the entire formation is extremely fossiliferous and especially rich in brachiopods. Rugose corals, nautiloids, and ammonoids are also richly represented in addition to fusulines in the lower part (unit 1). The nautiloids have been described by Teichert and Kummel (1973).

The rocks overlying the Dzhulfa beds were assigned by the Russian authors to a stratigraphic unit that they called the Induan Stage. It appears from the general discussion that the "Induan" Stage corresponds to the lower part of the Scythian Stage in the conventional sense. The lower part of the rock sequence of the "Induan" Stage was subdivided into informally named "beds," and since it is this part of the section on which we concentrated our investigations on the Iranian side of the Aras River, we quote the observations in the Russian report in somewhat greater detail. These subdivisions are as follows (Text-fig. 4):

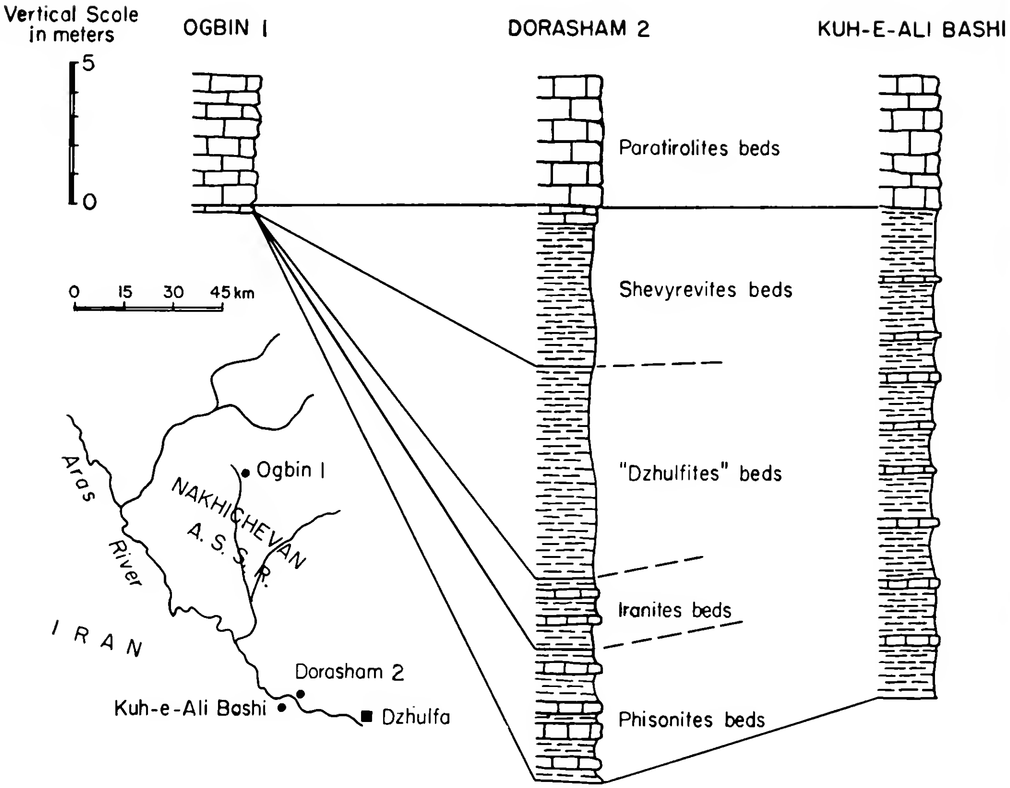
Unit	*Description*	*Thickness (meters)*
4	Beds with *Paratirolites.* Limestones, reddish brown, finely laminated, in places nodular argillaceous, with thin layers of brown shale	4.5–7.5
3	Beds with *Bernhardites.* Shales and limestones similar to the underlying beds, with *Bernhardites radiosus, B. nodosus,* and *Pseudogastrioceras abichianum*	5.5
2	Beds with *Dzhulfites.* Shales, brownish, greenish, or dark gray in color, with layers of varicolored marly limestones containing *Dzhulfites spinosus* and *D. nodosus*	7.5
1	Beds with *Tompophiceras.* Dark gray shales, alternating with light gray marly limestones; in	

the middle part of the beds is an horizon (0.5 m) of brown shales and limestones. *Tompophiceras transcaucasium* occurs here 2.5

Thus, this part of the "Induan" has, in the Dzhulfa section, a thickness of at least 20 m. From unspecified stratigraphic levels within these four numbered beds, the following species, possibly collected from float, are cited: Rugosa—*Plerophyllum dzhulfense, P. differentiatum, P. armenicum, P. cuneatum, Pleramplexus leptoconicus, P. minimus;* Ammonoidea–*Paratirolites kittli, P. waageni, P. vediensis, P. trapezoidalis, P. dieneri, Abichites stoyanowi, A. mojsisovicsi, A.*



Text-figure 3. Generalized stratigraphic column of Permian and Triassic formations in (A) Dzhulfa region, Transcaucasia (data from Ruzhentsev and Sarycheva, 1965) and (B), at Kuh-e-Ali Bashi, Julfa region, northwest Iran (data from Stepanov, Golshani, and Stäcklin, 1969).



Text-figure 4. Correlation of Ali Bashi Formation between Ogbin, Dorasham 2, and Kuh-e-Ali Bashi.

abichi; Brachiopoda—*Enteletes dzhagrensis, Orthotichia parva, Orthotetina* sp., *Spinomarginifera pygmaea, Haydenella kiangsiensis, H. minuta, Terebratuloidea* sp., *Araxthyris ogbinensis, A. araxensis minor;* nautiloids, small foraminifers, and bryozoans.

The authors, judging from the ammonoids, concluded that this part of the Triassic section belongs to the basal "Induan" Stage. They further stated that the beds with *Paratirolites* in Dzhulfa Gorge are conformably overlain by light gray, thinly bedded marly limestone containing the bivalves *Claraia stachei* and *C. aurita.* Higher up follow gray, thinly laminated, "fucoid" limestones up to 150 m thick, which are replaced upwards in the section by massive, commonly oolitic limestones having a thickness of 40 m. From these upper limestones, the bivalves *Eumorphotis, Velopecten,* and *Myophoria* are reported.

The chapter on the Triassic rocks is followed by one on the composition and development of the following fossil groups: fusulinids, Sphinctozoa, tabulate corals, rugose corals, nautiloids, ammonoids, bryozoans, brachiopods, trilobites, ostracods, fishes, algae—in that order. For each group, a detailed discussion of the occurrences of species of Guadalupian, Dzhulfian, and "Induan" age is given, and for each group a detailed list of species is compiled indicating the occurrence of individual species in the localities studied by the authors.

In the two following chapters are discussions of both biostratigraphic conclusions and the reasons for the change in the organic world at the boundary between the Paleozoic and Mesozoic eras. We are discussing the authors' opinions in these fields elsewhere in this paper to the extent that they have a bearing on our own studies and conclusions.

A greater part of the book (p. 135–432, text–figs. 4–59, plates 1–58) is given to systematic paleontology, containing descriptions of many new species and some new genera. In addition, numerous species are illustrated on the plates which have not been described in the text, but which had been named and described previously. Later in this paper we refer to those species whose representatives we found on the Iranian side of the Aras River.

All in all, the publication edited by Ruzhentsev and Sarycheva represents a monumental step forward in our understanding of the Permian and Triassic systems and their interrelationships in Transcaucasia and especially in the Dzhulfa area.

Tozer (1969) reinterpreted the evidence presented by Ruzhentsev and Sarycheva and their collaborators and concluded that the boundary between the Permian and Triassic Systems in the Dzhulfa area should be placed at the top of the *Paratirolites* beds. Furnish and Glenister (1970) also regarded *Paratirolites* as marking uppermost Permian.

Rostovtsev and Azaryan (1971a) restudied some of the Permian-Triassic sections in Transcaucasia. They came to the conclusion that in the Dzhulfa section all beds below the thin-bedded limestone with *Claraia* (unit G) are of Permian age. They quoted Kummel's (misspelt Kamme in the English translation) reinterpretation of Shevyrev's "*Tompophiceras*" and "*Bernhardites radiosus*" and listed as *nomina nuda* the generic names *Iranites* and *Shevyrevites,* which are being established in the present paper. For the beds from the base of the *Phisonites* Zone to the top of the *Paratirolites* Zone the authors propose a new chronostratigraphic term, Dorasham Stage. This would appear to be a synonym of the Changhsingian of Furnish and Glenister (1970).

NORTHWESTERN IRAN

At the time of the publication of the volume edited by Ruzhentsev and Sarycheva in 1965, nothing was known about the geology of the country immediately south of the Aras River opposite the Paleozoic and Triassic outcrops on the Soviet side to the north. The geological map of Iran, 1:2,500,000, published by the National Iranian Oil Company in 1959, shows only Triassic, no Permian, rocks in this area. This information was, no doubt, based in part on the map published by Bonnet and Bonnet (1947), who showed the presence of Triassic rocks south of the Aras River. No information on the geology of this part of Iran was available in the files of the Geological Survey of Iran.

The Bonnets' map and their descriptions, published in 1947, suggested to Teichert the possibility that Permian rocks might also be present on the Iranian side of the Aras River. On 16 February 1966, Teichert wrote to N. Khadem, Director of the Geological Survey of Iran, that "I believe that a stratigraphic section similar to that on the Russian side may exist on the Iranian side near Julfa," which is the counterpart to the Russian Dzhulfa on the north side of the Aras River. In the same letter, Teichert explained his general interest in problems of the Permian-Triassic boundary on a worldwide basis and inquired about the possibility of a reconnaissance visit to this area with logistic support from the Geological Survey of Iran, for the purpose of ascertaining the presence of such a Permian-Triassic section on the Iranian side of the border. With the kind intervention of Mr. Khadem, permission for Teichert to visit this border area was granted by authorities, and the date of 5 October 1966 was later agreed upon for the beginning of this reconnaissance visit, which was to last only a few days. Two or three days before that date, Teichert was informed in Teheran that he would be accompanied in the field by Helmut Flügel, of the University of Graz, Austria, and by D. L. Stepanov, of the University of Leningrad. Stepanov had then recently joined a United Nations advisory team working with the Geological Survey of Iran. Teichert, Flügel, and Stepanov met in Tabriz on 6 October, where they were joined by W. Gräf, of Graz, and M. Mehrnusch, of the Geological Survey of Iran.

A mountainous area several miles west of Julfa named Kuh-e-Ali Bashi was visited by the party on 7 October, and it was soon apparent that rocks of Permian age occupied a considerable area in that range. Presence of Triassic rocks was also confirmed. The locality visited was situated an estimated 8 km south of the Aras River and about the same distance west of Julfa. Rain foiled an attempt to return to the same locality on 9 October, and Teichert returned to Teheran on that same day.

Subsequently, suggestions to set up a joint research project with the Geological Survey of Iran in which Teichert and Kummel would concentrate on the Permian-Triassic boundary and Survey-connected geologists would study the general stratigraphy and paleontology of the Permian and Triassic sequences in Kuh-e-Ali Bashi were rejected. Instead, the Geological Survey of Iran developed its own project, sending a small party to Kuh-e-Ali Bashi in the summer of 1967 for the special purpose of studying the Permian-Triassic boundary and the major aspects of the Permian section. This work has been reported on in a paper by Stepanov, Golshani, and Stöcklin (1969).

These authors describe Permian and Triassic sections from Kuh-e-Ali Bashi and from two localities in the Alborz Mountains: from the upper Chalus Valley in the western Alborz Mountains and from a locality 20 km south of Amol in the eastern Alborz Mountains. They also figured, but did not describe, many species of Permian and Triassic fossils from these areas. At Kuh-e-Ali Bashi, the Permian-Triassic section was subdivided as follows (text–fig. 3):

Triassic	*Description*	*Thickness* (*meters*)
H.	Upper part of Elikah Formation: massive to thick-bedded barren dolomite	200+
G.	Lower part of Elikah Formation: thin-bedded limestone and some shale containing *Claraia*	282.2
F.	*Paratirolites* limestone: nodular, red limestone, cliff-forming, containing *Paratirolites waageni* Stoyanow, *Abichites, Prionolobus, Pseudogastrioceras,* tabulate and rugose corals (*Michelinia, Plerophyllum, Pleramplexus*), and brachiopods (*Orthotetina, Spinomarginifera, Araxathyris, Pseudowellerella*)	3.6
E.	Permian-Eotriassic transition beds: *Bernhardites* Zone, *Dzhulfites* Zone, *Tompophiceras* Zone, containing, in addition to these cephalopods, a fauna of tabulate and rugose corals, brachiopods, and orthocerid cephalopods	12.75
Permian		
	Permian-Eotriassic transition beds: *Phisonites-Comelicania* Zone, containing *Michelinia, Comelicania,* and *Phisonites*	5.1
D.	Upper Julfa beds (*Haydenella-Pseudowellerella* Zone) (unit D), limestone and shale containing rugose corals, brachiopods, *Araxoceras, Vedioceras,* and nautiloids	11.35
C.	Lower Julfa beds (unit C): *Pseudogastrioceras-Permophricodothyris* Zone, *Araxilevis-Orthotetina* Zone, limestone and shale, richly fossiliferous (mostly brachiopods, some nautiloids, and ammonoids)	11.41
B.	Khachik beds (unit B), dark gray, well-bedded limestone, with chert nodules, rich in brachiopods, but also containing algae, foraminifers (including fusulines), rugose and tabulate corals, gastropods, nautiloids, and one trilobite (*Pseudophillipsia*)	168.00

A.	Gnishik beds (unit A), dark gray, thick-bedded limestone, with rare chert nodules, and rich fauna, mainly of brachiopods, but also containing algae, foraminifers, tabulate and rugose corals, gastropods, and one trilobite (*Pseudophillipsia*)	308.00
	Total thickness	1002.41+

Stepanov *et al.* gave the age of the Gnishik and Khachik beds as Guadalupian and the age of the Julfa beds as Dzhulfian. In the latter stage they also included the lowermost unit (*Phisonites-Comelicania* Zone) of their "Permo-Triassic transition beds" without stating specific reasons. In the zonation of the upper part of the "transition beds" by ammonoid genera, Stepanov *et al.* adopted the scheme proposed by Shevyrev (*in* Ruzhentsev and Sarycheva, 1965), but their conclusions were based on extremely limited material, not on critical paleontological studies.

PRESENT INVESTIGATIONS

After Teichert's reconnaissance in October, 1966, Teichert and Kummel visited Kuh-e-Ali Bashi together in the summer of 1968, spending two weeks on field studies in the general area visited by the Iranian party in the previous year. They discovered that the information published by Stepanov *et al.* (1969) had been obtained essentially from a single section, measured by F. Golshani and B. Hamzepour.

In the place chosen by these investigators, the "transition beds" are poorly exposed and very difficult of access. Thus, Kummel and Teichert extended their investigations along the strike of the beds in a small valley where this unit is exposed for a distance of about 1 kilometer. Here, efforts were concentrated on four localities (Text–figs. 5–10). In two of these, outcrops were too poor to allow detailed measurement of the sections, but fossils were collected from carefully determined intervals within stratigraphic distances of about 2 meters. Thus, while contamination from higher beds naturally occurred, stratigraphically highest occurrences of most species could be determined. In the remaining two localities outcrops were sufficiently continuous to allow measurements of the sections and, accordingly, exact determination of the stratigraphic position of many fossils, although, here too, fossils were also collected from "float."

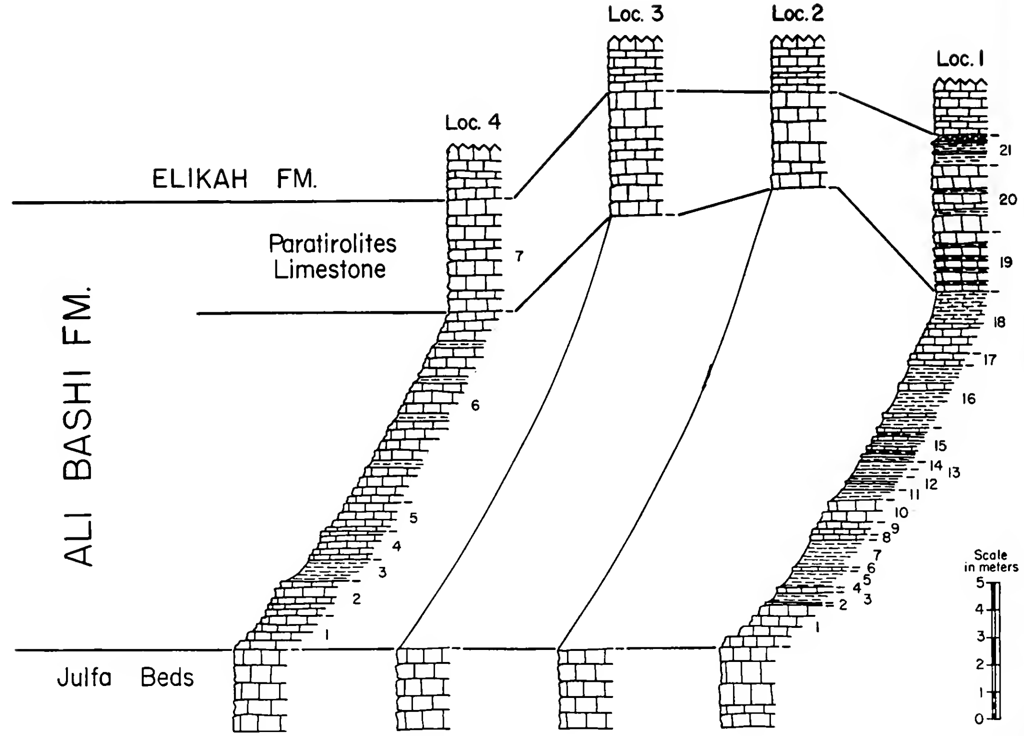
Subsequent examination of their large fossil collections has led Teichert and Kummel to conclude that the "Permian-Eotriassic transition beds" of Stepanov *et al.* (1969) were in fact of latest Permian age and that, indeed, the Permian-Triassic boundary should be placed at the top of the *Paratirolites* beds. Detailed documentation for these conclusions is presented in this paper. A preliminary account of their views was presented at the International Permian-Triassic Conference at Calgary, Alberta, 23–26 August 1971, an abstract of which was published in the Bulletin of Canadian Petroleum Geology (Kummel and Teichert, 1971: 336–337). The full paper was presented by Kummel at the Calgary meeting on 23 August 1971, and the manuscript was immediately transmitted for publication in the Proceedings of that meeting (Alan Logan and L. V. Hills, editors).

Teichert was able to return to Kuh-e-Ali Bashi for a brief visit in June, 1970, mainly for the purpose of taking new photographs of their localities.

It is interesting to record publication of a paper by Waterhouse in May, 1972, in which he expressed views that are identical to Kummel and Teichert's. To the best of their knowledge, Waterhouse never visited Kuh-e-Ali Bashi nor has he ever studied fossils from this area. He did, however, attend the Permian-Triassic Conference at Calgary in August, 1971, and the manuscript of his paper was submitted on 27 September 1971.

STRATIGRAPHY OF THE ALI BASHI FORMATION

We propose the name Ali Bashi Formation for the lithologic unit that lies between the top of the Julfa beds and the base of the thin-bedded medium gray limestone, con-



Text-figure 5. Stratigraphic sections of latest Permian and early Triassic formations at Kuh-e-Ali Bashi, northwest Iran.

taining *Claraia*, that can be correlated with the Elikah Formation of the Alborz Mountains. The Ali Bashi Formation includes beds 52–61 of the stratigraphic section published by Stepanov *et al.* (1969: 35–36, 40), and is equivalent to the "Permian-Triassic transition beds," including the *Phisonites* Zone, as well as the *Paratirolites* limestone (unit F) as described in that publication.

Lithology. The bulk of the Ali Bashi Formation consists of alternating impure aphanitic limestone and shale. Its top part is made up of grayish red limestone containing *Paratirolites*. This limestone forms such a distinct lithologic unit that it may well be distinguished formally as a member of the Ali Bashi Formation although we have refrained from doing so. For details of the lithology of the Ali Bashi Formation, the reader is referred to the description of the stratigraphic sections, especially at Localities 1 and 4.

Thickness. According to our measurements, the thickness of the formation varies from 16.5 m at Locality 4 to 20.5 m at Localities 2 and 3. These figures are in agreement with the total thickness given by Stepanov *et al.* for their beds 52–61, which was 21.6 m. The locality where Golshani and Hamzepour (*in* Stepanov et al., 1969) measured their section lies about 300 m to the north of our Locality 4. At our Locality 1, which lies about 200 m south of our Locality 2, the thickness of the formation is 18.8 m.

The thickness of the uppermost part of the formation, herein referred to as *Paratirolites* limestone, is 5.8 m at Locality 1, 3.5 m at Locality 2, 4.5 m at Locality 3, and 4.2 m at Locality 4. At the locality described in Stepanov *et al.* (1969) it is 3.6 m.

Type locality. In the absence of good

maps, the exact location of the type locality of the Ali Bashi Formation is somewhat difficult to describe. It is indicated in Figure 2 of this paper only in a very general way as lying about 10 km due west of the town of Julfa. It is reached by driving about 7 km along a gravel road leading southwest from Julfa in the direction of Khoy, then leaving the road and turning northwest to drive for about 6 km over a uniformly rising pediment surface in the direction of the only large valley visible at this point from the road. One can reach by jeep the foot of the mountains on the western side of this valley. From here, it is necessary to proceed up the valley on foot for another 2 km until the first outcrops of dark-colored Khachik Limestone are reached. At this point, one turns northeast, crosses a low ridge consisting of Julfa beds, and descends into a much smaller and narrower valley on the northeastern side. Turning north in this small valley, the outcrops of the Ali Bashi Formation studied by us may be followed and are easily accessible for about 1 km on the eastern side. They probably extend for some distance farther north, where, however, they are almost inaccessible.

The outcrops in the lower part of the valley, as described above, are here designated as the type locality of the Ali Bashi formation (Text–figs. 6–10). In this belt, four stratigraphic sections were selected for detailed study, but in only two were the rocks sufficiently well exposed to warrant detailed measuring. Because time did not permit us to make our own reconnaissance

Text-figure 6. View of strike valley at Kuh-e-Ali Bashi. Locality 3 is the prominent nose of the escarpment behind the individuals in the picture. The Julfa beds include the strata from the left of the picture to the top of the hard bed in the middle of the slope. The Ali Boshi Formation extends from there to the base of the prominent scarp, which is made of the Elikah Formation (Kummel photograph).

Text-figure 7. Locality 4 is in the mid-part of the right hand side of this photograph. The massive limestone beds at the top of the slope are the Elikah Formation. These are underlain by the Ali Bashi Formation. The top of the underlying Julfa beds is the prominent hard bed at the mid-part of the slope (Kummel photograph).

map, the exact positions of the sections cannot be pinpointed. However, this is not judged to be a serious shortcoming because the studied outcrops extend across merely a few hundred meters.

A description of the sections that we term Localities follows. Locality 1 is the southernmost (Text–fig. 9), Locality 4 the northernmost (Text–fig. 7); the distance between them is about 500 m. Localities 2 and 3 (Text–figs. 6, 8) are close together, about halfway between 1 and 4. The section measured by Golshani and Hamzepour (*in* Stepanov *et al.*, 1969) lies about 300 m to the north of our Locality 4.

Age and correlation. It is the purpose of this paper to document more thoroughly that the Ali Bashi Formation in its entirety is of latest Permian age and that no part of it can be assigned to the Triassic. This conclusion has already been presented in two previous publications (Kummel and Teichert, 1971, 1973). The conclusion reached by Stepanov *et al.* (1969) that these beds, with the exception of the lowest 5 meters, are of Triassic age is not supported by a reevaluation of the paleontological evidence provided by the study of our fossil collections.

North of the Aras River, in Armenian Dzhulfa, the correlative strata are bed 5 of the Dzhulfian Stage and beds 1–4 of the Lower Triassic ("Induan") of Arakelyan, Grunt, and Shevyrev (*in* Ruzhentsev and Sarycheva, 1965). Taraz (1971a, b) adopted the same correlation for what he regarded as equivalent beds in a Permian-Triassic section of the Abadeh region in central Iran.

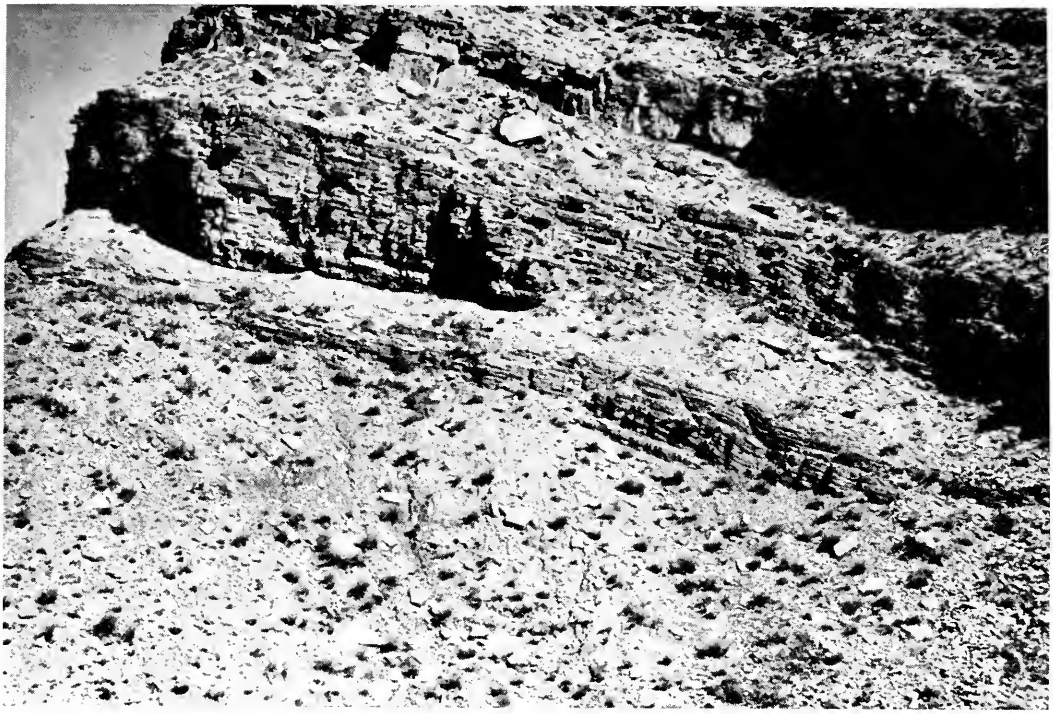
Text-figure 8. The Ali Bashi Formation at Locality 2. The formation includes the strata between the small hard ledge near the base of the picture and the more prominent ledge toward the top of the picture (Kummel photograph).

Description of Stratigraphic Sections at Type Locality of Ali Bashi Formation, Kuh-e-Ali Bashi

(Distribution of Conodonts is summarized in Table 7)

LOCALITY 1

Bed	*Description*	*Thickness (meters)*
	ELIKAH FORMATION	
22	Limestone, medium gray, thin-bedded to platy, in part aphanitic, hard, containing *Claraia* (Conodont samples 22L, 22M, 22U).	
	ALI BASHI FORMATION	
21	Shale, in alternating yellowish gray and light olive gray beds, each about 20 cm thick; also olive gray limestone beds; poorly exposed; seemingly unfossiliferous (Conodont sample 21).	1.1
20	Limestone, aphanitic, grayish red, nodular, with some shaly interbeds; contains *Paratirolites* and, microscopically, several types of nonfusulinid foraminifers, shell fragments, large numbers of ostracod shells, and some echinoderm remains (Conodont samples 20L, 20M, 20U).	2.5
19	Limestone, aphanitic, grayish red, in beds 5–15 cm thick, separated by shaly beds, 2–3 cm thick; partly nodular; some beds bioturbated; contains *Paratirolites kittli, P. mojsisovicsi* and, microscopically, at least 2 types of nonfusulinid foraminifers, very numerous ostracod shells, both articulated and disarticulated, and some echinoderm remains; a thin basal bed contains an abundance of bairdiid ostracods associated with *Hollinella* sp. (Conodont samples 19L, 19U).	2.2
18	Limestone, grayish red, in part very argillaceous, grading upward into calcareous shale, thin-bedded, bioturbated; in thin section nu-	



Text-figure 9. Locality 1, the upper part of the Ali Bashi Formation overlain by the lower part of the Elikah Formation. The *Paratirolites* limestone is the lower scarp separated by a bench from the overlying, more conspicuous scarp (Kummel photograph).

	merous ostracod shells, both articulated and disarticulated, and some echinoderm fragments (Conodont samples 18L, 18U).	2.3
17	Limestone, aphanitic, pale red, hard, ledge-forming, nodular in part; in thin section few ostracod shells, both articulated and disarticulated. Contains *Shevyrevites shevyrevi* (Conodont sample 17).	0.4
16	Shale, light to medium gray, with several beds of aphanitic argillaceous limestone beds, 2–8 cm thick, forming thin resistant ledges; most limestone beds bioturbated, containing greater or lesser amounts of ostracod shells, both articulated and disarticulated, some echinoderm remains, and, possibly, nonfusulinid foraminifers, also *Iranites transcaucasius* (in place) (Conodont samples 16L, 16M, 16U).	2.3
15	Limestone, aphanitic, argillaceous, light olive gray, in beds 2–8 cm thick, alternating with layers of dark gray shale; limestone in thin section contains scattered ostracod shells, most of them disarticulated, and few echinoderm remains; some limestone beds weakly bioturbated, showing remnants of original lamination (Conodont samples 15M, 15U).	1.25
14	Siltstone, yellowish gray, no megafossils (Conodont sample 14).	0.3
13	Shale, very dark red, poorly exposed.	0.3
12	Shale, very dark red, with some thin, hard, light olive gray, aphanitic limestone beds; these contain, microscopically, some scattered, mostly disarticulated ostracod shells (Conodont sample 12).	0.5
11	Shale, very dark red, poorly exposed.	0.4
10	Limestone, aphanitic, argillaceous, pale brown to light brown-	

Text-figure 10. The Triassic Elikah Formation at Kuh-e-Ali Bashi (Kummel photograph).

	ish gray; contains *Iranites transcaucasius* (in place), *Paratirolites spinosus* (in place), *Pleuronautilus* sp. indet. and, microscopically, abundant, mostly disarticulated, ostracod shells (Conodont samples 10M, 10U).	0.8
9	Limestone, aphanitic, argillaceous, light olive gray; bioturbated, in beds 2.5–5 cm thick, with interbeds of dark shale; contains disarticulated and articulated ostracod shells (Conodont sample 9).	0.45
8	Limestone, aphanitic, argillaceous, grayish orange pink; ledge-forming; bioturbated; contains few disarticulated and articulated ostracod shells (Conodont sample 8).	0.2
7	Shale, pale brown; *Strigogoniatites* sp. indet. was found at this level (Conodont sample 7).	1.0
6	Limestone, aphanitic, argillaceous, light olive gray; weakly bioturbated; seemingly unfossiliferous.	0.1
5	Shale, pale brown, poorly exposed (Conodont sample 5).	0.6
4	Limestone, aphanitic, argillaceous, pale brown; strongly bioturbated; few ostracod shells, both articulated and disarticulated (Conodont sample 4).	0.2
3	Shale, very dark red, poorly exposed.	0.4
2	Limestone, aphanitic, argillaceous, light brownish gray; strongly bioturbated; just one hard bed; scattered ostracod shells, both articulated and disarticulated (Conodont sample 2).	0.1
1	Limestone aphanitic, very argillaceous, light olive gray, thin-bedded; strongly bioturbated; contains *Michelinia vesiculosa*, *Liroceras* sp. indet. (Conodont sample 1).	1.4
	JULFA BEDS	
	Limestone, aphanitic, argillaceous, light brownish gray; slightly bioturbated; abundant ostracod shells, mostly disarticulated; taken 1 m below base of	

	Ali Bashi Formation (Conodont sample 0).	
Total thickness of Ali Bashi Formation		18.8

LOCALITY 2

Quality of outcrops insufficient for detailed stratigraphic section. Thickness of Ali Bashi Formation to base of *Paratirolites* beds is 17 m.

Paratirolites beds, only part of formation well exposed, are 3.5 m thick; they are aphanitic, argillaceous limestone, pale red, strongly bioturbated; containing, in addition to *Paratirolites,* much organic debris: gastropod and cephalopod fragments, articulated and disarticulated ostracod shells, echinoderm fragments, including crinoid columnals; in one thin section a transverse section of a keeled cephalopod shell 3 mm in diameter, possibly representing the early ontogenetic stage of a xenodiscid of the type of *Xenodiscites.*

Ufimia sp. was found at 4.5 m and 13.5 m above the base of the Ali Bashi Formation; *Pleramplexus leptoconicus* at 0.7, 1.0 and 13.5 m; *Iranites transcaucasius* was found at 0.7, 2.1, 2.2, 3, 3.5, 4.5, 7.5, 9, and 10.5 m above base of formation; "*Pseudotirolites*" sp. indet. at 2.1 m above base of formation; *Pseudogastrioceras abichianum* at 0.9 and 4.5 m above base of formation; *Shevyrevites shevyrevi* at 7.5, 9, and 10.5 m above base of formation; *Paratirolites kittli* in place in *Paratirolites* beds, *Paratirolites spinosus* at 13.5 m above base of formation, *Paratirolites mojsisovicsi at* 9 m above base of formation; *Strigogoniatites* sp. indet. at 2.1 m above base of formation; *Tainoceras* sp. indet. at 4.5 m above base of formation. Distribution of conodonts is summarized in Table 7.

LOCALITY 3

Quality of outcrop insufficient for detailed stratigraphic section. Thickness of Ali Bashi Formation to base of *Paratirolites* beds is 16 m. The *Paratirolites* beds, the only part of formation exposed, are 4.5 m thick and are similar in lithology and fossil content to those at Locality 2.

Pleramplexus leptoconicus was found at 4.5 m and 7. 5 m above the base of the Ali Bashi Formation; *Iranites transcaucasius* at 4.5, 6, and 7.5 m above base of formation; *Pseudogastrioceras abichianum* at 4.5 and 7.5 m above base of formation; *Shevyrevites shevyrevi* at 7.5 m above base of formation; *Xenodiscus dorashamensis* at 1.5 m above base of formation; *Phisonites triangulus* at 1.5 m above base of formation; *Paratirolites kittli* from *Paratirolites* beds, also at 11 m above base of formation; *P. mojsisovicsi* at 3 m above base of formation; *Strigogoniatites* sp. indet. at 4.5 m above base of formation; *Temnocheilus* sp. indet. at 3 m above base of formation; ?*Neocycloceras* sp. indet. at 4.5 m above base of formation; *Araxathyris araxensis minor* and *Araxathyris* sp. at 4.5 m above base of formation.

LOCALITY 4

(Distribution of Conodonts is summarized in Table 7)

Bed	*Description*	*Thickness (meters)*
	ALI BASHI FORMATION	
7	Limestone, aphanitic, argillaceous, pale red; cliff-forming; contains brachiopods at 1 m (*Araxathyris araxensis minor*), *Paranautilus* sp. indet. at 2.3 m, *Paratirolites* sp., and, microscopically, abundant articulated and disarticulated ostracod shells, scattered echinoderm fragments (Conodont samples 7L, 7M, 7U).	4.2
6	Limestone, aphanitic, argillaceous, grayish red, nodular; slope-forming; strongly bioturbated; few interbeds of reddish shale; contains abundant debris of ostracod shells, but few articulated specimens (Conodont sample 6).	7.0
5	Limestone, aphanitic, argillaceous, pale red, nodular, hard; weakly bioturbated; contains *Paratirolites kittli, Pleuronautilus* sp. indet., *Pleramplexus leptoconicus,* and, microscopically, scattered, mostly fragmented, ostracod shells (Conodont sample 5).	0.4–1.0
4	Limestone, red, nodular, crinoidal in upper part.	1.1
3	Shale, "reddish," contains *Plerophyllum dzhulfense, Araxathyris araxensis minor, Lopingoceras* sp.,	

	Domatoceras sp. indet., *Urartoceras* sp. indet., and crinoid stems.	0.75
2	Limestone, aphanitic, argillaceous, pale red, nodular, thin-bedded, ledge-forming; bioturbated; contains few disarticulated ostracod shells, some echinoderm fragments, including crinoid columnals, *Phestia* sp. indet., *Araxathyris araxensis minor* (Conodont sample 2).	1.3
1	Limestone, aphanatic, argillaceous, pale red, thin-bedded; slope-forming; bioturbated; contains some debris of ostracod shells and few echinoderm fragments, including crinoid columns (Conodont sample 1).	1.2
	Total thickness of Ali Bashi Formation about	16.5

FAUNA OF ALI BASHI FORMATION

Our collections from the Ali Bashi Formation have yielded specimens referable to approximately 40 genera of fossil invertebrates; however, only a few of these can be identified as to species. The collections include corals, bryozoans, brachiopods, bivalves, nautiloids, ammonoids, ostracods, crinoid stems, and conodonts. Mega-invertebrate fossils are by no means abundant, but the dominant element by far is the ammonoids. Nautiloids are second in abundance, while all other groups are sparsely represented in our collections, some by only a single specimen. Among the microfossils conodonts are very abundant, as are ostracods in certain beds.

Anthozoa

In our collections from the Ali Bashi Formation at Kuh-e-Ali Bashi, *Pleramplexus* is by far the most abundantly represented genus. This is in contrast to the relative proportions of genera reported from the north side of the Aras River.

Below we discuss the following species that we have identified from the Ali Bashi Formation:

Michelinia vesiculosa Chudinova
Plerophyllum dzhulfense Ilina
Ufimia sp.
Pleramplexus leptoconicus (Abich)

All four species are also represented in our collections from the Julfa beds, immediately below the Ali Bashi Formation, where we collected them close to our Locality 4.

From the "Induan Stage" of Soviet Dzhulfa (Dorasham 1 and 2), Ilina (1962) and Chudinova (*in* Ruzhentsev and Sarycheva, 1965) listed or described the following species of corals:

Khmeria pumila Chudinova
Plerophyllum armenicum Ilina
P. cuneatum Ilina
P. differentiatum Ilina
P. dzhulfense Ilina
Pleramplexus leptoconicus (Abich)
P. minimus Ilina

Plerophyllum differentiatum is the species most abundantly represented in the collections available to Ilina and Chudinova. *Khmeria pumila, Plerophyllum dzhulfense* and *Pleramplexus leptoconicus* are the only species surviving from the preceding Dzhulfian Stage, whereas the other four species first appear in the "Induan."

Stepanov *et al.* (1969) mentioned *Michelinia* sp., *Pleramplexus minimum* [*sic*] Ilina, and *Plerophyllum* sp. from their "Transition beds" at Kuh-e-Ali Bashi.

Bryozoa

Our collections from the Ali Bashi Formation contain a fragment of an annulated orthocone completely encrusted by a trepostomatous bryozoan. R. S. Boardman studied the specimen and informed us (written communication to Teichert, 28 May 1971) that it is generically unidentifiable but probably belongs to the family Stenoporidae.

Morozova (*in* Ruzhentsev and Sarycheva, 1965) recorded only one species of Bryozoa from the "Induan" of Soviet Dzhulfa. This is *Polypora dorashamensis* Nikiforova, a cryptostomate. This species also occurs in the underlying Dzhulfian beds where it is represented by 50 specimens in the Soviet collections. Morozova listed only two specimens from the "Induan." The species is also represented in the Upper Permian Chandalaysk Group of the Vladivostok region.

Brachiopoda

Brachiopods are relatively rare in the Ali Bashi Formation at Kuh-e-Ali Bashi; our collections contain only ten specimens. From this small sample G.A. Cooper (written communication, 13 February 1970) identified *Araxathyris araxensis minor* Grunt and *Araxathyris* sp. indet. It is of interest to note that from Soviet Dzhulfa Sarycheva, Sokolskaya, and Grunt (*in* Ruzhentsev and Sarycheva, 1965) recorded 454 specimens from the "Induan", but 389 of these are assigned to one species, *A. araxensis minor* Grunt, the same species that makes up the bulk of the specimens from the Ali Bashi Formation. All the remaining species recognized from the "Induan" of Soviet Dzhulfa are represented by few specimens, and some by only one.

Sarycheva, Sokolskaya, and Grunt (*in* Ruzhentsev and Sarycheva, 1965) described or listed the following species of brachiopods from the "Induan Stage" of Soviet Dzhulfa:

Spinomarginifera pygmaea Sarycheva
Haydenella kiangsiensis (Kayser)
H. minuta Sarycheva
Araxathyris araxensis minor Grunt
A. ogbinensis Grunt
Orthotichia parva Sokolov
Enteletes dzhagrensis Sokolov
Orthotetina sp.
Terebratuloidea sp.

These authors commented on this assemblage as follows (translation of Ruzhentsev and Sarycheva, 1965, by D.A. Brown, 1968: 75): "The lower Triassic Induan assemblage is strongly impoverished in numbers and in systematic relationships as compared with the brachiopod assemblage of the upper beds of the Dzhulfian Stage. Of the 9 species occurring here, 5 pass up from the Permian; unknown in the underlying deposits are *Enteletes dzhagrensis*, *Orthotichia parva*, *Orthotetina* sp. and *Terebratuloidea* sp. Let us note that the first three genera appeared even in the Middle Carboniferous and the last genus, in the Early Permian; they all died out at the boundary with the Triassic, if we ignore the present region of Trans-Caucasia."

Bivalves

Our collections from the Ali Bashi Formation at Kuh-e-Ali Bashi contain one small specimen of *Phestia* sp. indet. identified for us by N.D. Newell (written communication to Kummel, 16 December 1969). The monograph on the Permian and Triassic strata of Soviet Dzhulfa edited by Ruzhentsev and Sarycheva (1965) contains no data on bivalves.

Nautiloidea

Our collections from the Ali Bashi Formation at Kuh-e-Ali Bashi yielded the following nautiloids:

?*Dolorthoceras* sp.
Neocycloceras sp.
Lopingoceras sp.
Tainoceras sp. indet.
Metacoceras sp. indet.
Pleuronautilus sp. indet.
Temnocheilus sp. indet.
Domatoceras sp. indet.
Liroceras sp. indet.
Paranautilus sp. indet.

Shimanskiy (*in* Ruzhentsev and Sarycheva, 1965) recognized the following nautiloids from the Ali Bashi Formation of Soviet Dzhulfa:

?*Neocycloceras* sp.
Tainoceras sp. 1 (ex. gr. *changlingpuense* Chao)
T. sp. 2 (ex. gr. *changlingpuense* Chao)
T. sp. 3
Metacoceras sp. 2 (ex. gr. *dorsoarmatum* Abich)
?*Foordiceras* sp. 2
Pleuronautilus ex. gr. *dieneri* Krafft
?*P.* sp.
Tainionautilus sp.
Domatoceras sp. 2
?*Paranautilus* sp.
Syringonautilus vagus Shimanskiy

Most of the genera in these two faunas are characteristic forms of the late Paleozoic, namely Late Carboniferous and Permian. Only *Syringonautilus* has previously been recorded from the Middle and Upper Triassic. However, this identification is doubtful. Kummel (1953) has demonstrated that there was no significant change in the composition of nautiloid faunas across the Permian-Triassic boundary. He (Kummel, 1953: 1) summarized this relationship as follows: "Evolution of the nautiloids in the Triassic is mostly one of culminating patterns and modes started in the late Paleozoic." The nautiloids thus can make no significant contribution to the determination of the Permian-Triassic boundary.

Straight "nautiloids" (orthocerids) are reasonably common and are represented by the genera ?*Dolorthoceras, Neocycloceras,* and *Lopingoceras*. Some representatives of the last-named genus are very similar, and possibly identical, to the type species, *Lopingoceras lopingense* (Stoyanow), which was first reported from the Upper Permian of Soviet Dzhulfa. This genus was not reported by Shimanskiy (*in* Ruzhentsev and Sarycheva, 1965) from the equivalents of the Ali Bashi Formation in Soviet Dzhulfa, but *Neocycloceras* occurs there, both in the Dzhulfian beds and in the overlying lower "Induan."

Ammonoidea

Our collections of ammonoids from the Ali Bashi Formation near Iranian Julfa contain specimens of the following 15 species in 13 genera:

Pseudogastrioceras abichianum (von Möller)
Strigogoniatites sp. indet.
?*Propopanoceras* sp. indet.
Neoaganides n. sp.
"*Pleuronodoceras*" sp. indet.
"*Pseudotirolites*" sp. indet.
"*Pseudostephanites*" sp. indet.
Phisonites triangulus Shevyrev
Xenodiscus dorashamensis Shevyrev
Iranites transcaucasius (Shevyrev)
Shevyrevites shevyrevi Teichert and Kummel, n. g., n. sp.
Urartoceras sp. indet.
Paratirolites kittli Stoyanow
P. mojsisovicsi Stoyanow
P. spinosus (Shevyrev)

Ruzhentsev and Sarycheva (1965) listed the following 17 species and 9 genera from the Ali Bashi Formation of Soviet Dzhulfa:

Pseudogastrioceras abichianum (Moeller)
Stacheoceras tschernyschewi (Stoyanow)
Phisonites triangulus Shevyrev
Xenodiscus dorashamensis Shevyrev
Tompophiceras transcaucasium Shevyrev
Bernhardites radiosus (Frech)
B. nodosus Shevyrev
Dzhulfites spinosus Shevyrev
D. nodosus Shevyrev
Paratirolites kittli Stoyanow
P. waageni (Stoyanow)
P. vediensis Shevyrev
P. trapezoidalis Shevyrev
P. dieneri Stoyanow
Abichites stoyanowi (Kiparisova)
A. mojsisovicsi (Stoyanow)
A. abichi Shevyrev

These ammonoids range stratigraphically through five beds (or zones) as follows (from top to bottom):

Beds with *Paratirolites*
Beds with *Bernhardites*
Beds with *Dzhulfites*
Beds with *Tompophiceras*
Beds with *Phisonites*

The complete sequence of these ammonoid beds is present apparently only at locality Dorasham 2 in Dzhulfa Gorge. In the remaining regions of Transcaucasia the beds with *Phisonites* and those with *Tompophiceras* are apparently absent. The beds with *Paratirolites* are widely distributed in Transcaucasia and are present in all sections studied by the Soviet geologists. The beds with *Dzhulfites* and *Bernhardites* are more restricted in their distribution and are quite thin in most sections other than that of Dorasham 2. According to our systematic revisions of the taxa in the Ali Bashi Formation, these Soviet faunas consist of nine species belonging to seven genera.

The most significant aspect of our ammonoid fauna is the number of additional genera over that of previous reports on the ammonoids from this formation. The additional genera are *Strigogoniatites, Neoaganides, "Pleuronodoceras," "Pseudotirolites," "Pseudostephanites,"* and *Urartoceras.* Of these, *"Pleuronodoceras," "Pseudotirolites,"* and *"Pseudostephanites"* are of particular interest as they were first illustrated, but not described, by Chao (1965) from the highest Permian strata in China which were selected as the type of the Changhsingian Stage by Furnish and Glenister (1970). These three genera are known only from northwestern Iran and China.

Strigogoniatites is a relatively rare goniatite that ranges through much of Permian time. To date only six species have been assigned to this genus and these are based on very few specimens. In its morphological features the genus is gradational with *Pseudogastrioceras.* On the basis of the available data, angularity of the venter develops at progressively younger stages through Permian time. One of our specimens has an acute venter at a diameter of 18 mm. This is the smallest diameter for the appearance of this feature noted so far, suggesting that this is the youngest representative of this genus so far recorded.

The lowest beds of the Ali Bashi Formation contain specimens of *Phisonites triangulus* Shevyrev and *Xenodiscus dorashamensis* Shevyrev. These species were first described from the same stratigraphic position in Soviet Dzhulfa. *Phisonites* is a monotypic genus known only from the Dzhulfa region. *Xenodiscus* is a fairly common ammonoid of Upper Permian deposits wherever they occur. It is a very generalized form, considered to be ancestral to the Early Triassic ophiceratids and glyptophiceratids. Schindewolf (1954) was the first to distinguish clearly the morphological features that distinguish *Ophiceras* from *Xenodiscus.* The former has three umbilical lobes and the latter only two. Schindewolf (1954: 176) also discussed the possibility that the forms from the Lower Triassic *Ophiceras* beds of East Greenland placed by Spath (1935) in *Ophiceras* (*Metophiceras*) are perhaps more properly placed in *Xenodiscus.* He based his argument primarily on the suture of *Ophiceras* (*Metophiceras*) *subdemissum* (Spath, 1935, pl. 13, fig. 3). We find it difficult to accept this conclusion because the data are far too meager. The earliest Triassic ophiceratids are an extremely plastic stock that reflects a wide adaptive radiation. One expression of this radiation is the wide variation in shape of whorl section and degree of involution. The suture likewise shows extensive variation. *Ophiceras* (*Metophiceras*) is better understood as part of the ophiceratid radiation than as a surviving *Xenodiscus.* The record available suggests that *Xenodiscus* showed little significant evolutionary change throughout the Late Permian, but that it was one of its offspring, the ophiceratids, that underwent extensive radiation.

The best known goniatite from the Julfa region is *Pseudogastrioceras abichianum* (von Möller). In Soviet Dzhulfa, Shevyrev (*in* Ruzhentsev and Sarycheva, 1965) recorded only a single specimen from his *Bernhardites* Zone. Specimens of this species are quite common in the underlying *Phisonites* Zone, and predominant in the *Araxoceras* Zone. Our collections contain 12 specimens from the Ali Bashi Formation, the stratigraphically highest of which comes from a horizon 7.5 m above the base of the unit. This genus is widely distributed in Permian strata throughout the world. Stepanov *et al.* (1969: 40) record *Pseudogastrioceras* sp. from the *Paratirolites* beds.

The specimen we assign to *?Propopanoceras* is quite similar in overall appearance to *P. kweichowense* Chao (1965) from the Lower Permian of south China. However, the poor preservation of the specimen from the Ali Bashi Formation does not permit more than a suggested relationship. The only other species of *Propopanoceras* are from Lower Permian (Sakmarian) strata of the Urals and Western Australia.

Another interesting new taxon recorded here from the Ali Bashi Formation is *Neoaganides* n. sp. Our collections from the underlying Dzhulfian beds contain a specimen now being studied by W.M. Furnish and B. F. Glenister (written communication to Kummel, 15 December 1969) which they think is conspecific with the specimen from the Ali Bashi Formation. It is quite apparent that this is a very long-ranging genus, of little value for age determination.

Araxoceratids are a very characteristic element of the Dzhulfian strata both in the region of Soviet Dzhulfa and at Kuh-e-Ali Bashi in Iran. The specimen we assigned to *Urartoceras* sp. indet. is from float, 3 meters above the base of the Ali Bashi Formation, well within the *Phisonites* Zone. The genus was known previously only from the underlying *Vedioceras* Zone in Soviet Dzhulfa.

One of the most common ammonoids in the Ali Bashi Formation is the one assigned by Shevyrev (*in* Ruzhentsev and Sarycheva, 1965) to *Tompophiceras transcaucasium.* Shevyrev had only eight specimens, all from Dorasham 2, in Soviet Dzhulfa, a striking difference from its predominance in our collections from Kuh-e-Ali Bashi. Our material adds appreciably to knowledge of this species, which is discussed in detail in the systematic chapter. The primary conclusion is that *T. transcaucasium* is not congeneric with *T. fastigatum,* the type species of *Tompophiceras.* Popov (1961) clearly pointed out that fastigation of the venter of his type, and only, specimen, was confined to the outer volution, and that the inner volutions have broadly rounded venters. Tozer's (1969) contention that acuteness of the venter in *Tompophiceras fastigatum* is due to crushing is rejected by Popov (personal communication). Kummel was able to examine the type specimen in June 1970, and agrees completely with Popov's conclusions. Acuteness of the venter in the species from the Ali Bashi Formation is attained at a much earlier growth stage. The smallest specimen in our collection has an acute venter at a shell diameter of 13 mm.

The evolute, ribbed ammonoids of the Ali Bashi Formation, which Shevyrev assigned to his new genus *Bernhardites,* are extremely difficult to interpret. In the systematic chapter we explain in detail that the Ali Bashi species are not congeneric with *Celtites radiosus* Koken, the type species of *Bernhardites,* from the Lower Triassic of the Salt Range, West Pakistan. It is likewise pointed out that *Celtites radiosus* is not represented in the Lower Ceratite limestone as stated by Noetling (*in* Frech, 1905: 164), but rather occurs in the overlying Ceratite marls. Ammonoids of the general morphology of *Bernhardites* are fairly common in Upper Permian and Lower Triassic strata. The great difficulty in identification makes precise time correlations tenuous at best. For these reasons a new generic name, *Shevyrevites,* is introduced for the species represented in the Ali Bashi Formation.

The most characteristic ammonoids of the Ali Bashi Formation are assignable to species of *Paratirolites.* For this group of ammonoids Shevyrev (*in* Ruzhentsev and Sarycheva, 1965) recognized three genera (*Paratirolites* Stoyanow, *Dzhulfites* Shevyrev, and *Abichites* Shevyrev), containing ten species altogether. Paratirolitids are by far the most common and abundant ammonoids in our collections. Study of these specimens leads us to conclude that this group consist of only one genus and three species. The uniqueness of the paratirolitids rests in the suture. For a long time it was thought that they represented an endemic group confined to the Ali Bashi Formation. Now, however, they are known from correlative strata near Abadeh, central Iran (Taraz, 1969), and from an unknown horizon and locality in northern Madagascar (Tozer, 1969). In the Abadeh region the paratirolitids occur in a 19-meter bed of brownish red limestone that is reported also to contain *Pseudogastrioceras* and *Bernhardites.* Earlier interpretations of *Paratirolites* suggested affinities with *Stephanites* of the Upper Ceratite limestone in the Salt Range of West Pakistan, emphasizing the nodose ornamentation and deemphasizing differences in the suture. Examination of our large collection of *Paratirolites* clearly shows that its suture is very distinctive and its ornament much more variable than in the Salt Range species of *Stephanites.*

Ostracoda

It is apparent from thin-section studies on rock specimens from the Ali Bashi Formation at Kuh-e-Ali Bashi and from examination of residues prepared for conodont studies that ostracods are quite abundant at several levels (Plate 14). From one sample, a red mudstone bed immediately at the base of the *Paratirolites* beds, I.G. Sohn (written communication to Teichert, 21 December 1971) was able to identify:

Hollinella sp. cf. *H.? tuberculata* Belousova
Bairdia spp.
Bairdiacea gen. indet.

Sohn concluded that the sample was of Permian age on the basis of the presence of *Hollinella.*

Belousova (*in* Ruzhentsev and Sarycheva, 1965) recorded 19 species from the "Induan" of Soviet Dzhulfa. These species are:

Healdia incognita Belousova
Healdianella dorashamensis Belousova
H. splendida Belousova
Fabilicypris subgeinitziana Belousova
F. obuncus Belousova
F. geinitziana
F. hoxabarensis
Hollinella sp. aff. *H. cushmani*
Bairdia armenica Belousova
B. beedei
B. sp. aff. *B. hassi*
B. rhomboidalis
B. anbeedei Belousova
B. intermedia Belousova
B.? subglenensis Belousova
B. pseudoobuncus Belousova
B. subhassi Belousova
Orthobairdia sp. aff. *O. guadalupiana* Hamilton
Acratinella obscura Belousova

The essentially Paleozoic affinities of this fauna are evident.

Crinoidea

Crinoids are present in moderate abundance, represented by stem fragments only, among which several types of columnals can be distinguished. One of these is similar, or possibly identical, to the columns of *Erisocrinus araxensis* Yakovlev, described from uppermost Permian beds of Soviet Dzhulfa. Strangely enough, all our crinoid material was collected from beds 2 and 3 in Locality 4, although we spent less time in sampling this section than each of the other three.

No crinoids are mentioned from any part of the Permian or "Induan" in Ruzhentsev and Sarycheva's (1965) report.

Conodonts

Bulk samples from Permian-Triassic rocks at Kuh-e-Ali Bashi were processed for conodonts. General information about the number, size, weight, productivity, and stratigraphic distribution of the samples is summarized in Table 1, and information about the frequency and distribution of the conodont species represented is given in Table 7 (see p. 425).

As indicated in Table 1, 35 of the 48 samples are from the Ali Bashi Formation (units 52 through 61 of Stepanov *et al.*, 1969); one is from a level 1.0 m below the Ali Bashi Formation (in unit 51 of Stepanov *et al.*, 1969); and 12 are from the lower 38 m of the Elikah Formation. In addition to these samples, we have another (OSU*

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* Ohio State University.

TABLE 1. SAMPLE DATA

Section			Stratigraphic Position					
Teichert & Kummel	OSU	Number of Samples	Below Ali Bashi	Ali Bashi	Above Ali Bashi	Average Sample Weight (g)	Avg. No. Conodonts per kg	Total Conodonts Recovered
Loc. 1	69SA	38	1(0)*	25(1)	12(3)	0-20U: 1766 21-C8: 718	113 10.5	4722
Loc. 2	69SB	3	0	3(0)	0	1106	100	273
Loc. 3	69SC	7	0	7(0)	0	1593	109	1180
Bed 67	67GH	1	0	0	1	?	?	42

* Numbers in parentheses indicate number of samples that did not produce conodonts.

laboratory number 67GH-28) from unit 67 of the Elikah Formation. This sample represents matrix from the Elikah ammonoid identified as *Meekoceras* sp. by Stepanov *et al.* (1969: 41) and preliminary comments on conodonts recovered from it have already been published (*in* Stepanov *et al.,* 1969: 64).

As indicated in Table 1, 44 of the 48 samples were productive and yielded a total of 6,112 discrete conodont elements. An additional 42 specimens were derived from sample 67GH-28. These 6,154 elements represent eight species of four genera:

Anchignathodus isarcicus (Huckriede)
A. julfensis Sweet, n. sp.
A. typicalis Sweet?
Ellisonia gradata Sweet
E. teicherti Sweet
E. spp.
Neogondolella carinata carinata (Clark)
N. carinata subcarinata Sweet n. subsp.
N. carinata subcarinata?
N. orientalis (Barskov and Koroleva)
Xaniognathus sp. cf. *X. elongatus* Sweet

One of these species, *Anchignathodus julfensis* n. sp. has not been recognized previously and is named in this report. In addition, a previously undescribed subspecies of *Neogondolella carinata* (Clark) is recognized and named *N. carinata subcarinata* n. subsp.

Conodont elements in our collection from Kuh-e-Ali Bashi are unaltered, amber in color, and generally quite well preserved. A large number of the gondolelliform elements, which dominate the collections, are complete and unbroken; however, only a few of the ramiform elements are undamaged and a majority of the specimens at hand are faintly etched or pitted surficially. Several specimens (*e.g.,* Pl. 12, figs. 3, 13) have irregular tubular structures attached to them which we interpret as attached foraminifiers. From these features of preservation we conclude that the elements at hand were exposed to solution, currents, and to the activities of other organisms for some time after they accumulated on the sea floor.

AGE AND CORRELATION OF THE ALI BASHI FORMATION

The Age and correlation of the "Induan" beds of Soviet Dzhulfa have been a source of controversy for nearly a century. The views and interpretations of earlier researchers have been outlined in the previous chapter on "History of Research." It is the large monographic study of the stratigraphy and paleontology of these strata in Soviet Dzhulfa, edited by Ruzhentsev and Sarycheva (1965), that needs to be considered at this time. These Soviet authors came to the conclusion that the beds with *Tompophiceras* through those with *Paratirolites* are Early Triassic in age and belong to the Induan Stage of Kiparisova and Popov (1956, 1961, 1964). They based their arguments on age assignment entirely on ammonoids. They summarized their views as follows (translation of Ruzhentsev and Sarycheva, 1965, by D.A. Brown, 1968: 107–108):

"In these deposits we have recognized four stratigraphical levels (in ascending order): 1) beds with *Tompophiceras,* 2) beds with *Dzhulfites,* 3) beds with *Bernhardites,* and 4) beds with *Paratirolites.*

"In the beds with *Tompophiceras,* a new species, *T. transcaucasium* Shevyrev has been identified. Representatives of the genus *Tompophiceras* had so far been known only in Verkhoyansk, where they occur together with *Otoceras boreale* Spath, *O. indigirense* Popov, and *Glyptophiceras pascoei* Spath (Popov, 1961), that is, with species which, in East Greenland, are found at the base of the Lower Triassic. Therefore, we may consider the Dzhulfian beds with *Tompophiceras,* with reasonable confidence, as the stratigraphic equivalents of the zone of *Otoceras woodwardi* and *Ophiceras commune* of the above scale.

"The beds with *Dzhulfites* contain unusual forms of ceratites, unknown in other regions which, naturally, are difficult to correlate.

"In the overlying beds with *Bernhardites* this genus is represented by the species *B. radiosus* (Frech), which is also characteristic of the lower *Ceratite* limestone of the Salt Range. The latter, on its faunal assemblage, is correlated with the zone of "*Celtites*" *radiosus* of Spath and the zone of *Proptychites rosenkrantzi* of Kummel. On this basis the beds with *Bernhardites* may be considered as the equivalent of the zone of *Proptychites rosenkrantzi,* and the underlying beds with *Dzhulfites* may provisionally be correlated with the zone of *Vishnuites decipiens.*

"The beds with *Paratirolites* are also peculiar in their faunal relationships; ceratites unknown in other regions are found in them. The clarification of the position of these beds in the stratigraphic scale is served by two circumstances. First, the clear genetic association of the genera *Paratirolites* and *Abichites* with the older *Dzhulfites* and *Bernhardites* opposes any stratigraphic break between the third and fourth series of beds. Second, Sh.A. Azizbekov 1961, p. 83), citing determinations by L.D. Kiparisova, records from the deposits occurring in Nakhichevansk ASSR directly above the beds with *Paratirolites,* such species as *Claraia stachei* Bittner, *C. aurita* Hauer and *Proptychites discoides* Waagen. The last species is also known from the lower *Ceratite* limestone of the Salt Range. Consequently, the beds with *Paratirolites* may also be correlated with the zone of *Proptychites rosenkrantzi.*

"Thus, the palaeontologically characterized Lower Triassic deposits of Trans-Caucasia correspond precisely, in our opinion, with the lower half of the Induan Stage. At the transition on the zonal scale they embrace the entire *Otoceras* Horizon, that is, the zones of *Otoceras woodwardi* and *Ophiceras commune,* and half of the *Gyronites* Horizon with the zones of *Vishnuites decipiens* and *Proptychites rosenkrantzi.* Such an age determination for these beds is in considerable degree new, because several authors (Spath, 1934; Kummel, 1957, etc.) were inclined to accept the *Paratirolites* beds up to the zone of *Anasibirites multiformis,* recognized in the lower part of the Olenekian Stage."

The critical genera in the above discussion are *Tompophiceras, Dzhulfites, Bernhardites,* and *Paratirolites,* which are represented in the Ali Bashi Formation at Kuh-e-Ali Bashi, and are discussed in detail in the chapter on "Systematic Paleontology." A summary of their stratigraphic implications is given here.

The specimens assigned to *Tompophiceras* by Shevyrev (*in* Ruzhentsev and Sarycheva, 1965) are not conspecific with *Tompophiceras fastigatum* Popov from Siberia. Shevyrev had only eight fragmentary specimens, whereas our collections contain a large number of specimens of this form. Fastigation of the venter in *Tompophiceras fastigatum* Popov is present on the outer volution. We have specimens from the Ali Bashi Formation that are fastigate at a diameter of 13 mm. For these reasons we establish the new genus *Iranites* for these forms in the Ali Bashi Formation and the corresponding forms in Soviet Dzhulfa.

Dzhulfites Shevyrev is a synonym of *Paratirolites.* It differs from *Paratirolites* only in whorl section, the sutures being almost identical.

Ribbed, evolute ammonoids of the type Shevyrev placed in his genus *Bernhardites* are not uncommon in Late Permian and Early Triassic strata. They are very difficult to identify and differentiate. As a consequence, precise age determination is tenuous at best. Shevyrev (*in* Ruzhentsev and Sarycheva, 1965) selected *Celtites radiosus* Koken (*in* Frech, 1905) as the type of his new genus *Bernhardites.* This species was stated to have come from the Lower Ceratite limestone of the Salt Range, West Pakistan. However, Kummel's field experience in the Triassic formations of the Salt Range demonstrates that specimens of the species actually occur in the overlying Ceratite marl. It is our contention that the specimens assigned to *Bernhardites* from the "Induan" of Soviet Dzhulfa are not congeneric with "*Celtites*" *radiosus* Koken of the Salt Range.

Until recently *Paratirolites* was known only from the "Induan" of Soviet Dzhulfa and the Ali Bashi Formation of northwestern Iran. Recently Tozer (1969) has pointed out that the specimen from Madagascar assigned by Diener (1914) to *Xenodiscus douvillei* Diener is a paratirolitid. Unfortunately, no stratigraphic data are available for this specimen. Taraz (1969) reported *Paratirolites* from Abadeh in central Iran, and Teichert collected specimens from this locality in 1970. But Taraz's faunal list that includes this genus, in addition to *Pseudogastrioceras, Dzhulfites, Abichites,* and *Bernhardites,* is for a unit 19 m (62 feet) thick which probably represents the equivalent of the entire Ali Bashi Formation.

In the monograph edited by Ruzhentsev and Sarycheva (1965) an attempt was made to establish the age of the lower part of the "Induan" in Soviet Dzhulfa on the basis of the presence, in sequence, of four ammonoid genera, namely *Tompophiceras, Dzhulfites, Bernhardites,* and *Paratirolites.* With exception of *Paratirolites,* we consider these generic identifications to be wrong. In addition, none of these taxa unequivocally indicates a Late Permian or Early Triassic age.

Several additional genera of ammonoids, representatives of which we collected from the Ali Bashi Formation, are of considerable importance in assessing the age of the formation. Among these, the most interesting are "*Pleuronodoceras,*" "*Pseudotirolites,*" and "*Pseudostephanites.*" These genera were first illustrated, though not formally established, by Chao (1965) from highest Permian strata, the Changhsing limestone, of eastern China. The Changhsing district in northern Chekiang was selected as type locality of the Changhsingian Stage by Furnish and Glenister (*in* Kummel and Teichert, 1970). The remaining newly discovered genera are *Strigogoniatites, Neoaganides,* and *Urartoceras,* all of which are well-known from Permian strata but most of which have long ranges. Only six species of *Strigogoniatites* have been recorded so far, all of Permian age. On the evidence of these six species, acuteness of the venter appears to develop at progressively younger stages through Permian time. One of our specimens from the Ali Bashi Formation has a well-developed acute venter at a diameter of 18 mm. On the basis of earlier observations on species of this genus, this would suggest that our forms are very late Permian in age.

Neoaganides n. sp. was recognized by Teichert and Kummel on the basis of a single specimen. Our collections from the underlying Julfa beds contain a conspecific specimen now being studied by W.M. Furnish and B.F. Glenister. The specimen of *Urartoceras* sp. indet. from the Ali Bashi Formation is an interesting find. This genus is quite common in the underlying *Vedioceras* Zone in the Dzhulfian of Soviet Dzhulfa.

Phisonites is known only from the Ali Bashi Formation in Iran and in equivalent strata across the Aras River in Soviet Dzhulfa. The beds containing this genus were included in the Dzhulfian by Ruzhentsev and Sarycheva (1965), but we consider that they are more properly included in the Ali Bashi Formation.

Thus, our analysis of the ammonoid fauna of the Ali Bashi Formation leads us to the conclusion that it does not contain a single genus that can be considered as being Triassic in age.

The conodonts add significant data bearing on the question of the age of the Ali Bashi Formation. From Table 7 it is clear that *Neogondolella carinata* (Clark) is the dominant member of the conodont fauna of the Ali Bashi Formation, but representatives of *Ellisonia gradata* Sweet, *E. teicherti* Sweet, and, possibly, *Anchignathodus typicalis* Sweet are present from near or below the base of the formation to, or well above, its top. This assemblage of species, which continues to a level 13.5 m above the base of the Elikah Formation, is characteristic of the *Anchignathodus typicalis* Zone (Sweet, 1970b; Sweet *et al.*, 1971), which "straddles" the Permian-Triassic boundary in Pakistan (Sweet, 1970b), Kashmir (Sweet, 1970a), and East Greenland (Sweet, unpublished MS).

In the Salt Range and the Trans-Indus ranges of Pakistan, the top of the *Anchignathodus typicalis* Zone is in the Kathwai Member of the Mianwali Formation, a few feet below the highest occurrence of *Ophiceras*. In one section (Chhidru A, Kummel and Teichert, 1970), it occurs 9.6 feet above the lowest occurrence of that distinctive Early Triassic ammonoid. Conodonts characteristic of the *A. typicalis* Zone are also present at various levels in the upper 12 feet or so of the subjacent Chhidru Formation at four places in the Salt Range and Trans-Indus ranges, but the base of the *A. typicalis* Zone has not been located in those sections.

In the section of Permian and Triassic rocks at Guryul Ravine, Kashmir (Teichert, Kummel, and Kapoor, 1970; Sweet, 1970a; Nakazawa *et al.*, 1970), *Anchignathodus typicalis* and *Ellisonia teicherti* range from 29 feet below to 39 feet above the level at which Teichert, Kummel, and Kapoor (1970) placed the Permian-Triassic boundary. Nakazawa and his colleagues reported *Claraia, Otoceras, Ophiceras,* and *Proptychites* from various levels within the upper 39 feet of the *A. typicalis* Zone at Guryul Ravine, and the highest record of the *A. typicalis* conodont fauna is at about the same level as the highest *Ophiceras* reported from that section. The base of the *A. typicalis* Zone has not been located in the Guryul Ravine section, for the lowest conodont-bearing sample known there yields the zonal index species, *Ellisonia teicherti* and *E. triassica*.

In the Salt Range and Guryul Ravine sections, the *Anchignathodus typicalis* Zone is succeeded stratigraphically by a sequence of strata in which specimens of *Neogondolella carinata* (Clark) dominate conodont collections, and indexes to the *A. typicalis* Zone (*e.g., Anchignathodus typicalis, Ellisonia teicherti*) are absent. These strata were included by Sweet (1970a, 1970b) in a *Neogondolella carinata* Zone, which may or may not have stratigraphic utility in other sections. That is, the index species of the *N. carinata* Zone is also abundantly represented in the subjacent *A. typicalis* Zone and the boundary between the two is drawn at the level of disappearance of *A. typicalis* and its fairly constant companion, *Ellisonia teicherti*.

As noted previously, representatives of *Ellisonia teicherti* and, possibly, of *Anchignathodus typicalis* have been collected from as high as 13.5 m above the base of the Elikah Formation at Locality 1 (OSU section 69SA) (Table 7) in the Julfa region. Elikah strata above 13.5 m have produced only a few, mostly fragmentary, conodont elements. None of these is referable to *Neogondolella carinata.* Thus we cannot directly correlate the 13.5 m level at Locality 1 with the top of the *A. typicalis* Zone in either the Kashmir or the Salt Range sections. However, the 13.5 m level may be very close to the top of the *A. typicalis* Zone, because well-preserved specimens of *Anchignathodus isarcicus* (Huckriede) have been recovered from three samples in the lower 4.5 m of the Elikah Formation. Representatives of this same species occur about 5 feet above the lowest occurrence of *Ophiceras* in three sections in Pakistan (Sweet, 1970b) and a comparable distance below the highest level from which *A. typicalis* and *E. teicherti* have been found in those sections. In addition to suggesting a general correlation between the top of the *A. typicalis* Zone of Pakistan and Kashmir with the 13.5 m level in the Elikah Formation at Julfa Locality 1, the occurrence of *A. isarcicus* in the lower 4.5 m of that formation suggests not only that the sampled portion of the Elikah is entirely Triassic in age, but also that it represents essentially the same part of the Lower Triassic as the Kathwai Member of the Mianwali Formation of Pakistan. *A. isarcicus* also defines a thin interval near (but not at) the base of the Werfen Formation in the southern Alps of northern Italy (Staesche, 1964).

An important result of Sweet's study of Permian and Triassic conodonts from the Julfa region is location of the base of the *Anchignathodus typicalis* Zone. We define that level here at the lowest occurrence of *Neogondolella carinata* (Clark), which appears for the first time in the lowest samples from the Ali Bashi Formation at Localities 1 and 4. *Ellisonia teicherti* and fragmentary specimens reminiscent of *A. typicalis* appear 0.2 m above the base of the Ali Bashi Formation at Locality 4, and neither these species nor *N. carinata* are represented in any of the few samples we have from strata older than the Ali Bashi Formation in Iran or nearby Soviet Transcaucasia. We feel this boundary to be an especially significant one, for it represents the level of evolutionary transition from *Neogondolella orientalis* (Barskov and Koroleva) to *N. carinata* (Clark).

It is of interest to note that the *Anchignathodus typicalis* Zone, as now defined, includes not only the latest Permian Changhsingian Stage of Furnish and Glenister (1970), but also much, if not all, of the earliest Triassic Griesbachian Stage of Tozer (1967). Clearly, conodonts were either far less sensitive chronometers than ammonoids in latest Permian and earliest Triassic time or the *A. typicalis* Zone has been too broadly conceived. That the latter is probably the case is suggested by some of the new material described in this report. That is, in *Neogondolella carinata* (Clark), the most abundantly represented conodont species of the Ali Bashi Formation, we can distinguish two vertically segregated but morphologically intergradational subspecies. *N. carinata subcarinata* Sweet, n. subsp., ranges from the base to the top of the Ali Bashi Formation (*i.e.*, essentially through the Changhsingian Stage), whereas *N. carinata carinata* makes its first appearance 4.5 m below the top of the Ali Bashi Formation, is represented by a single Elikah specimen (sample 67GH-28) from near the top of the *A. typicalis* Zone in Iran, and is the only subspecies of *N. carinata* represented in the largely Lower Triassic *A. typicalis* faunas of Pakistan and Kashmir (Sweet, 1970a, 1970b). Possible division of the present *A. typicalis* Zone into two major parts is thus suggested, as is further subdivision of these by segregation of intervals with *Anchignathodus julfensis* Sweet, n. sp., and *A. isarcicus* (Huckriede).

We do not at this time propose formally to dismember the *Anchignathodus typicalis* Zone along the lines just suggested, for we do not know that the divisions outlined would have biostratigraphic utility even in sections close to the Julfa region. However, if additional material from other regions supports no more than a division into two parts, a lower one characterized by *Neogondolella carinata subcarinata* and an upper distinguished by *N. carinata carinata,* some light would be shed on currently divergent conclusions about correlation of the uppermost part of the Chhidru Formation of Pakistan. In fact, even without division of the *A. typicalis* Zone, we can now set at least a lower limit for the age of the uppermost part of that formation, and this should help in determining the magnitude of the stratigraphic gap that is supposed to separate Permian and Triassic rocks in the Salt Range and Trans-Indus ranges of Pakistan.

From their study of the worldwide distribution of species of the ammonoid *Cyclolobus,* Furnish and Glenister (1970) concluded that strata referable to the uppermost Permian Changhsingian Stage are missing in Salt Range sections, even though no specimens of *Cyclolobus* have been collected from the uppermost 36 feet or so of the Chhidru Formation, which is believed to be the youngest Permian unit in the Salt Range. On brachiopod evidence from the Chhidru and superjacent Mianwali Formation, Grant (1970) concluded that the Chhidru is most likely Guadalupian and the overlying Kathwai Member of the Mianwali Formation probably Dzhulfian in age. With respect to Furnish and Glenister's conclusion, we point out that *Neogondolella carinata carinata* dominates a sample (K4-2) from about 12 feet below the top of the Chhidru Formation at Chhidru (Sweet, 1970b), and it is now known that *N. carinata* ranges no lower than the base of the Ali Bashi Formation of Iran which probably represents the base of the Changhsingian Stage. Thus, strata of the Changhsingian may well be present in the upper Chhidru Formation, even though diagnostic ammonoids are lacking. Moreover, if *N. carinata carinata* has the same stratigraphic distribution in Iran and Pakistan, the upper beds of the Chhidru Formation would correlate with the uppermost 4.5 m of the Ali Bashi Formation of the Julfa region (*i.e.*, with the Paratirolites limestone of Stepanov *et al.*, 1969, and of this report). In short, the upper beds of the Chhidru Formation of the Salt Range and Trans-Indus ranges may be of very latest Permian age and the Permian section of Pakistan may well be virtually complete.

Rebuttal to Grant's (1970) suggestion that the Chhidru Formation is most likely Guadalupian in age is implicit in the foregoing discussion. If by suggesting a Dzhulfian age for the overlying Kathwai Member of the Mianwali Formation, Grant was following the definition of that stage given by Ruzhentsev and Sarycheva (1965) (*i.e., Araxilevis* through *Phisonites* beds), then conodont evidence now at hand is contradictory. *Neogondolella carinata,* which occurs in the upper 12 feet or so of the Chhidru, appears at the base of the Ali Bashi Formation in the Julfa region, and the base of the Ali Bashi is essentially the same as the base of the uppermost Dzhulfian *Phisonites* beds *sensu* Ruzhentsev and Sarycheva. Thus the *Phisonites* beds are the lowest Dzhulfian unit with which the Kathwai or immediately underlying upper Chhidru beds could possibly be correlated. However, *N. carinata carinata,* the subspecies represented in the uppermost Chhidru and Kathwai, does not appear in Iran until the base of the *Paratirolites* beds, some 12 m above the top of the Dzhulfian *sensu* Ruzhentsev and Sarycheva. Furthermore, *Anchignathodus isarcicus* in both the lower unit of the Kathwai and the basal 4.5 m of the Elikah suggests correlation of these units, not a correlation of the Kathwai of Pakistan with beds in Iran or Soviet Transcaucasia as old as the *Phisonites* beds of the lower Ali Bashi Formation.

While the evidence for a Late Permian age of the Ali Bashi Formation, based on detailed analysis of the ammonoid and conodont faunas, may be considered as conclusive, it is worth pointing out that this conclusion is strongly supported by the study of other faunal elements. All four species of corals described by us from the Ali Bashi Formation were found by us in the underlying Julfa beds. The single bryozoan specimen found in the Ali Bashi is a member of the typically Paleozoic family

Stenoporidae. Brachiopods are represented by fewer species than in the "Induan" of the Dzhulfa area, but *Araxathyris araxensis minor* Grunt was reported from the upper Dzhulfian by Sarycheva, Sokolskaya, and Grunt (*in* Ruzhentsev and Sarycheva, 1965).

Most of the nautiloid genera reported by us from the Ali Bashi Formation are characteristic Late Paleozoic forms, with the possible exception of *Syringonautilus,* which was not previously known from pre-Triassic rocks. The typical Permian aspect of the ostracod fauna of the Ali Bashi Formation has already been stressed. The crinoids, represented by stems only, clearly were Paleozoic types.

All in all, it seems to us that the fauna of the Ali Bashi Formation of Kuh-e-Ali Bashi and of the corresponding beds in Transcaucasia is composed of populations that survived from the preceding Dzhulfian. On the whole these populations were impoverished with respect to species and very few new forms were added, none of them suggestive of demonstrably post-Paleozoic affinities.

SYSTEMATIC PALEONTOLOGY

In the following descriptions MCZ indicates Museum of Comparative Zoology, Harvard University; KU University of Kansas Museum of Invertebrate Paleontology; OSU Orton Museum of Geology, The Ohio State University. The descriptions of Conodontophorida are by Sweet and reference to them should be made as "Sweet *in* Teichert, Kummel, and Sweet, 1973." All other descriptions are by Teichert and Kummel and the correct reference is "Teichert and Kummel *in* Teichert, Kummel, and Sweet, 1973."

Phylum **COELENTERATA**

Class **ANTHOZOA** Ehrenberg, 1834

Subclass **TABULATA** Milne-Edwards and Haime, 1850

Order *FAVOSITIDA* Sokolov, 1950

Family MICHELINIIDAE Waagen and Wentzel, 1886

Subfamily MICHELINIINAE Waagen and Wentzel, 1886

Genus *Michelinia* de Koninck, 1841

Type species, *Calamopora tenuisepta* Phillips, 1836

Discussion. Chudinova (*in* Ruzhentsev and Sarycheva, 1965: 35) did not record any species of *Michelinia* from the "Induan" of the Soviet Dzhulfa area but reported two species, *M. parva* and *M. nana,* from the Dzhulfian and two others, *M. miranda* and *M. vesiculosa,* from Guadalupian strata of that area. Other species of *Michelinia* were reported from localities in the Transcaucasus. Gräf (1964) described as *Michelinia indica* Waagen and Wentzel a specimen from Dizdere, a locality somewhere south or southeast of Julfa, the exact position of which we find difficult to identify. No stratigraphic details are known.

Michelinia vesiculosa Chudinova
Plate 1, figures 8–10

Michelinia vesiculosa Chudinova, *in* Ruzhentsev and Sarycheva, 1965: 152, pl. 8, fig. 2.

Discussion. Our collections contain one fairly large colony of *Michelinia* whose longest diameter is about 80 mm. The diameter of the corallites varies from about 5 to 7.5 mm. They are subhexagonal in transverse section and essentially straight. Wall pores are present, but their density is difficult to determine; they are probably up to 0.5 mm in diameter. Septa are absent, but septal tubercles are present. Tabulae are strongly convex upward and somewhat variable in distance between about 0.5 and 3.0 mm.

We assign this specimen to *Michelinia vesiculosa* because of size of corallum and corallites and nature of the tabulae, although Chudinova (*in* Ruzhentsev and Sarycheva, 1965: 152) reports this species only from the Gnichik Formation of early Guadalupian age in the Transcaucasus. Of the two "Induan" species, *M. parva* and *M. nana,* described by Chudinova from the Transcaucasus, *M. parva* has concave, or at least less strongly convex, tabulae; and *M.*

nana, a very small corallum consisting of only two or three corallites.

Occurrence. Loc. 1, 1 m above base of bed 19.

Repository. MCZ 9409.

Subclass **RUGOSA** Milne-Edwards and Haime, 1850

Order *STREPTELASMATIDA* Wedekind, 1927

Family PLEROPHYLLIDAE Koker, 1924

Genus *Plerophyllum* Hinde, 1890

Type species, *Plerophyllum australe* Hinde, 1890

Plerophyllum is common in Permian rocks in Asia and Australia (Schindewolf, 1942) and is among the few Late Permian survivors of the Rugosa. Ilina (1962, 1965) described the following species from the Ali Bashi Formation equivalents ("Induan" Stage) of the Transcaucasus: *P. armenicum, P. cuneatum, P. differentiatum, P. dzhulfense. P. dzhulfense* is the only one of these species that extends from the Dzhulfian into the "Induan." All four species occur in the Soviet Dzhulfa area at Dorasham 1 and 2.

Plerophyllum dzhulfense Ilina

Plate 1, figures 1–7

Plerophyllum dzhulfense dzhulfense Ilina, 1962: 75–76, pl. 1, figs. 4, 5 (Engl. transl., 1964: 1611–1612, pl. 1, figs. 4, 5).

Plerophyllum dzhulfense Ilina, 1965: 47–52; pl. 3, fig. 9; pl. 4, figs. 1–11; pl. 5, figs. 1–5.

Discussion. In our collections the genus *Plerophyllum* is represented by six small coralla, not much more than about 15 mm long. They are slightly curved, slowly expanding. We are placing these specimens in *Plerophyllum dzhulfense* because they seem to be closer to this species than to any of the other three described by Ilina from the Transcaucasus.

We are figuring four cross sections (Pl. 1, figs. 2, 4, 6, 7) from three different specimens, the larger of which (Pl. 1, fig. 7) is about 14.5 mm wide. One of them (Pl. 1, fig. 2) is perhaps somewhat similar to *Plerophyllum differentiatum* because most major septa are tapering inward rather than being rhopaloid in transverse section, but Ilina has also illustrated specimens of *P. dzhulfense* having septa of this kind (Ilina, 1965, pl. 4, fig. 11b).

One of the figured specimens (Pl. 1, fig. 6) seems to us to be closer to *P. dzhulfense,* the other (Pl. 1, fig. 4), closer to *P. differentiatum.* In the specimen illustrated in Figure 4, the number of septa in the alar quadrants is two less than in the counter quadrants and the alar and counter-lateral septa are distinctly rhopaloid whereas the cardinal and counter septa are not. In the specimen illustrated on Plate 1, figure 6, none of the major septa is rhopaloid, except the cardinal septum, which is only very weakly rhopaloid.

It should not be overlooked that these characters vary in other species of *Plerophyllum.* Thus, both Gerth (1921, pl. 146, figs. 16, 17) and Schindewolf (1942, text–figs. 45c, d) illustrated specimens of *P. radioforme* Gerth having rhopaloid as well as nonrhopaloid septa. This species occurs in Timor in the Basleo Formation of Guadalupian age. It closely resembles *P. dzhulfense,* but no detailed comparisons can be made on the basis of our limited material. Gräf (1964) described a species from the Permian of the Abadeh area in central Iran as *P. radiciforme* which may well be conspecific with either *P. dzhulfense* or *P. differentiatum.*

Occurrence. One specimen (MCZ 9404) from Loc. 2, 70 cm above base of Ali Bashi Formation; 1 specimen (MCZ 9405) from Loc. 2, 1 m above base of Ali Bashi Formation; 1 specimen (MCZ 9406) from Loc. 3, 4.5 m above base of Ali Bashi Formation; 3 specimens (KU 73289, 73290, 73292) from Loc. 4, bed 3.

Respository. MCZ 9404 (Pl. 1, figs. 5–7), MCZ 9405 (Pl. 1, figs. 3–4), MCZ 9406 (Pl. 1, figs. 1–2). Unfigured specimens KU 73289, 73290, 73292.

Genus *Ufimia* Stuckenberg, 1895

Type species, *Ufimia carbonaria* Stuckenberg, 1895

Ufimia resembles *Plerophyllum* but differs in that the cardinal septum is short in the adult stage. Some authors, *e.g.*, Schindewolf (1942) and Flügel (1968), consider it to be a subgenus of *Plerophyllum.* Ilina (1965) described two species as *Ufimia elongata* (Gerth) and *U. alternata* (Huang). Both species occur in the Gnishik Formation of Guadalupian age of the Transcaucasus, though not in the Dzhulfa region. The stratigraphic range of the genus is Middle Devonian to Upper Permian and it occurs in Europe, Asia, and Australia (Ilina, 1965: 71).

Ufimia sp.

Plate 2, figures 3, 4, 7, 8

Discussion. Our collections contain four specimens which we assign to *Ufimia*, but which do not warrant a specific assignment. Specimen KU 73282 is a fragment that is 8 mm long and 8.5 mm wide at its proximal end. Most septa taper inwardly and only some are weakly rhopaloid in cross section. The cardinal septum is less than half as long as the alar septa. Specimen no. MCZ 9407 is similar in all respects. The corallum is 1.4 mm long (Pl. 2, fig. 3), and the illustration on Plate 2, figure 4 represents a cross section 10 mm from the tip of this corallum. Here, too, the cardinal septum is a little less than half as long as the alar septa.

There is no doubt that both specimens belong to the same species, and they are probably conspecific with one of the two Guadalupian species described by Ilina (1965) from the Transcaucasus, but on the basis of our limited material we are unable to decide with which.

The type material of *Ufimia elongata*, originally assigned to *Tachylasma* by Grabau (1928: 69), came from cherty limestone of Permian (probably Guadalupian) age in Anhwei Province, eastern China. The specimens from the Transcaucasus and Kuh-e-Ali Bashi may well be conspecific with the Chinese specimens, although in two transverse sections figured by Grabau (1928, pl. 1, figs. 13a, d) some of the major septa, especially the counter-laterals, are more distinctly rhopaloid than in any of the specimens considered here.

Occurrence. 1 specimen (MCZ 9407) from Loc. 2, 7.5 m above base of Ali Bashi Formation (Pl. 2, figs. 3, 4); 1 specimen (KU 73282) from Loc. 2, 4.5 m above base of Ali Bashi Formation (Pl. 2, figs. 7, 8); 1 specimen from Loc. 2, 13.5 m above base of Ali Bashi Formation (KU 73283), 1 specimen (KU 73291) from Loc. 4, bed 3.

Repository. MCZ 9407 (Pl. 2, figs. 3, 4), KU 73282 (Pl. 2, figs. 7, 8). Unfigured specimens, KU 73283, KU 73291.

Genus *Pleramplexus* Schindewolf, 1940

Type species, *Pleramplexus similis* Schindewolf, 1940

The genus *Pleramplexus* has been thoroughly discussed in recent publications by Ilina (1965) and by Flügel (1970). It includes members of the family Plerophyllidae having fully developed major septa in early growth stages only. In the mature stage, the septa are much reduced in size. According to Flügel (1970), the genus is known from the Permian of northern Iran, the Transcaucasus, Timor, Sicily, and perhaps Hungary. In the Transcaucasus and in the Alborz Mountains of Iran, the genus occurs only in rocks of Dzhulfian age.

Pleramplexus leptoconicus (Abich)

Plate 2, figures 1, 2, 5, 6

Clisiophyllum leptoconicum Abich, 1878: 87, pl. 2, figs. 7, 7a.

Pleramplexus leptoconicus (Abich), Flügel, 1968: 289–291, text-fig. 5, pl. 25, fig. 3. (Contains full synonymy.)

Description. Pleramplexus leptoconicus is the predominant species in our coral collections from the Ali Bashi Formation, where it is represented by eight specimens. It has been well described by Heritsch (1937), Ilina (1962, 1965), and by Flügel (1968). On the basis of 28 peels of transverse sections available to us, which measure from 3.9 to 15.0 mm in diameter, the Ali Bashi form agrees in every respect with the Dzhulfian forms described by Ilina and by Flügel. The maximum diameter of any one corallum is 15 mm.

The protosepta are well developed at a diameter of the corallum of about 6 mm

(Pl. 2, fig. 5) when the total number of major septa is about 13. At a diameter of 14 mm (Pl. 2, fig. 6), the number of major septa is 20. These are of subequal length with cardinal, alar, and counter-lateral septa only slightly more emphasized than the other septa. A minor septum is inserted between each two major septa. In another specimen measuring 14 mm in cross section, the number of major septa is 26. The counter-laterals are the longest as the counter septum is very short. From this area, the septa become progressively shorter through the counter-lateral quadrants; the alar septa are slightly longer, and the septa in the alar quadrants are again shorter, and the cardinal septum is no longer, but very slightly thicker, than the septa in the alar quadrants.

In several sections the septa appear slightly wavy as described for this species by Ilina (1962, 1965). In intermediate growth stages, some of the major septa tend to become rhopaloid in transverse section, as is also shown in some specimens illustrated by Ilina (1965), although there is little regularity in the position of the rhopaloid septa (compare Ilina, 1965, pl. 14, fig. 2, and pl. 15, fig. 4b). The same feature was earlier demonstrated by Heritsch (1937, *e.g.*, pl. 2, fig. 10).

Discussion. The specimens from the Ali Bashi Formation agree in every respect with the many specimens of *Pleramplexus leptoconicus* described and illustrated from the Dzhulfian of the Transcaucasus by Heritsch (1937) and by Ilina (1962, 1965), and from the Nesen Formation of the Alborz Mountains by Flügel (1968). In regard to size, they are intermediate between the maximum diameter of 11 mm noted by Flügel and the maximum diameter of 22 mm given by Ilina.

This species seems to be very similar to the type species of *Pleramplexus*, *P. similis* Schindewolf, from the Basleo beds of Timor (see especially Schindewolf, 1942), which seems to differ mainly in having a short cardinal septum. A specimen described under this name by Gräf (1964) from the vicinity of Abadeh is possibly conspecific with *P. leptoconicus*.

Occurrence. 1 specimen (KU 73284) from Loc. 3, 4.5 m above base of Ali Bashi Formation; 1 specimen (KU 73285) from Loc. 3, 7.5 m above base of Ali Bashi Formation; 2 specimens (KU 73293, 73294) from Loc. 4, bed 5; 5 specimens (MCZ 9408; KU 73286, 73287, 73288) from unspecified localities.

Repository. MCZ 9408 (Pl. 2, figs. 1, 2), KU 73288 (Pl. 2, figs. 5, 6). Unfigured specimens KU 73284, 73285, 73286, 73287, 73293, 73294.

Phylum **BRYOZOA**

Class **GYMNOLAEMATA** Busk, 1852

Order *TREPOSTOMATA* Ulrich, 1882

Family STENOPORIDAE Waagen and Wentzel, 1886

Genus and species indeterminate

Plate 2, figure 10

Description. A fragment of an annulated orthocone, probably *Neocycloceras* sp. indet., and probably all phragmocone, is almost completely encrusted by a trepostomatous bryozoan. The specimen was submitted to R. S. Boardman, U. S. National Museum, for examination. He reported that it probably belongs to the family Stenoporidae, but that its generic affinities could not be identified with certainty. He stated (letter to Teichert, 28 May 1971) that the occurrence of a stenoporid of this age was, in itself, of considerable interest. The range of the family Stenoporidae is stated as Silurian to Permian by Bassler (1953: 101).

Discussion. Morozova (*in* Ruzhentsev and Sarycheva, 1965) did not report occurrence of Trepostomata in the equivalents of the Ali Bashi Formation in the Dorasham section or from equivalents of the Julfa beds. Obviously, the Ali Bashi specimen is a very late straggler of the family, and it is hoped that more and better-preserved specimens will be found in the future.

Occurrence. Loc. 3, 4.5 m above base of Ali Bashi Formation.

Repository. MCZ (no number).

Phylum **BRACHIOPODA**

Class **ARTICULATA** Huxley, 1869

Family ATHYRIDIDAE McCoy, 1844

Genus *Araxathyris* Grunt *in* Ruzhentsev and Sarycheva, 1965

Type species, *Spirigera protea* Abich, 1878

Araxathyris araxensis minor Grunt *in* Ruzhentsev and Sarycheva, 1965

Plate 2, figures 11–16

We are indebted to G. A. Cooper (letter to Kummel, 13 February 1970) for the identification of our brachiopod specimens, two of which are illustrated here. *Araxathyris araxensis minor* is the most common form in the "Induan" beds of Soviet Dzhulfa as reported by Ruzhentsev and Sarycheva (1965).

Occurrence. All specimens within 4.5 m from base of Ali Bashi Formation.

Repository. MCZ 9828 (Pl. 2, figs. 11–13), MCZ 9827 (Pl. 2, figs. 14–16). Unfigured specimens MCZ 9829–9833, KU 73315, 73316 (Loc. 3, at 4.5 m), KU 73321–73329 (Loc. 4, bed 2), KU 73317–73320 (Loc. 4, bed 3).

Phylum **MOLLUSCA**

Class **BIVALVIA** Linné, 1758

Subclass **PALAEOTAXODONTA** Korobkov, 1954

Family NUCULANIDAE Adam and Adam, 1958

Genus *Phestia* Chernyshev, 1951

Type species, *Leda inflatiformis* Chernyshev, 1939

Phestia sp. indet.

Plate 2, figure 9

Kummel and Teichert are indebted to N. D. Newell (letter to Kummel, 16 December 1969) for the identification of the only bivalve collected by them from the Ali Bashi Formation. No bivalves were reported from the same stratigraphic interval in Soviet Dzhulfa (Ruzhentsev and Sarycheva, 1965). The presence of the genus *Phestia* adds little to determination of the age of the Ali Bashi Formation as it ranges from Devonian through Lower Triassic.

Occurrence. Float.

Respository. MCZ 18005.

Class **CEPHALOPODA** Cuvier, 1798

Order *ORTHOCERIDA* Kuhn, 1940

Included in our collections from the Ali Bashi Formation are 13 conch fragments of orthocerids, which we are assigning to three genera.

Superfamily PSEUDORTHOCERATACEAE Flower and Caster, 1935

Family PSEUDORTHOCERATIDAE Flower and Caster, 1935

We here follow the systematic treatment suggested by Sweet (*in* Teichert *et al.*, 1964). Barskov (1963) proposed to raise the superfamily Pseudorthocerataceae to the rank of an order that he named Pseudorthoceratida and proposed to place it in the superorder Actinoceratoidea. However, it seems to us that the structures of both endosiphuncular and cameral deposits of the pseudorthoceratids are significantly different from those of actinocerids, although some pseudorthoceratid genera are considered to be homeomorphs of actinocerids (Flower, 1957).

Genus *Dolorthoceras* Miller, 1931

Type species, *Dolorthoceras circulare* Miller, 1931

?*Dolorthoceras* sp. indet.

Plate 9, figure 6

Description. One fragment of an internal mold of a phragmocone, 39 mm long, consisting of 16 camerae; cross section somewhat elliptical, longest diameter of conch increasing from 6 mm at adapical end to 11.5 mm at the adoral end. It is not possible to measure accurately the shorter conch diameter because the specimen is attached to the rock with one of its broad sides. Sutures form very shallow lobes across the exposed broad side of specimen. In the first of the camerae, cameral deposits are present, but their structure cannot be determined. The siphuncle seems to be in a near-central position.

Remarks. Up till now, no representatives of *Dolorthoceras* seem to have been reported from rocks of Late Permian age.

The stratigraphic range of the genus is given by Sweet (*in* Teichert *et al.,* 1964) as Lower Devonian to Lower Permian, by Shimanskiy (1968) as Ordovician to Lower Permian. Because of lack of detailed knowledge of the exact shape of the cross section, exact position of siphuncle, and structure of cameral deposits, the present specimen can be assigned to *Dolorthoceras* only with reservation. A closely similar genus, *Shikhanoceras* Shimanskiy (1954), is so far known only from rocks of Early Permian (Sakmarian and Artinskian) age and is distinguished from *Dolorthoceras* mainly by having a bulbous protoconch. Since this stage cannot be observed in the Ali Bashi specimen, no firm decision about its affinity to one genus or the other can be made. As far as we have been able to ascertain, no similar form has been reported from Upper Permian beds anywhere.

Occurrence. The figured specimen is from float at an undetermined locality and horizon; a second specimen, poorly preserved and unfigured, came from Loc. 2, 13.5 m above base of Ali Bashi Formation.

Repository. MCZ 9723 (Pl. 9, fig. 6). Unfigured specimen KU 73299.

Family and Superfamily uncertain

Genus *Neocycloceras* Flower and Caster, 1935

Type species, *Neocycloceras obliquum* Flower and Caster, 1935

Neocycloceras sp. indet.

Plate 9, figure 7

Remarks. In our collections, *Neocycloceras* is represented by five fragmentary specimens, all of them poorly preserved, ranging in length from 12 to 48 mm. With one exception the specimens are badly squashed, but in some fragments of phragmocones it can be seen quite clearly that the annulations are oblique with respect to sutures. The largest specimen (Pl. 9, fig. 7) is the adoral part of a phragmocone, 16 mm long, consisting of five fragmentary camerae, and an incomplete living chamber, 32 mm long. Although the specimen is distorted, it can be clearly seen that the annulations cross the sutures at a low angle.

All five specimens can be matched with specimens from the underlying Julfa beds that we have described as *Neocycloceras* cf. *N. obliqueannulatum* (Waagen) (Teichert and Kummel, 1973).

From the equivalents of the Ali Bashi Formation (lower "Induan") in the Armenian Dzhulfa area, Shimanskiy (*in* Ruzhentsev and Sarycheva, 1965) recorded six specimens of "*?Neocycloceras* sp." but did not illustrate any.

Occurrence. Loc. 3 at 2.10 m (KU 73295), 3 m (KU 73297, 73298), and 4.5 m (KU 73296) above base of Ali Bashi Formation, and in float (MCZ 9724).

Repository. MCZ 9724 (Pl. 9, fig. 7). Unfigured specimens KU 73295–73298.

Genus *Lopingoceras* Shimanskiy, *in* Ruzhentsev, 1962

Type species, *Lopingoceras lopingense* Shimanskiy *in* Ruzhentev, 1962.

For diagnosis and discussion of this genus see Teichert and Kummel (1973).

Lopingoceras sp.

Plate 9, figure 8

Remarks. In our collection the genus *Lopingoceras* is represented by six poorly preserved fragments of phragmocones, ranging in length from 10 to 24 mm. Although all specimens are squashed, it can be clearly seen that the annulations of the shell are straight and transverse, and in a few places it can be established that one annulation occurs per camera, situated between two sutures. The specimens are comparable to similarly poorly preserved specimens from the underlying Julfa beds that we have identified as *Lopingoceras lopingense* (Stoyanow) (Teichert and Kummel, 1973).

Shimanskiy (*in* Ruzhentsev and Sarycheva, 1965) did not list *Lopingoceras* from equivalents of the Ali Bashi Formation in the Armenian Dzhulfa area.

Occurrence. Loc. 2, 7.5 m; Loc. 3, 1.5

and 4.5 m above base of Ali Bashi Formation; Loc. 4, bed 3; and float.

Repository. MCZ 9779 (Pl. 9, fig. 8). Unfigured specimens MCZ 9750, KU 73300, 73301, 73302.

Order *NAUTILIDA* Agassiz, 1847

Superfamily TAINOCERATACEAE Hyatt, 1883

Family TAINOCERATIDAE Hyatt, 1883

Genus *Tainoceras* Hyatt, 1883

Type species, *Nautilus quadrangulus* McChesney, 1860

Tainoceras sp. indet.

Plate 9, figure 3

Discussion. A specimen consisting of half a volution of a phragmocone can readily be identified as an indeterminate species of the genus *Tainoceras.* The most characteristic features are the nodes on the ventral shoulders and the double row of nodes on the midline of the venter. *Nautilus dorsoplicatus* Abich (1878: 23) is clearly a species of the genus *Tainoceras.* The description and illustration of this species, however, are not sufficient for comparison with our specimen.

Shimanskiy (*in* Ruzhentsev and Sarycheva, 1965) records three specimens of *Tainoceras dorsoplicatum* (Abich) from the *Araxoceras* Zone, two specimens specifically indeterminate from the *Phisonites* Zone, and two specimens specifically indeterminate from the Ali Bashi Formation. Shimanskiy did not describe his specimens but illustrated some of them. The specimen he assigned to *Tainoceras* sp. 2 (ex. gr. *changlingpuense* Chao) is probably conspecific with the specimen recorded here.

Species of the genus *Tainoceras* are fairly common in mid-Pennsylvanian through Permian formations. The only Triassic form assigned to the genus is *Trematodiscus klipsteini* Mojsisovics (1882) from the Karnian of the Alps.

Occurrence. Float, Loc. 2, 4.5 m above base of Ali Bashi Formation.

Repository. MCZ 9721 (Pl. 9, fig. 3).

Genus *Metacoceras* Hyatt, 1883

Type species, *Nautilus (Discus) sangamonensis* Meek and Worthen, 1861

Metacoceras sp. indet.

Discussion. This genus is recognized from a fragmentary phragmocone representing a quarter volution of a conch. It has a broad, low, arched venter with prominent nodes on the ventral shoulders.

Shimanskiy (*in* Ruzhentsev and Sarycheva, 1965) recorded *Metacoceras dorsoarmatum* from the *Araxoceras* Zone of the Dzhulfian, and indeterminate forms from the *Vedioceras* and *Phisonites* zones.

Occurrence. Float from Ali Bashi Formation.

Repository. MCZ 9745.

Genus *Pleuronautilus* Mojsisovics, 1882

Type species, *Pleuronautilus trinodosus* Mojsisovics, 1902

The genus *Pleuronautilus* encompasses evolute nautiloids having dorsoventral and lateral whorl cross sections of approximately equal dimensions and with lateral ribs. The genus is quite common in Triassic formations and is represented by approximately 35 species. The type species is from Anisian strata in the Alps. A comprehensive review of the genus by Kummel (1953) demonstrated that it is almost equally common in Permian formations.

Shimanskiy (*in* Ruzhentsev and Sarycheva, 1965) recognized five species of *Pleuronautilus* from Dzhulfian strata plus two forms of uncertain specific identity. The great majority of the species and specimens came from the lowest Dzhulfian horizon, the *Araxoceras* Zone. The highest Permian horizon recognized by Ruzhentsev and Sarycheva (1965), the *Phisonites* Zone, yielded only one specimen, which Shimanskiy compared with *Pleuronautilus dieneri* Krafft, and two specimens that he questionably identified as *Pleuronautilus.* Their collections contained only one specimen from the lower "Induan" that Shimanskiy assigned with question to *Pleuronautilus.* Species of *Pleuronautilus* have, for the most part, been narrowly conceived, and this is especially true for those recognized from the Dzhulfa region. It needs to be emphasized also that the preservation of these specimens leaves much to be desired.

Pleuronautilus sp. indet.

Plate 9, figures 1, 2

Discussion. Two specimens are in our collection. One (Pl. 9, fig. 1) consists entirely of a body chamber with a whorl height of about 35 mm and a whorl width of about 42 mm. The lateral areas bear prominent radial ribs. The other specimen (Pl. 9, fig. 2) consists of a nearly complete volution of phragmocone. The adoral 2 cm appear to be part of the body chamber. The specimen has a diameter of 68 mm, a whorl height of 23 mm, a whorl width of 26 mm, and an umbilical diameter of 27 mm. No shell is preserved.

These specimens compare well with most of the previously described species from the Dzhulfa region. We suspect that at most probably no more than one or, possibly, two species are present in these faunas. Better collections are needed to properly appraise their affinities.

Occurrence. Loc. 1, bed 10, 5 m above base of formation (MCZ 9719), Loc. 4, bed 5 (MCZ 9720).

Repository. MCZ 9719 (Pl. 9, fig. 1), MCZ 9720 (Pl. 9, fig. 2).

Family KONINCKIOCERATIDAE Hyatt *in* Zittel, 1900

Genus *Temnocheilus* McCoy, 1844

Type species, *Nautilus (Temnocheilus) coronatus* McCoy, 1844

Temnocheilus sp. indet.

Plate 9, figures 4, 5

Discussion. A fragmentary phragmocone can be assigned to *Temnocheilus.* Its whorls are depressed, lateral areas convex, and they converge toward the dorsum. The ventral shoulders bear prominent nodes spaced about one cm apart. A small portion of an inner whorl, with a height of 12 mm, is preserved, and, in this, the whorl section is more rounded in cross section and the whorl sides only slightly convergent.

Kummel (1953) assigned to this genus 23 species of Pennsylvanian and Permian age. Our specimen is too incomplete for meaningful comparison with other recorded species. *Temnocheilus* was not recorded by Shimanskiy (*in* Ruzhentsev and Sarycheva, 1965) from any part of the section in Soviet Dzhulfa.

Occurrence. Loc. 3, float from 3 m above base of Ali Bashi Formation.

Repository. MCZ 9722 (Pl. 9, figs. 4, 5).

Superfamily TRIGONOCERATACEAE Hyatt, 1884

Family GRYPOCERATIDAE Hyatt *in* Zittel, 1900

Genus *Domatoceras* Hyatt, 1891

Type species, *Domatoceras umbilicatum* Hyatt, 1891

Domatoceras sp. indet.

Plate 8, figures 10, 11

Discussion. Our collections contain two fragmentary specimens that clearly belong to a species of *Domatoceras.* One specimen (Pl. 8, figs. 10, 11) is a phragmocone. The other consists of half a volution of a conch that appears to be mainly part of a body chamber.

Shimanskiy (*in* Ruzhentsev and Sarycheva, 1965) recorded five species from the *Araxoceras* Zone of Soviet Dzhulfa. In the overlying *Vedioceras* Zone, from which he had far fewer specimens, he records only two forms, not specifically identifiable. From equivalents of the Ali Bashi Formation, Shimanskiy had only one small and fragmentary specimen, which he named *Domatoceras* sp. 2 and which he figured (pl. 16, fig. 3) but did not describe. Published data are insufficient to establish whether it is conspecific with the specimens recorded here.

Occurrence. Float from Loc. 4, bed 3. Ali Bashi Formation.

Repository. MCZ 9718 (Pl. 8, figs. 10, 11), KU 73330.

Superfamily CLYDONAUTILACEAE Hyatt *in* Zittel, 1900

Family LIROCERATIDAE Miller and Youngquist, 1949

Genus *Liroceras* Teichert, 1940

Type species, *Coloceras liratum* Girty, 1911

Liroceras sp. indet.

Plate 8, figure 9

Discussion. Two specimens in our collections are readily assignable to *Liroceras*, whose principal features are the smooth, extremely involute, globular conch and simple sutures. Both specimens are somewhat deformed: one (Pl. 8, fig. 9) has a diameter of approximately 64 mm, the other, of about 95 mm. These specimens are too incomplete to allow a specific identification or meaningful comparison with other species of the genus. However, there is no question as to the generic assignment.

Shimanskiy (*in* Ruzhentsev and Sarycheva, 1965) did not record *Liroceras* from any part of the section near Soviet Dzhulfa.

Occurrence. Loc. 1, bed 1 (MCZ 9717), and float from Ali Bashi Formation (MCZ 9781).

Repository. MCZ 9717 (Pl. 8, fig. 9). Unfigured specimen MCZ 9781.

Genus *Paranautilus* Mojsisovics, 1902

Type species, *Nautilus simonyi* Hauer, 1850

Paranautilus sp. indet.

Plate 9, figures 9, 10

Discussion. A single specimen consisting of half a volution of a phragmocone belongs to *Paranautilus*. The conch is smooth, slightly compressed, and has a well-rounded venter.

Paranautilus ranges through the Permian and Triassic, but no Lower Triassic (Scythian)species are known. Shimanskiy (*in* Ruzhentsev and Sarycheva, 1965) listed five specimens of ?*Paranautilus* sp., as coming from horizons above the *Phisonites* Zone. However, he neither described nor illustrated them.

Occurrence. Specimen collected in place at Loc. 4, 1 m below the top of Ali Bashi Formation.

Repository. MCZ 9727 (Pl. 9, figs. 9, 10).

Subclass **AMMONOIDEA** Agassiz, 1847

Family PARAGASTRIOCERATIDAE Ruzhentsev, 1951

Genus *Pseudogastrioceras* Spath, 1930

Type species, *Goniatites abichianus* von Möller (as figured *in* Arthaber, 1900, pl. 18, figs. 5a–d)

Pseudogastrioceras abichianum (von Möller)

Plate 4, figures 2–4; Text-figures 11A, B

Goniatites striatus Martin, –Abich, 1878: 9, pl. 1, figs. 1, 1a, 2, 2a, 3; pl. 2, figs. 2, 2a.

Goniatites Abichianus von Möller, 1879: 239.

Gastrioceras Abichianum, –Karpinsky, 1890: 89; Arthaber, *in* Frech and Arthaber, 1900: 219, pl. 18, figs. 5a–d; Stoyanow, 1910: 103, 105; Diener, 1921: 14.

Pseudogastrioceras abichianum, Spath, 1930: 8; Miller and Furnish, 1940: 91; Miller *in* King *et al.*, 1944: 88; Glenister and Furnish, 1961: 718; Ruzhentsev and Sarycheva, 1965, pl. 17, fig. 2; Furnish, 1966: 279; Taraz, 1969: 691.

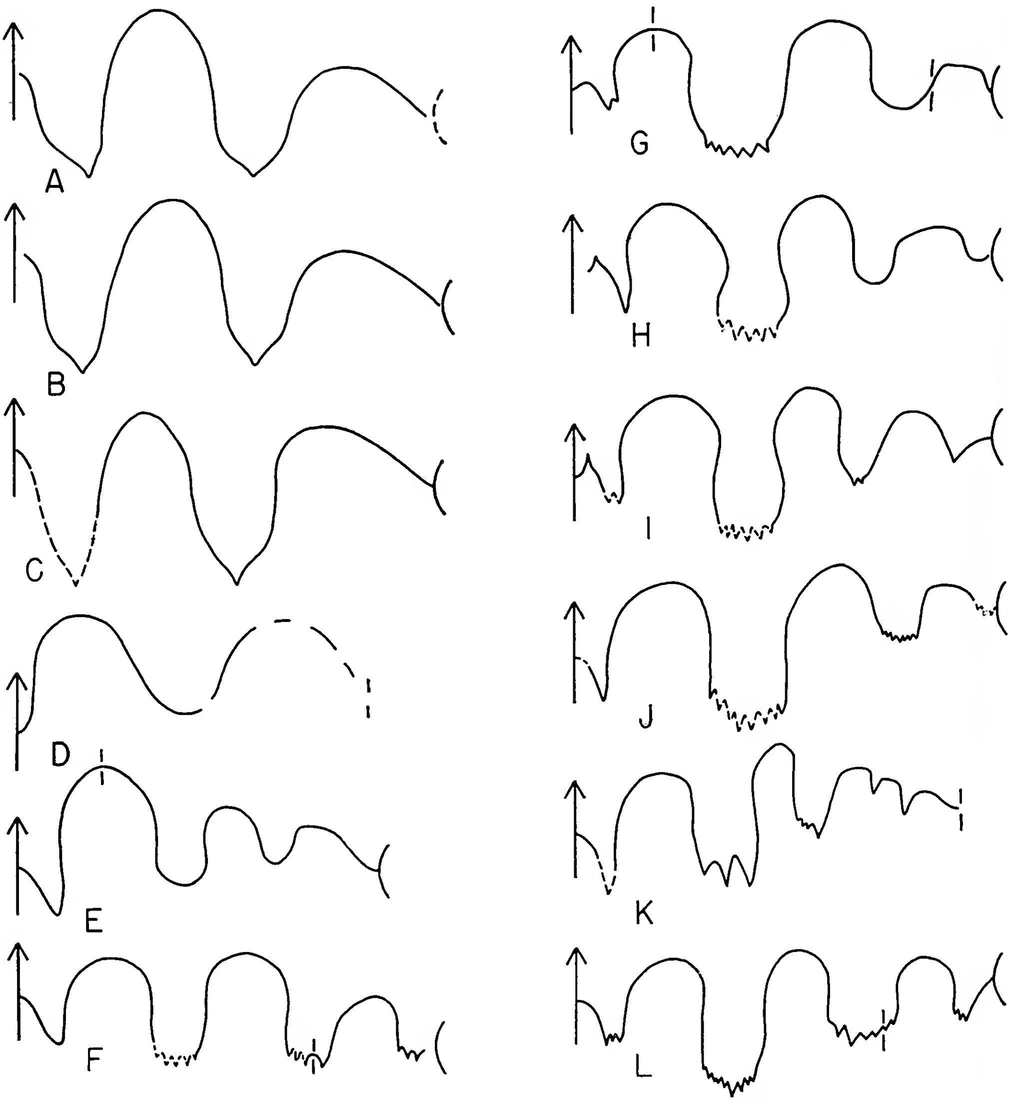
Discussion. Our collections from the Ali Bashi Formation have yielded 12, mostly fragmentary, specimens of *Pseudogastrioceras* from float. The stratigraphically highest specimen comes from a bed 7.5 m above the base of the formation.

Measurements (in millimeters) of three of the most completely preserved specimens are as follows:

	Diameter	*Width*	*Whorl height*	*Umbilical diameter*
Pl. 4, fig. 2	73.0?	?	39.0?	8.5?
Pl. 4, figs. 3, 4	33.8	11.5?	19.6	4.5?
MCZ 9710	21.1	9.1	13.5	1.8

The largest specimen in the collection is a fragment of a phragmocone from which it can be estimated that the complete specimen had a diameter of at least 100 mm. This specimen shows the striations well preserved in the ventral region. The sutures of two of our specimens are shown in Text–figures 11A, B.

The genus *Pseudogastrioceras* has been exhaustively discussed by Miller and Furnish (1940), Miller (*in* King et al., 1944), Glenister and Furnish (1961), and Furnish



Text-figure 11. Diagrammatic representation of the suture of ammonoids, all from the Ali Bashi Formation, except D. A, *Pseudogastrioceras abichianum* (von Möller) at a diameter of approximately 25 mm, MCZ 9692; B, *Pseudogastrioceras abichianum,* at a diameter of approximately 18 mm, MCZ 9744; C, *Strigogoniatites* sp. indet., at a diameter of 26 mm, MCZ 9695; D, *Neoaganides* n. sp., from Dzhulfian beds, at a diameter of 20 mm, MCZ 9782; E, *"Pleuronodoceras"* sp. indet., at a diameter 26 mm, MCZ 9693; F, *Phisonites triangulus* Shevyrev, at a whorl height of 17 mm, MCZ 9711; G, *Xenodiscus dorashamensis* Shevyrev, at a whorl height of 6 mm, MCZ 9687; H, *Iranites transcaucasius,* at a diameter of 20 mm, MCZ 9670; I, *Shevyrevites shevyrevi n.g.,* n. sp., at a diameter of 23 mm, MCZ 9680; J, *Shevyrevites shevyrevi* n.g., n.sp., at a whorl height of 11 mm, MCZ 9679; K, *Urartoceras* sp. indet., at a diameter of 25 mm, MCZ 9683; L, *Phisonites triangulus* Shevyrev, at a whorl height of 21 mm, MCZ 9712.

(1966). It is widely distributed in Permian strata throughout most of the world. The specimens in our collections add nothing to the understanding of the morphology of *P. abichianum,* but the numbers of specimens clearly show that the species is more abundant in the Ali Bashi Formation than was previously believed.

Pseudogastrioceras is extremely well represented in the Julfa beds. In the Dzhulfa sections studied by Ruzhentsev and Sarycheva (1965), this species is by far the most common one in the *Araxoceras* Zone. It is likewise predominant, but less so, in the overlying *Vedioceras* Zone; and it is the second most common species in the *Phisonites* Zone. Above this, Ruzhentsev and Shevyrev (*in* Ruzhentsev and Sarycheva, 1965) recorded only a single specimen from the *Bernhardites* Zone.

Occurrence. Ali Bashi Formation, Loc. 2, 90 cm and 4.5 m above base and Loc. 3, 4.5 m and 7.5 m above base (MCZ 9698); Loc. 4, float (MCZ 9692); Loc. 4, KU 73311–73314; float, no locality (MCZ 9691, 9744).

Repository. MCZ 9691 (Pl. 4, fig. 2), MCZ 9692 (Pl. 4, figs. 3, 4), suture specimens MCZ 9744, 9692 (Text–figs. 11A, B). Unfigured specimens MCZ 9698, KU 73311–73314.

Genus *Strigogoniatites* Spath, 1934
[= *Grabauites* Sun, 1947]

Type species, *Glyphioceras angulatum* Haniel, 1915: 51, text-figs. 11, 12

Strigogoniatites sp. indet.

Plate 4, figures 9–12; Text-figure 11c

Discussion. Three specimens are definitely assignable to *Strigogoniatites* but are not sufficiently complete to allow specific determination. One of them (Pl. 4, fig. 9) is a portion of phragmocone. The whorl is compressed, having converging flanks and an acutely rounded venter. Between the venter and the beginning of the first lateral saddle is a series of narrow strigations, the exact number of which cannot be determined because of poor preservation. Another specimen (Pl. 4, fig. 12) is a fragment similarly preserved but consisting of body chamber only, as no suture is visible. The whole section, venter, and strigations are like those of the first-mentioned specimen.

The third specimen is a fairly well-preserved phragmocone of 27 mm diameter. The adoral whorl has a width of 9.1 mm, a height of 16.6 mm, and an umbilical diameter of 1.5 mm. Its whorl section is compressed with flanks that converge markedly to form an acute venter. The umbilical shoulders are sharply rounded and the umbilical walls steep. Six narrow strigations are seen between the venter and approximately the mid-part of the first lateral lobe. The suture is shown in Text–figure 11C.

Strigogoniatites appears to be a rare form that ranges through much of the Permian. Most authors who have studied this genus have emphaszed its gradational character to *Pseudogastrioceras*. Only six species have been assigned to it. The type species, *Glyphioceras angulatum* Haniel (1915), is from an unknown horizon and locality in Timor. Haniel (1915: 51) thought it probably came from Noil Boewan, Timor. Smith (1927: 28) and Spath (1934: 15) expressed the opinion that the specimen was probably Early Permian in age. Miller and Furnish (1940: 94) were inclined to assign a Late (?) Permian age to the specimen because the Noil Boewan region has yielded a Basleo fauna, and their American species, *Strigogoniatites fountaini*, occurs in the Upper Permian Lamar Limestone of Texas.

Chao (1965) has listed two species of *Strigogoniatites* of Early Permian age from the "Kufeng" siliceous shale in the Liukiang district, Kwangsi, China. One of these, *S. liuchowensis* (*nom. nud.*), has a more inflated conch than the forms described here, and the acute venter does not appear until the conch reaches a diameter of approximately 40 mm. The other species, *S. nodosus* (*nom. nud.*), is very similar except for part of the ornamentation. *Gastrioceras* (*Girtyites*) *liui* Grabau (1924: 478) from the Paoan shale of Hupeh, China, is most probably a representative of *Strigogoniatites* (Spath, 1934: 15). This species, based on a crushed specimen, was made the type of the genus *Grabauites* by Sun (1947).

The North American species, *Strigogoniatites fountaini*, from the Lamar Limestone of West Texas was based on three incomplete specimens (Miller and Furnish, 1940). One of them, with a diameter of 28 mm, has a rounded venter. A fragment of a phragmocone, very similar to the specimens here illustrated (Pl. 4, figs. 9, 12), is part of a specimen that probably was at least 100 mm in diameter. In this specimen the venter is described as subangular. *Strigogoniatites kingi* Miller (*in* King *et al.*, 1944: 92) is a more inflated form, in which angularity of the venter does not appear until a diameter of approximately 40 mm. In addition, strigations entirely cover the lateral areas.

It needs to be emphasized that the six known species of *Strigogoniatites* have been established on the basis of very few specimens; in fact, three of the species were established on the basis of a single specimen each. As far as one may judge from available data, angularity of the venter develops at a progressively earlier stage through Permian time. The small complete specimen recorded here (Pl. 4, figs. 10, 11) has an angular venter at a diameter of 18 mm. This is the smallest diameter at which the appearance of this feature has been noted so far.

Shimanskiy (*in* Ruzhentsev and Sarycheva, 1965) did not record *Strigogoniatites* from anywhere in the Soviet Dzhulfa area.

Occurrence. Float from Ali Bashi Formation; specimen of Plate 4, figure 9, from Loc. 2, 2.1 m above base; that of Plate 4, figure 12, from Loc. 3, 4.5 m above base; and that of Plate 4, figures 10, 11, from Loc. 1, 3.5 m above base of the formation.

Repository. MCZ 9694 (Pl. 4, fig. 9), MCZ 9695 (Pl. 4, figs. 10, 11), MCZ 9696 (Pl. 4, fig. 12).

Family Popanoceratidae Hyatt, 1900

Genus *Propopanoceras* Tumanskaya, 1938

Type species, *Popanoceras lahuseni* Karpinsky, 1889: 67, pl. 5, figs. 1–3

?*Propopanoceras* sp. indet.

Plate 4, figure 1

Discussion. Our collections contain a crushed specimen in which no trace of a suture is preserved. The undistorted shell was involute with a compressed whorl section and a rounded venter. The greater part of the outer half of the whorl sides bears prominent ribs that increase in size toward the ventral shoulders.

This specimen is quite similar to *Propopanoceras kweichowense* Chao (*nom. nud.*, 1965) from the Chihsia Formation (Waitoushen shale), east of Maokou, Linchi district, Kweichow Province, China, and is considered to be of Lower Permian age. The only other species of this genus are from strata of Sakmarian age on the western slope of the Urals (Chao, 1965).

Shimanskiy (*in* Ruzhentsev and Sarycheva, 1965) did not record *Propopanoceras* from the Soviet Dzhulfa area.

Occurrence. Loc. 4, float from undetermined horizon in Ali Bashi Formation.

Repository. MCZ 9690 (Pl. 4, fig. 1).

Family PSEUDOHALORITIDAE Ruzhentsev, 1957

Genus *Neoaganides* Plummer and Scott, 1937

Type species, *N. grahamensis* Plummer and Scott, 1937: 350, pl. 40, figs. 4–9; text-fig. 72

Neoaganides n. sp.

Plate, 4, figures, 5, 6; Text-figure 11D

Discussion. We are indebted for the generic identification of this form to W.M. Furnish and B.F. Glenister of the University of Iowa. The single small specimen available is tightly involute, slightly compressed, and smooth. The ammonoids we collected from the underlying Dzhulfian strata are being studied by Furnish and Glenister. This collection contains a specimen of somewhat larger dimensions that will be described as a new species of *Neoaganides*. In addition, Furnish and Glenister believe the small specimen recorded here is conspecific with the Dzhulfian specimen. Our specimen does not lend itself to the drawing of a suture but that of the Dzhulfian specimen is shown in Text–figure 11D.

It now appears that this genus is very long ranging and of wide geographic extent. It is very common in Upper Pennsylvanian strata of Kansas, Oklahoma, and Texas. Furnish and Glenister (personal communication) have in preparation a study on the Permian representatives of this genus. They advise us that they have specimens from West Texas, Sicily, Arabia, the Alborz Mountains of Iran, and Hunan in China. In addition they have our specimen from the Julfa beds of northwest Iran. In regard to the stratigraphic implication of *Neoaganides*, Furnish and Glenister (written communication, letter of February, 1970) wrote us as follows: "The forms with simple suture, *Neoaganides*, are regarded as secondarily primitive. They have no value of exact age determination and are not even specifically identifiable unless most characters can be observed."

Occurrence. Float from approximately middle of Ali Bashi Formation.

Repository. MCZ 9692 (Pl. 4, figs. 5, 6).

Family "PLEURONODOCERATIDAE" Chao, 1965 (*nom. nud.*)

Genus "*Pleuronodoceras*"[1] Chao, 1965 (*nom. nud.*)

Illustrated specimen, "*Pleuronodoceras dushanense*" Chao, 1965, text-fig. 3d, pl. 2, figs. 23, 24 (*nom. nud.*)

"*Pleuronodoceras*" sp. indet.

Plate 4, figures 7, 8; Text-figure 11E

Discussion. A single specimen in an imperfect state of preservation can be assigned to "*Pleuronodoceras.*" It has a diameter of 30.5 mm, a whorl width of 8.9 mm, a height of 11.7 mm, and an umbilical diameter of 11.3 mm. The whorls are subquadrate in cross section, flanks flattened, converging very slightly toward the venter. The umbilical and ventral shoulders are rounded and the venter is marked by a prominent keel. The lateral areas of the whorls have slightly forward-projecting ribs that curve more distinctly forward on the ventral shoulder. The adoral half of the last volution has ten such ribs. The suture is illustrated on Text–figure 11E. The absence of denticulations of the lobes is believed to be entirely due to weathering.

The only specimen previously assigned to "*Pleuronodoceras*" is "*P. dushanense*" Chao (1965, pl. 2, figs. 23, 24) from the Changhsing limestone, Tushan, Kwangteh District, Anhwei Province, China. The illustrated specimen is approximately twice the size of the specimen recorded here, but in all other morphological features such as whorl shape, size of umbilicus, ornamentation, the Ali Bashi specimen appears to be identical with it. The sutures are likewise very similar.

Chao (1965) recorded this genus from a number of localities in eastern China where it is associated with *Pseudogastrioceras*, "*Pseudotirolites*," "*Pachydiscoceras*," and other ammonoid genera, and occurs at a horizon regarded by him as youngest Permian.

Shimanskiy (*in* Ruzhentsev and Sarycheva, 1965) did not record similar forms from the Soviet Dzhulfa area.

Occurrence. Float from undetermined horizon in Ali Bashi Formation.

Repository. MCZ 9693 (Pl. 4, figs. 7, 8).

Family "PSEUDOTIROLITIDAE" Chao, 1965 (*nom. nud.*)

Genus "*Pseudotirolites*" Chao, 1965 (*nom. nud.*)

Illustrated specimen, "*Pseudotirolites orientalis*" Chao, 1965, pl. 2, figs. 12, 13 (*nom. nud.*)

"*Pseudotirolites*" sp. indet.

Plate 5, figures 16–19

Discussion. Two fragmentary specimens, each consisting of half a volution of a body chamber, appear to belong to this genus. The whorls are depressed and have a broad venter marked by an acute crest. The lateral areas bear prominent ribs that increase in size toward the ventral shoulders and are slightly projected forward.

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[1] In an important paper published in 1965, Chao Kingkoo created a number of new names for what were intended to be new taxa on the family, genus, and species level. Although these new forms were well illustrated, they were not formally described and their names are therefore to be regarded as *nomina nuda*. Our use of them here for purposes of morphological comparisons is not to be construed as an attempt to validate these names.

Chao (1965) illustrated two "species" of his new genus; both come from the Talung Formation of China from his youngest Permian horizon. The associated fauna contains *Stacheoceras, Pseudogastrioceras, "Pleuronodoceras," "Pseudostephanites,"* and other genera. No similar forms seem to be known in the Soviet Dzhulfa area.

Occurrence. Float from undetermined horizon in Ali Bashi Formation. Loc. 2 (MCZ 9710), Loc. 4 (MCZ 9709).

Repository. MCZ 9709 (Pl. 5, figs. 16, 17), MCZ 9710 (Pl. 5, figs. 18, 19).

Genus *"Pseudostephanites"* Chao, 1965 (*nom. nud.*)

Illustrated specimen, *"Pseudostephanites costatus"* Chao, 1965, pl. 2, figs. 14–16 (*nom. nud.*)

"Pseudostephanites" sp. indet.

Plate 4, figure 13

Discussion. A single, small, incomplete specimen can be assigned to *"Pseudostephanites."* The whorls are depressed and have a broadly rounded venter. The rounded lateral areas bear large nodes or ribs that occupy the whole area. The specimen has an approximate diameter of 25 mm with an umbilical width of 9 mm. The sutures are not preserved.

The distinctive large lateral ribs are the primary basis for the taxonomic assignment of this specimen. The specimen of *"Pseudostephanites"* illustrated by Chao is from the Talung Formation, Chaotian, Kwangywan District, Szechwan Province, China, where it is found in association with *Stacheoceras, Pseudogastrioceras, "Pseudotirolites," "Tapashanites," "Pleuronodoceras,"* and other genera. This assemblage characterizes the youngest Permian horizon recognized by Chao (1965) in South China.

Occurrence. Float from undetermined horizon in Ali Bashi Formation.

Repository. MCZ 9697 (Pl. 4, fig. 13).

Family XENODISCIDAE Frech, 1902

Genus *Phisonites* Shevyrev *in* Ruzhentsev and Sarycheva, 1965

Type species, *Phisonites triangulus* Shevyrev *in* Ruzhentsev and Sarycheva, 1965

Phisonites triangulus Shevyrev

Plate 8, figures 1–8; Text-figure 11L

Phisonites triangulus Shevyrev *in* Ruzhentsev and Sarycheva, 1965: 168–169, pl. 21, figs. 4, 5.

Discussion. Our collections contain 20 specimens of *Phisonites triangulus* of which most are fragments, and many are crushed. Shevyrev states that his own collections from Soviet Dzhulfa contained only 12 specimens from a single locality (Dorasham 2) and that these also were mainly fragments. The new material from Kuh-e-Ali Bashi does add, however, to our knowledge of this unusual ammonoid.

The smallest specimen in this collection has a diameter of 32 mm and the flared umbilical shoulder is quite prominent, but the whorl cross section is not as markedly triangular as it is in later growth stages (Pl. 8, fig. 5). The inner whorls are not preserved in any of our specimens, and the same appears to be true of Shevyrev's specimens. The largest specimen in our collection has a diameter of approximately 90 mm; its suture is shown in Text-figure 11L.

Occurrence. Float from lowest part of Ali Bashi Formation.

Repository. MCZ 9711 (Pl. 8, figs. 1, 2), MCZ 9712 (Pl. 8, figs. 3, 4), MCZ 9713 (Pl. 8, fig. 5), MCZ 9714 (Pl. 8, fig. 6), MCZ 9715 (Pl. 8, figs. 7, 8), unfigured specimens MCZ 9716, KU 73365–73380.

Genus *Xenodiscus* Waagen, 1879

[= *Xenaspis* Waagen, 1895]

Type species, *Xenodiscus plicatus* Waagen, 1879: 34, pl. 2, fig. 1

Xenodiscus dorashamensis Shevyrev

Plate 3, figures 9–17; Text-figure 11G

Xenodiscus dorashamensis Shevyrev *in* Ruzhentsev and Sarycheva, 1965: 166, pl. 21, figs. 2, 3.

Xenaspis araxensis Shevyrev *in* Ruzhentsev and Sarycheva, 1965: 166, pl. 21, fig. 1.

Discussion. Our collections contain 12 specimens of *Xenodiscus dorashamensis* in a moderately good to poor state of preservation. The largest specimen has a diameter of 49 mm, the smallest a diameter of 18.5 mm. Some of the specimens are essentially smooth, except for traces of growth lines; others have radial ribs. There is much variation in the prominence of the ribs. The morphology of our specimens is identical with that described and illustrated by Shevyrev. The suture of one specimen is illustrated in Text–figure 11G.

No general consensus exists as to whether *Xenodiscus* and *Xenaspis* are synonyms. The type species of *Xenodiscus* is *X. plicatus* Waagen (1879), that of *Xenaspis* Waagen (1895) is *Ceratites carbonarius* Waagen (1872), both from the Chhidru Formation of the Salt Range. These two genera were differentiated on the basis of ornamentation, *plicatus* having radial ribs, *carbonarius* being essentially smooth. Waagen had only one specimen of *X. plicatus* and four of *X. carbonarius*, none of which is well preserved, a fact not noticeable in the fine line drawings Waagen reproduced in his monograph. Photographs of these specimens have been published by Kummel (1970) and illustrations of topotype specimens were reproduced by Schindewolf (1954). Schindewolf (1954) presented convincing arguments for placing *Xenaspis* in synonymy of *Xenodiscus*, and this is the procedure followed here, as it was by Teichert (1966) and Kummel (1970). At the same time, Furnish (1966), following "convention," retained both genera, as did Shevyrev (*in* Ruzhentsev and Sarycheva, 1965).

Occurrence. Float from Ali Bashi Formation, all specimens collected from within 1.5 m of the base of the Formation.

Repository. MCZ 9684 (Pl. 3, figs. 9, 10), MCZ 9685 (Pl. 3, figs. 11, 12), MCZ 9686 (Pl. 3, figs. 13, 14), MCZ 9687 (Pl. 3, fig. 15), MCZ 9688 (Pl. 3, figs. 16, 17), unfigured specimens MCZ 9689, KU 73331–73334.

Genus *Iranites* Teichert and Kummel n. gen.

Type species, *Tompophiceras transcaucasium* Shevyrev *in* Ruzhentsev and Sarycheva, 1965: 169, pl. 21, fig. 6.

One of the more common ammonoids in the Ali Bashi Formation is an evolute ceratite with a narrowly rounded to acute venter and a variable pattern of radial ribs on the flanks. Shevyrev (*in* Ruzhentsev and Sarycheva, 1965) assigned these forms to the genus *Tompophiceras* Popov (1961). The type species of *Tompophiceras, T. fastigatum* Popov, is based on a single, incomplete specimen from the *Otoceras* Zone of the eastern Verkhoyansk region, eastern Siberia. Popov (1961) emphasized that the sharpening of the venter is confined to the outer volution and that the inner whorls are rounded. Tozer, on the basis of personal examination of the type specimen, recently came to the conclusion that "The venter of the only known specimen is not well preserved. Examination of this specimen left me unconvinced that it was truly fastigate" (Tozer, 1969: 353). On the appearance of the above statement we questioned our friend Yu. N. Popov about the holotype of *Tompophiceras fastigatum* and he reaffirmed his original observation (letter to Kummel, 27 January 1970). In addition, Popov emphasized that, as he had stated in the original description of the species (Popov, 1961: 27), it was only the outer volution in which the venter was fastigate and that the inner volutions had rounded venters. Subsequently, Kummel, in June, 1970, has had the opportunity to examine this specimen and agrees completely with Popov's interpretation.

Shevyrev (*in* Ruzhentsev and Sarycheva, 1965) assigned eight specimens from Dorasham 2 to *Tompophiceras transcaucasium*. One would judge that all are fragmentary since the only specimen illustrated consists of only one-third of a volution of a conch. Tozer (1969: 353) stated that the specimen is crushed and the "fastigation apparent." Shevyrev differentiated *T. transcaucasium* from *T. fastigatum* entirely on the basis of minor differences in the suture. The smallness of the samples and rather indifferent preservation has made interpretation of these two species of *Tompophiceras* difficult. In addition to the eight specimens of *T. transcaucasium,* Shevyrev recorded 37 specimens of the genus which he left indeterminate. All specimens came from the *Tompophiceras* Zone, the lowest "Induan" in Shevyrev's terminology.

Our collections have yielded a large number of specimens that help to clarify the nature of this taxon. First it needs to be emphasized that whether or not Shevyrev's type specimen is crushed as stated by Tozer (1969: 353), one of the common ammonoids of the Ali Bashi Formation near Julfa is an evolute form with a narrow to acute rounding of the venter. The smallest nondeformed specimen in our collection has an acute venter at a diameter of 13 mm. This feature may appear earlier, but this cannot be determined from the material available. The true and most significant difference between *Tompophiceras fastigatum* Popov and *Tompophiceras transcaucasium* Shevyrev is in the time of appearance of the acute rounding of the venter. In the Siberian species fastigation appears only in the outer volution and in the species from the Ali Bashi Formation it appears at a very early growth stage. It is clear from this difference that these two species are not congeneric and thus we introduce the generic name *Iranites* for the taxon in the Ali Bashi Formation. Fastigation of the venter occurred repeatedly in various lineages of Late Permian and Early Triassic ammonoids. In most cases it can be established that such forms are offshoots of forms with rounded venters and rarely are ancestral to other lineages.

Iranites transcaucasius (Shevyrev)

Plate 5, figures 1–15; Text-figure 11H

Tompophiceras transcaucasium Shevyrev *in* Ruzhentsev and Sarycheva, 1965: 169, pl. 21, fig. 6; Shevyrev, 1968: 85, pl. 1, fig. 6.

Discussion. Our collections contain 53 specimens of *Iranites transcaucasius,* the great majority being fragments of body chambers. The main features of the conch are the acutely rounded to angular venter, the ovoid whorl section, and the lateral ribs. It is quite apparent that the rib pattern varies considerably, as demonstrated by the specimens illustrated on Plate 5, figures 1–15. The best-preserved and undeformed specimen is that shown on Plate 5, figures 1–3. This is a phragmocone of 22 mm diameter that clearly shows sharpening of the venter down to a diameter of 13 mm. At smaller diameters the venter cannot be seen. The suture (Text–figure 11H) has two ceratitic lateral lobes; the serrations of the second lateral lobe are minute.

A number of Late Permian and Early Triassic ammonoid genera with narrowly rounded to acute venters are known. *Xenodiscites* Miller and Furnish (1940), known from the Upper Permian of Mexico and Texas, is a more involute form having radial ribs confined entirely to the earliest whorls and a more simplified suture. A closely related genus, *Cibolites* Plummer and Scott (1937), is more compressed and smooth, and has a suture with two goniatitic lateral lobes. *Cibolites* has the same geographic and stratigraphic distributions as *Xenodiscites.* In the Lower Triassic (Scythian) there are many more genera of ammonoids with narrowly rounded to acute venters. In the lowest Scythian zone, that of *Otoceras* and *Ophiceras,* only *Tompophiceras* has such a venter, and it is developed only on the outer volution. At a slightly higher horizon *Vishnuites* Diener (1897) and *Subinyoites* Spath (1930) make their appearance, but their shells are much more involute and quite unlike *Iranites.* In the mid-Scythian we find such forms as *Subvishnuites* Spath (1930), *Preflorianites* Spath (1930), and *Inyoites* Hyatt and Smith (1905), but each of these genera is quite distinct from *Iranites.*

Most of the Upper Permian and Lower Triassic genera mentioned above are known from few species and specimens. This fact, combined with the relatively simple nature of the conch, makes comparison very difficult. There is nothing inherent in the morphology of *Iranites transcaucasius* to suggest a precise age assignment except that it may be anywhere from Late Permian through Early Triassic.

Occurrence. Loc. 1, bed 10 (MCZ 9701), Loc. 2 (MCZ 9704, 9705, 9706, 9707, 9708); Loc. 3 (MCZ 9699, 9700), float from Ali Bashi Formation. The stratigraphically highest specimen was found 10.5 m above the base of the formation.

Repository. MCZ 9699 (Pl. 5, figs. 1–3), MCZ 9700 (Pl. 5, figs. 4, 5), MCZ 9701 (Pl. 5, figs. 6, 7), MCZ 9702 (Pl. 5, fig. 8), MCZ 9703 (Pl. 5, fig. 9), MCZ 9704 (Pl. 5, fig. 10), MCZ 9705 (Pl. 5, fig. 11), MCZ 9706 (Pl. 5, figs. 12, 13), MCZ 9707 (Pl. 5, figs. 14, 15), unfigured specimens MCZ 9708, KU 73342–73364.

Genus *Shevyrevites* Teichert and Kummel, n. gen.

Type species, *Shevyrevites shevyrevi* Teichert and Kummel, n. sp.

The ammonoid fauna of the Ali Bashi Formation includes evolute shells having a subrectangular whorl section, radial ribs, and a simple two-lobed ceratitic suture. These forms we regard as congeneric with forms that Shevyrev (*in* Ruzhentsev and Sarycheva, 1965) described as *Bernhardites radiosus* and *B. nodosus,* but we believe that the generic assignments were incorrect. Shevyrev (*in* Ruzhentsev and Sarycheva, 1965) introduced the new genus *Bernhardites* (type species *Celtites radiosus* Koken *in* Frech, 1905), stated to be from the Lower Ceratite limestone at Chhidru in the Salt Range. He included in this new genus *Celtites fortis* Koken (*in* Frech, 1905) from the Lower Ceratite limestone of the Salt Range in West Pakistan and described a new species, *Bernhardites nodosus,* from the equivalents of the Ali Bashi Formation in the Dzhulfa region. Shevyrev's collections contain 29 specimens that he identified as *B. radiosus* and only two of *B. nodosus.*

Ammonoids with evolute shells having somewhat compressed, subquadrate whorl sections, a low rounded venter, lateral ribs, and a simple suture with two denticulated lateral lobes were common in Late Permian and Scythian times. The genus *Bernhardites* is such a form. Ammonoids of this general morphology are very difficult to identify and their phylogenetic relationships are not at all well known. Is the whole complex of such forms the product of a complex iterative pattern of evolution or are the many genera of the "form" no more than parts of a single, linear evolutionary series? The range of intraspecific variation for most of the many species and genera in this group of ammonoids is poorly known. One can be sure of their identification only when they are associated with a fairly large and distinctive fauna from which an age can be deduced with a fair amount of certainty.

Noetling (*in* Frech, 1905: 164) listed *Celtites radiosus* from the Lower Ceratite limestone and in fact named what he believed to be the lowest zone of the Salt Range Triassic sequence after this species, designating the Lower Ceratite limestone as the content of that zone. The Lower Ceratite limestone of Waagen (1895) is the basal unit of the Mittiwali Member of the Mianwali Formation (Kummel, 1966). In 1961–62, during approximately four months of field work studying the Triassic formations of the Salt Range and Surghar Range, Kummel did not once encounter this species in the Lower Ceratite limestone. He found, however, that it occurs in fair abundance in the overlying Ceratite marl of Waagen (1895). In addition, several specimens collected and identified by Koken were available for study. Matrix on some of the specimens in the Koken collection also suggests that they came from the Ceratite marl and not from the Lower Ceratite limestone. The many specimens in Kummels' collections show considerable variation in whorl width and rib pattern. The lateral ribs vary from narrow and rather delicate to broad and blunt. Likewise the whorl section varies from slightly compressed to a shape in which width and height are approximately equal. *Celtites* *fallax* Noetling, (*in* Frech, 1905, pl. 22, fig. 5) falls well within the range of intraspecific variation observed in *Celtites radiosus.* Frech (1905: 164) distinguished the middle part of the Ceratite marl as the *Celtites fallax* Zone. The sequence of zones for the Lower Triassic formation of the Salt Range established by Noetling is in need of complete revision. Restudy of the ammonoid faunas by Kummel is now in progress.

The specimens of "*Bernhardites*" from the Ali Bashi Formation have slightly compressed whorl sections with ribs on the lateral areas that extend and expand from the umbilical shoulder to the ventral shoulder. The maximum width of the ribs is at the ventral shoulder. This is not the rib pattern of *Celtites radiosus* or *Celtites fallax.* In these species the ribs expand very slightly from the umbilical shoulder to the ventral shoulder, but terminate before reaching the ventral shoulder. It is primarily on the basis of these features that the species from the Ali Bashi Formation is considered not to be congeneric with the Salt Range species. Thus a new generic and a new specific name, *Shevyrevites shevyrevi,* is here proposed.

Shevyrevites shevyrevi Teichert and Kummel, n. sp.

Plate 3, figures 1–6; Text-figures 11I, K

Bernhardites radiosus Shevyrev (non *Celtites radiosus* Koken, *in* Frech, 1905) *in* Ruzhentsev and Sarycheva, 1965: 171, pl. 21, fig. 7; Shevyrev, 1968: 86, pl. 1, fig. 7; pl. 2, fig. 1; Taraz, 1969: 691.

Bernhardites nodosus Shevyrev, *in* Ruzhentsev and Sarycheva, 1965: 171, pl. 21, fig. 7; Shevyrev, 1968: 87, pl. 2, fig. 2; Taraz, 1969: 691.

Description. Evolute, with slightly compressed whorl section that bears lateral ribs with maximum prominence at the ventral shoulder; venter rounded. Suture simple with two denticulated lateral lobes and partial auxiliary on umbilical seam.

Discussion. Our collections contain 16 specimens, mainly fragments, of rather indifferent preservation. Though our material is fragmentary it is quite apparent that considerable variation in rib spacing and expression exists. The range of variation is shown by the specimens illustrated on Plate 3. "*Bernhardites*" *nodosus* was differentiated by Shevyrev on the basis of inflated ribs on the inner whorls. Shevyrev had only two specimens of this species. Their rib pattern is believed to fall well within the variation range of that of *S. shevyrevi.*

Occurrence. Loc. 1 (MCZ 9678), Loc. 2 (MCZ 9681, 9682), Loc. 3 (MCZ 9679), float from Ali Bashi Formation (MCZ 9680). The stratigraphically highest specimens were collected 10.5 m above base of the formation.

Repository. Holotype, MCZ 9678 (Pl. 3, figs. 1, 2); paratypes, MCZ 9679 (Pl. 3, fig. 3), MCZ 9680 (Pl. 3, figs. 4, 5), MCZ 9681 (Pl. 3, fig. 6), unfigured specimens MCZ 9682, KU 73335–73341.

Family *Araxoceratidae* Ruzhentsev, 1959

Genus *Urartoceras* Ruzhentsev, 1959

Type species, *Urartoceras abichianum* Ruzhentsev, 1959: 64, figs. 1G, 2G

Urartoceras sp. indet.

Plate 3, figures 7, 8; Text-figure 11K

Discussion. We are indebted to W. M. Furnish and B. F. Glenister for advice on the identification of a single, somewhat poorly preserved specimen that can be assigned to *Urartoceras.* It has a diameter of 28 mm and is crushed, and one side is very badly weathered. The venter is fastigate, the lateral areas concave, and the umbilical region flared. The umbilicus is distorted by crushing and has a diameter of approximately 3.5 mm. The suture is shown in Text–figure 11K.

The araxoceratids were first recognized from the Dzhulfian strata of Soviet Dzhulfa. They are a highly complex and variable group of ammonoids in need of much taxonomic clarification (Furnish and Glenister, written communication to Kummel). Our specimen most closely resembles *Urartoceras.* This genus is monotypic and the type species was established on the basis of two specimens from the *Vedioceras* Zone of the

Soviet Dzhulfian Stage (Ruzhentsev and Sarycheva, 1965: 48). The suture of our specimen is almost identical with that of the type species.

Occurrence. Ali Bashi Formation, Loc. 4, bed 3, 3 m above base of formation.

Repository. MCZ 9683 (Pl. 3, figs. 7, 8).

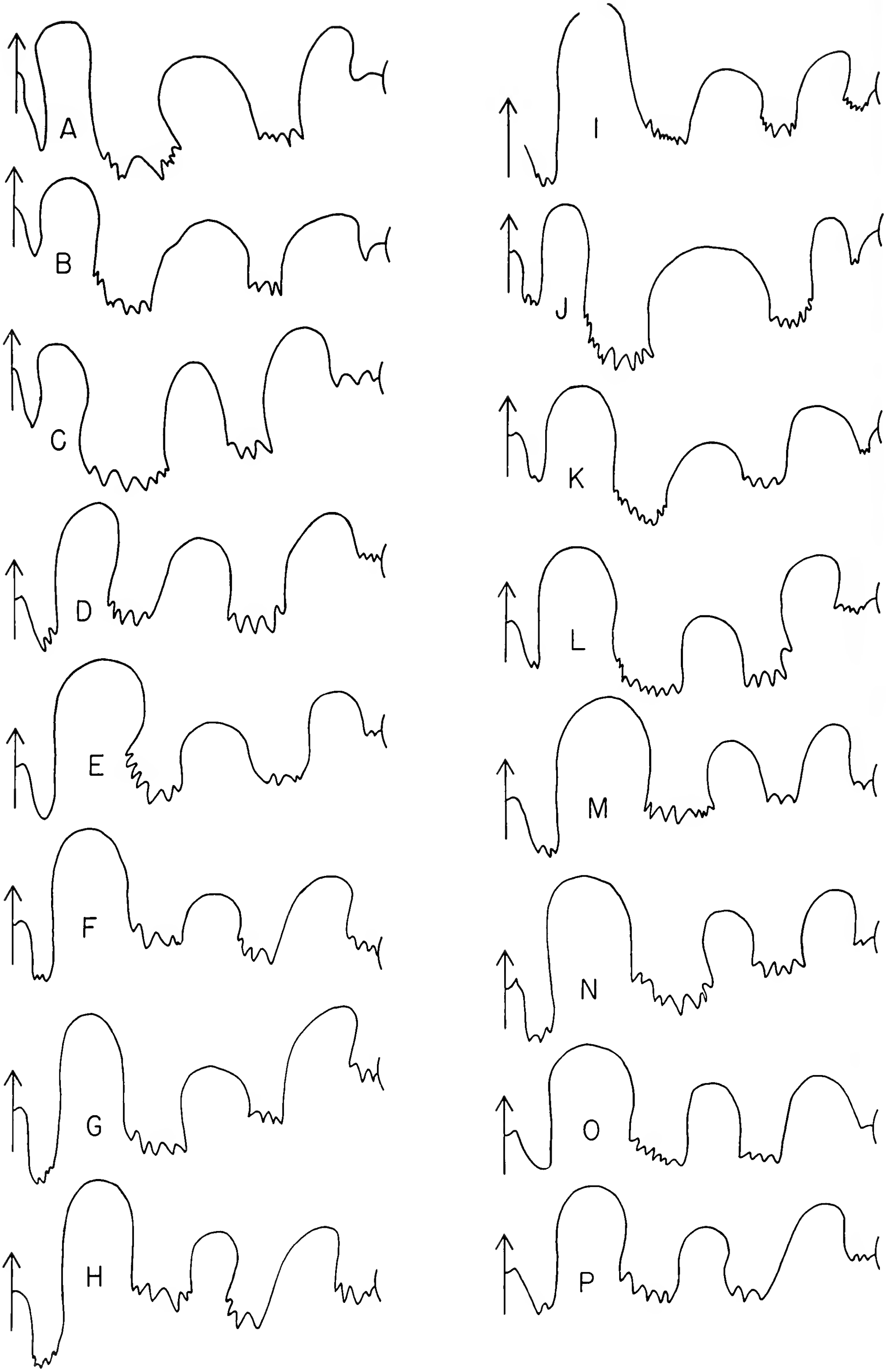
Family DZHULFITIDAE Shevyrev, 1965
Genus *Paratirolites* Stoyanow, 1910
[= *Dzhulfites, Abichites* Shevyrev *in* Ruzhentsev and Sarycheva, 1965]
Type species, *P. kittli* Stoyanow, 1910

The most characteristic and common ammonoids of the Ali Bashi Formation are members of the genus *Paratirolites.* From the *Tompophiceras, Dzhulfites, Bernhardites,* and *Paratirolites* beds, as recognized in the Soviet Dzhulfa region by Ruzhentsev and Sarycheva (1965), Shevyrev had available for study a total of 181 specimens of ammonoids from this group of which 116 belong to the family Dzhulfitidae divided among three genera and ten species. They are indeed a peculiar and most interesting group of ammonites. All three genera are evolute forms with ventrolateral nodes and lateral ribs. *Dzhulfites* was defined as having a subquadrate whorl section, *Paratirolites* a subtrapezoidal one, and *Abichites* a whorl section that is somewhat compressed and subquadrate. It is in the suture that one can see the close genetic relationship between these three "genera." The suture is unique because of the low saddle separating two denticulated lateral lobes. Unfortunately, the ontogenetic development of the suture is not known, so that one cannot be sure if this is a true first lateral saddle or merely an adventitious indentation in a broad lateral lobe. Regardless of this, the patterns of the suture of all described species and genera are nearly identical (Text–fig. 12). Shevyrev distinguished *Dzhulfites* primarily on its simple-pronged ventral lobe, a character we feel is hardly of generic significance. Aside from the so-called simplicity of the ventral lobe in *Dzhulfites,* the overall shapes of the sutures of this genus and those of *Paratirolites* and *Abichites* are remarkably alike. There are, however, strong variations in whorl shape and ornamentation. In light of the identity of the sutures we regard the differences in whorl shape as indications of differentiation on the species level only. We thus believe that *Dzhulfites* and *Abichites* are synonyms of *Paratirolites.* The ten species of the Dzhulfitidae described by Shevyrev were distinguished largely on the basis of differences in ornamentation. Unfortunately, Shevyrev gave little or no data on the range of variability of each ornament pattern. Our collections of approximately 60 specimens clearly show that there is great variation in ornament pattern and much gradation. Experience with many large populations of ornamented Scythian ammonites has clearly demonstrated that node and rib patterns commonly are highly variable, both in numbers and in strength (Kummel and Erben, 1968; Kummel, 1969). In Soviet Dzhulfa the two recorded species of "*Dzhulfites*" came from a single thin stratum, as did the five species of *Paratirolites* and the three species of "*Abichites.*"

Until recently *Paratirolites* was considered an endemic genus confined to the Ali Bashi Formation and its equivalents in the Dzhulfa region. Now Taraz (1969) has reported the genus from the Abadeh region of central Iran, about 1,100 km (680 miles) southeast of Julfa. In addition Tozer (1969) reported that the holotype of *Xenodiscus douvillei* Diener (1914: 918, pl. 1, figs. 1a–d), from an unknown horizon in Madagascar, is a species of *Paratirolites.* Since it shows the characteristic suture, there is no reason to doubt this identification. The lack of stratigraphic data for this specimen is unfortunate, but this record does extend considerably the geographic range of *Paratirolites.*

Paratirolites kittli Stoyanow
Plate 6, figures 1, 3–5, 7, 10, 11; Plate 7, figures 3, 7, 9

Paratirolites Kittli Stoyanow, 1910: 82, pl. 9, figs. 1, 2; Spath, 1934: 366, fig. 125; Kiparisova, 1947: 169, pl. 40, fig. 4; Kummel *in* Arkell *et al.*,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1957: L147, fig. 179,1; Shevyrev *in* Ruzhentsev and Sarycheva, 1965: 174, pl. 22, fig. 4; Shevyrev, 1968: 90, pl. 3, fig. 1.

Stephanites? Waageni Stoyanow, 1910: 89, pl. 8, fig. 3; Kiparisova, 1947: 167, pl. 40, fig. 3.

Stephanites sp. ind. Stoyanow, 1910: 89, pl. 7, fig. 8.

Paratirolites waageni, Spath, 1934: 367; Shevyrev *in* Ruzhentsev and Sarycheva, 1965: 175, pl. 22, figs. 5, 6; Shevyrev, 1968: 90, pl. 2, figs. 6, 7.

Paratirolites vediensis Shevyrev *in* Ruzhentsev and Sarycheva, 1965: 176, pl. 23, fig. 1; Shevyrev, 1968: 92, pl. 5, fig. 1.

Paratirolites trapezoidalis Shevyrev *in* Ruzhentsev and Sarycheva, 1965: 177, pl. 24, fig. 1; Shevyrev, 1968: 92, pl. 4, fig. 1.

Discussion. This is by far the dominant species, approximately 60 specimens, of this genus in the Ali Bashi Formation at Kuh-e-Ali Bashi and in Soviet Dzhulfa. Our specimens are for the most part fragmentary but show clearly that there is great variation in whorl cross section and ornamentation. The few specimens illustrated on Plates 6 and 7 give some idea of this variation. Because of fragmentary preservation, our collection is not suited for a detailed analysis of this variation. However, because the specimens are all from a single unit (approximately 3 m thick) within a very limited geographic range, we believe it more prudent to assume they are a single species; otherwise the only limit on the number of species recognized would be the number of specimens available.

Occurrence. Loc. 1, 1 m above base of Paratirolites limestone (MCZ 9728, 9751, KU 73381–73386); Loc. 2, 13.5 m above base of formation (MCZ 9748); Loc. 2, 20 cm above base of Paratirolites limestone (MCZ 9731, 9733, 9749, KU 73396–73402); Loc. 3, 11 m above base of formation (MCZ 9783); Loc. 4, bed 5 (MCZ 9784); float from Ali Bashi Formation but exact locality unknown (MCZ 9730, 9735, 9737, 9740, 9742, 9746, KU 73403–73467).

Repository. MCZ 9728 (Pl. 6. fig. 1), MCZ 9730 (Pl. 6, figs. 3, 4), MCZ 9731 (Pl. 6, fig. 5), MCZ 9733 (Pl. 6, fig. 7), MCZ 9735 (Pl. 6, figs. 10, 11), MCZ 9737 (Pl. 7, fig. 3), MCZ 9740 (Pl. 7, fig. 7), MCZ 9742 (Pl. 7, fig. 9), unfigured specimens MCZ 9746, 9748, 9749, 9751, 9783, 9784; KU 73381–73386, 73396–73467.

Paratirolites spinosus (Shevyrev)
Plate 6, figures 2, 6; Plate 7, figures 4, 5, 10, 11

Dzhulfites spinosus Shevyrev *in* Ruzhentsev and Sarycheva, 1965: 173, pl. 21, fig. 9; pl. 22, fig. 1; Shevyrev, 1968: 88, pl. 2, figs. 3, 4; Taraz, 1969: 691.

Dzhulfites nodosus Shevyrev *in* Ruzhentsev and Sarycheva, 1965: 174, pl. 22, figs. 2, 3; Shevyrev, 1968: 89, pl. 2, fig. 5; pl. 3, fig. 4.

Discussion. The two species brought together here were assigned by Shevyrev (*in* Ruzhentsev and Sarycheva, 1965) to his new genus *Dzhulfites.* As stated above, we do not believe the differences between these forms and other paratirolitids sufficient to warrent separation on the generic level. As in Soviet Dzhulfa, the species at Kuh-e-Ali Bashi is not common. Our collections contain nine specimens.

Occurrence. Loc. 2, 13.5 m above base of formation (MCZ 9729); float from Ali

Text-figure 12. Diagrammatic representation of suture of ammonoids from the "Induan" of the Dzhulfa area: A, *Dzhulfites spinosus* (1965, fig. 14a), at a whorl height of 20.3 mm; B, *Dzhulfites spinosus* Shevyrev (1965, fig. 14b), at a whorl height of 18.5 mm; C, *Dzhulfites nodosus* Shevyrev (1965, fig. 14c), at a whorl height of 27.9 mm; D, *Paratirolites kittli* (Shevyrev, 1965, fig. 15a), at a whorl height of 15.8 mm; E, *Paratirolites kittli* (Shevyrev, 1965, fig. 15b), at a whorl height of 9.7 mm; F, *Paratirolites waageni* (Shevyrev, 1965, fig. 16a), at a whorl height of 25.2 mm; G, *Paratirolites waageni* (Shevyrev, 1965, fig. 16b), at a whorl height of 23 mm; H, *Paratirolites waageni* (Shevyrev, 1965, fig. 16c), at a whorl height of 17.8 mm; I, *Paratirolites vediensis* Shevyrev (1965, fig. 17a), at a whorl height of 17.6 mm; J, *Paratirolites trapezoidalis* Shevyrev (1965, fig. 17b), at a whorl height of 24 mm; K, *Paratirolites trapezoidalis* Shevyrev (1965, fig. 17c), at a whorl height of 14.6 mm; L, *Paratirolites dieneri* (Shevyrev, 1965, fig. 18), at a whorl height of 10.5 mm; M, *Abichites mojsisovicsi* (Shevyrev, 1965, fig. 19a), at a whorl height of 12.2 mm; N, *Abichites stoyanowi* Shevyrev (1965, fig. 19b), at a whorl height of 11.9 mm; O, *Abichites stoyanowi* Shevyrev (1965, fig. 19c), at a whorl height of 13 mm; P, *Abichites abichi* Shevyrev (1965, fig. 19d), at a whorl height of 10.3 mm. [All references to Shevyrev, 1965, are to Shevyrev *in* Ruzhentsev and Sarycheva, 1965.]

Bashi Formation but exact locality unknown (MCZ 9732, 9738, 9743, 9747, KU 73392–73395).

Repository. MCZ 9729 (Pl. 6, fig. 2), MCZ 9732 (Pl. 6, fig. 6), MCZ 9738 (Pl. 7, figs. 4, 5), MCZ 9743 (Pl. 7, figs. 10, 11), unfigured specimens MCZ 9747, KU 73392–73395.

Paratirolites mojsisovicsi (Stoyanow)

Plate 6, figures 8, 9; Plate 7, figures 1, 2, 6, 8

Xenodiscus (*Paratirolites?*) *Mojsisovicsi* Stoyanow, 1910: 79, pl. 8, fig. 1.

Abichites mojsisovicsi, Shevyrev *in* Ruzhentsev and Sarycheva, 1965: 180, pl. 23, fig. 4; Shevyrev, 1968: 95, pl. 4, fig. 3.

Xenodiscus radians Stoyanow, 1910: 86, pl. 9, fig. 5.

Xenodiscus sp. ind. Stoyanow, 1910: 87, pl. 9, fig. 6.

Kashmirites? stoyanowi Kiparisova, 1947: 149, pl. 35, fig. 1.

Abichites stoyanowi, Shevyrev *in* Ruzhentsev and Sarycheva, 1965: 179, pl. 24, figs. 2, 3; Shevyrev, 1968, pl. 3, fig. 5, pl. 4, fig. 2; Taraz, 1969: 691.

Abichites abichi Shevyrev *in* Ruzhentsev and Sarycheva, 1965: 181, pl. 24, fig. 4; Shevyrev, 1968: 181, pl. 24, fig. 4.

Paratirolites Dieneri Stoyanow, 1910: 83, pl. 8, fig. 2; Spath, 1934: 366, fig. 125e; Shevyrev *in* Ruzhentsev and Sarycheva, 1965: 178, pl. 23, figs. 2, 3; Shevyrev, 1968: 93, pl. 3, figs. 2, 3.

Discussion. Brought together here are the more compressed paratirolitids for which Shevyrev (*in* Ruzhentsev and Sarycheva, 1965) established the genus *Abichites.* These forms are only slightly more common than those assigned to *Dzhulfites* but still far inferior in numbers to *Paratirolites kittli* in our collections from Kuh-e-Ali Bashi and in Shevyrev's collections from Soviet Dzhulfa. Our collections contain only four specimens, but they are rather well preserved. The species brought together here were originally differentiated on minor variations in ornament or whorl shape.

Occurrence. Loc. 1, 1 m above base of Paratirolites limestone (MCZ 9734); Loc. 2, 9 m above base of formation (MCZ 9736); Loc. 3, 3 m above base of formation (MCZ 9739); from unknown horizon and locality in Ali Bashi Formation MCZ 9741, KU 73387–73391.

Repository. MCZ 9734 (Pl. 6, figs. 8, 9), MCZ 9736 (Pl. 7, figs. 1, 2), MCZ 9739 (Pl. 7, fig. 6), MCZ 9741 (Pl. 7, fig. 8), unfigured specimens KU 73387–73391.

Phylum **ARTHROPODA**

Class **CRUSTACEA** Pennant, 1777

Subclass **OSTRACODA** Latreille, 1806

Orders *PALAEOCOPIDA* Henningsmoen, 1953, and *PODOCOPIDA* Müller, 1894

Ostracods are quite common in rocks of the Ali Bashi Formation, but we succeeded in securing only a very few identifiable specimens. Out of 37 thin sections of Ali Bashi rocks, ostracods were present in 26, and in many of these in considerable abundance (Pl. 14). The small assemblage that I. G. Sohn (written communication to Teichert, 21 December 1971) was able to identify has already been mentioned. It came from the very base of the *Paratirolites* beds at Locality 1.

According to Sohn, the carapace of *Hollinella* sp. cf. *H? tuberculata* Belousova, 1965, has a straight frill and a configuration of nodes and lobe similar to the specimen figured by Belousova in Ruzhentsev and Sarycheva (1965, pl. 46, fig. 2a). In addition this small assemblage includes species of *Bairdia* and other indeterminate Bairdiacea.

Phylum **ECHINODERMATA**

Class **CRINOIDEA** Miller, 1821

INTRODUCTION

Our collections include about 50 parts of crinoid stems, occurring both as columnals and pluricolumnals. Since Moore and Jefford (1968) have demonstrated that the study of dissociated columnals of crinoids is of potential stratigraphic value, and since very little is known of Permian crinoid columnals, we decided to describe our crinoid material in some detail. In describing the morphological features of the columnals, we follow closely the morphological terminology proposed by Moore, Jeffords, and Miller (1968a). For the benefit of readers who are not familiar with this terminology, which is largely new, or who do not have easy access to the original publication, some diagrammatic figures published by Moore, Jeffords, and Miller (1968a, figs. 1 and 2) are here reproduced (Text-fig. 13). They are essentially self-explanatory, but for further guidance the following explanations of new or little-known terms are supplied. They are copied from Moore, Jeffords, and Miller (1968a: 27–30).

Glossary of Selected Terms Applied to Crinoid Parts

areola (pl., **areolae**). Generally smooth, featureless area of columnal articulum between lumen (or perilumen, if present) and inner margin of crenularium; may be granulose or marked by fine vermicular furrows and ridges.

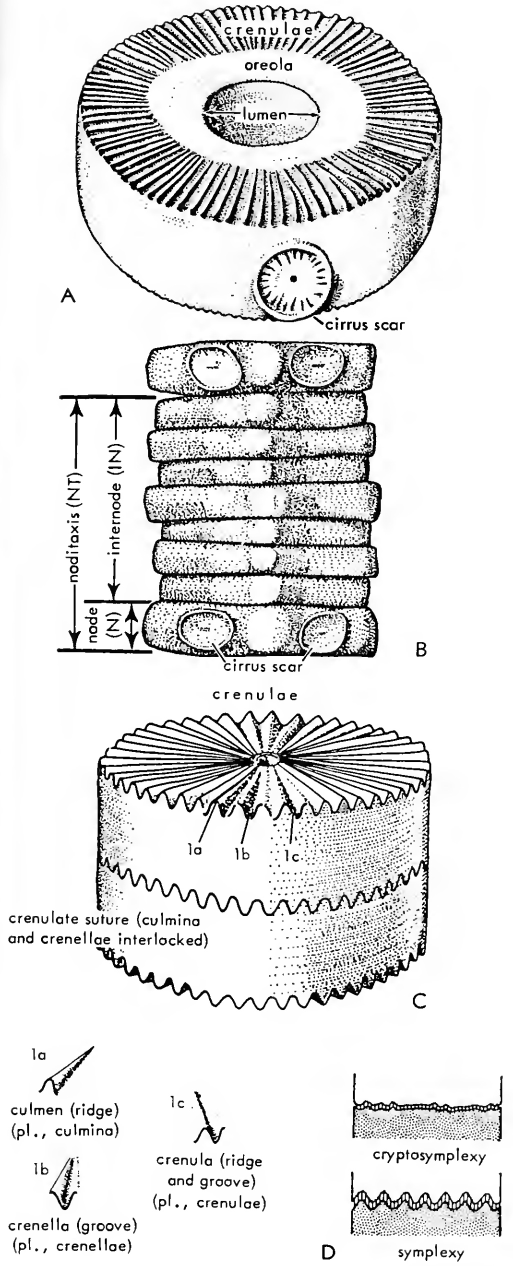
articulum (pl., **articula**). Smooth or sculptured surface of columnal or cirral serving for articulation with contiguous stem element, may be intercolumnal, intercirral, or nodicirral (between nodal columnal and most proximal cirral); *syn.*, articular facet. All columnal and cirral articula are divisible into lumen and surrounding area designated zygum.

axial canal. Longitudinal passageway penetrating columnals and cirrals, generally but not invariably located centrally; may be single and either simple or complex or multiple (main canal accompanied by smaller accessory canals).

claustrum (pl., **claustra**). Thick or thin inward projection of columnal medulla constricting axial canal, inner extremity acuminate to bluntly rounded, truncate with rabbeted edges, or clavate, composed of dense stereom or showing microstructure of fine annular lamellae subparallel to mid-plane of columnal, with or without intersecting longitudinally disposed lamellae which form microscopic cribwork.

crenularium (pl., **crenularia**). Portion of columnal and cirral articula occupied by crenulae.

heteromorphic (column or pluricolumnal). Sequent columnals dissimilar, some consisting of nodals and others of internodals, latter commonly divis-



Text-figure. 13. Some morphological features of crinoid columnals and pluricolumnals. A. Single columnal showing nearly straight sides and features of the facet. B. Side view of pluricolumnal showing nodals with cirrus scars, and internodals of three orders, entire noditaxis composed of eight columnals. C. Straight-sided columnals joined by interlocked ridges and grooves of articular surfaces marked externally by crenulate suture, single ridge (1a, culmen) and groove (1b, crenella) together forming a crenula (1c). D. Diagrammatic transverse profiles of juxtaposed articular facets showing two types of articulation described in this paper. (From Moore, Jeffords, and Miller, 1968a, fig. 1. Published by permission of the authors.)

ible by order of their intercalation into prim-, secund-, tert-, and quartinternodals or higher-rank ones. Nodals and internodals may be clearly distinguishable along sides of axial canal, as seen in longitudinal sections, but not in views of columnal latera.

homeomorphic (column or pluricolumnal, cirrus or pluricirral). Composed of identical or essentially identical skeletal elements. Pluricolumnals from different parts of xenomorphic crinoid columns may be homeomorphic within themselves but dissimilar when compared with one another.

jugulum (pl., **jugula**). Localized constriction of axial canal produced by approximated adaxial edges of claustrum, may be longitudinally very short to moderately tall and transversely circular or pentagonal to strongly pentastellate.

latus (pl., **latera**). Surface of crinoid columnal or cirral exclusive of articular facets, equivalent to epifacet.

perilumen (pl., **perilumina**). Raised inner border of columnal articular zygum, surrounding lumen as rim or tabular field with smooth, granulose, tuberculate, or vermiculate surface. Internally, perilumen of some columnals corresponds to dense inner medulla, which is very distinct from reticulate to spongy outer medulla between areolae and possibly part of crenularia of opposite articula.

pluricolumnal. Two or more columnals attached to one another.

spatium (pl., **spatia**). Localized widening of columnal axial canal opposite interarticular sutures.

zygum (pl., **zyga**). All of columnal or cirral articulum surrounding lumen.

For further guidance of the reader, the following list of explanations of symbols used in text and tables of the present paper is given.

Explanation of Symbols Used in this Paper

A —Areolar width: twice the interval between two radial intercepts of the areola.

Ai —Areolar index: $\frac{A}{KD}$.

C —Crenularial width: twice the interval between two radial intercepts of the crenularium.

Ci —Crenularial index: $\frac{C}{KD}$.

IN —Internodal (without cirri).

KD —Columnal diameter (for straight-sided columnals this is also the width of the articular facet).

KH —Columnal height, longitudinal dimension of columnal.

KHi —Columnal height index: $\frac{KH}{KD}$.

L —Luminal diameter.

Li —Luminal index: $\frac{L}{KD}$.

N —Nodal; having one or more cirri.

P —Periluminal width: twice the interval between radial intercepts of the perilumen.

Pi —Periluminal index: $\frac{P}{KD}$.

SPM —Specimen.

We have given much consideration to the question of whether or not we should formally name the crinoid specimens studied by us in the manner proposed by Moore and Jeffords (1968) and practiced by Soviet paleontologists such as Yu. A. Dubatolova, G. A. Stukalina, and R. S. Yeltysheva (cited in Moore, Jeffords, and Miller, 1968b: 12, 14). However, we decided to divide up our material into informally named types. Obviously, all specimens are similar enough morphologically that they must belong to one genus. However, we find it difficult to decide whether or not these "types" represent taxonomic units on the species-group level. Further, we show that the bulk of the specimens seems to be parts of juvenile individuals. Lastly, there is a strong possibility that all specimens may belong to an already named species of fistulate crinoids, *Erisocrinus araxensis* Yakovlev (1933). These considerations form the basis for our decision not to apply formal taxonomic names to the crinoid remains from the Ali Bashi Formation.

For purposes of comparison, we have included in this study the description of a few crinoid columnals from the Julfa beds that underlie the Ali Bashi Formation.

At the University of Kansas, R. C. Moore has assembled, over a period of years, what is probably the world's largest collection of disarticulated crinoid remains, including stem fragments. It has, of course, been impossible to check these huge collections. We have, however, selected a few specimens from Pennsylvanian and Permian rocks for comparative studies. We wish to thank Dr. Moore for his permission to study these specimens.

SYSTEMATIC DESCRIPTIONS

Order and family uncertain

Type 1

Plate 10, figures 5, 15

Description. Known only from internodals that are circular to elliptical in transverse section, straight latera; articulation unknown, probably symplectic or cryptosymplectic; articular facet with medium culmina that retain approximately the same thickness throughout their length; broad areola; perilumen absent or very faint; small, circular lumen; number of culmina 22 or 23. Measurements (in mm) and indices of specimen KU 73118 are: KD, 3.8; L, 0.3; Li, 18.1; A, 2,3; Ai, 60.0; C, 0.7; Ci, 34.0; KH, 3.5; KHi, 91.0.

Discussion. The collection contains one specimen definitely assignable to Type 1. A second specimen has no perilumen but is elliptical in transverse section. Illustrated specimens that resemble Type 1 include *Cyclocyclicus schizinicus* Dubotolova and Shao-Tze (1959, pl. 1, figs., 18a,b) from the Middle Triassic of northern China which differs only in having a more squared symplectic articulation (see fig. 18b, longitudinal view). *Erisocrinus araxensis* Yakovlev (1933; Yakovlev and Ivanov, 1956, pl. 19, figs. 2a,b) probably bears the closest resemblance to Type 1 (Pl. 10, figs. 1a,b). This species occurs in the uppermost Permian beds at Dorasham near Dzhulfa in the Nakhichevan ASSR. Unfortunately, a second crinoid species, *Spaniocrinus transcaucasicus* Yakovlev (1933), which occurs in the same beds, cannot be compared because its columnals are not known.

Forms similar in circular to elliptical cross section are *Encrinus liliiformis* (Quenstedt, 1876, pl. 107, fig. 18) from the Middle Triassic of southern Germany and *Eugeniacrinus compressus* (*ibid*, pl. 106, fig. 19) from the Upper Jurassic of southern Germany. Both species have small lumina, well-developed crenularia, an areola, and no perilumen.

Specimen PH 105 from the Word Formation (Guadalupian) of the Glass Mountains, Texas, which is in the R. C. Moore collection of the Paleontological Institute, University of Kansas, resembles Type 1 except for greater convexity of its latera and the possible presence of a spatium.

Measurements and indices for specimens in published literature and from the R. C. Moore collection are given in Tables 2 and 3.

Occurrence. Loc. 3A, bed 2.

Repository. KU 73118 (Pl. 10, figs. 15a, b), possibly 73151 (Pl. 10, fig. 5).

Type 2

Plate 10, figures 3, 9, 10, 11, 14

Description. Stem heteromorphic, circular to elliptical in transverse section; nodals and internodals present; diameter of cirrus scars not greater than one-half the height of columnals; latera concave, convex, or straight; articulation cryptosymplectic; articular facet small with relatively fine culmina and crenellae; culmina probably develop by bifurcation from 15 original ones, which remain as bumps on the inner margin of the crenularium, others intercalated between bifurcating pairs, probably in manner similar to that described by Bather (1917: 250–251); medium to broad crenularium; areola of medium to narrow width but always present; perilumen present, approximately circular. Measurements and indices are given in Table 4.

Discussion. A specimen with elliptical transverse section (KU 73154) has the same articular pattern and so is included in this group; it has approximately 30–45 culmina including intercalated ones. Specimens intermediate between Types 2 and 3 in number of culmina exist (KU 73120, 73138). Type 2 specimens from Locality 3A, bed 2, seem to have a smaller Ci and a larger Ai than those from Locality 4, bed 3. The relationship between the diameters of colum-

Table 2. Measurements (in mm) and Indices for Crinoid Stems from the Literature

SPM	KD	L	Li	P	Pi	A	Ai	C	Ci	KH	KHi	Similar to Type
1 a (upper)	8.5	0.8	9.4	0	0	4.2	49.5	3.2	37.6	4.5	53.0	1
b (lower)	8.5	1.9	22.5	0	0	4.0	47.1	2.2	26.0	—	—	1
2	11.5	1.5	13.1	0	0	5.0	43.5	5.0	43.5	5.5	48.0	1
*3	7.2	0.4	5.6	0	0	4.4	61.1	2.2	30.5	7.6	106.0	1
*4	12.0	0.9	7.5	0	0	9.0	75.0	3.4	28.0	9.5	79.0	1
5	3.0	0.6	19.2	0	0	1.4	47.0	1.0	34.0	3.0	100.0	1
6	9.0	0.7	7.7	0	0	6.9	77.0	1.4	15.0	6.2	69.0	1
*7 a	4.0	—	—	—	—	—	—	—	—	3.1	78.0	1
b	4.9	0.3	9.1	0	0	3.3	68.0	1.3	28.0			1
8	4.4	0.7	16.1	0	0	2.7	61.0	1.0	23.0	—	—	1
9	7.0	1.0	14.3	0	0	2.2	31.4	3.0	42.8	1.5	21.4	1
10	5.7	0.8	14.1	0	0	1.5	26.3	3.0	52.6	1.4	24.6	1
11	2.9	0.5	16.9	0	0	1.3	43.1	1.0	32.3	—	—	1
12	2.5	0.3	13.0	0.7	22.0	1.5	58.0	0.5	20.0	1.5	60.0	3

* These specimens have measurements and indices with closest resemblance to those described in this report.

1. *Apiocrinus* stem, Upper Jurassic, southern Germany (Quenstedt, 1876, pl. 102, fig. 14)
2. *Apiocrinus* stem, lower Upper Jurassic, southern Germany (Quenstedt, 1876, pl. 104, fig. 7)
3. *Encrinus liliiformis,* Middle Triassic (Hauptmuschelkalk), Germany (Quenstedt, 1876, pl. 107, fig. 18)
4. *Cyclocyclicus schizinicus,* Middle Triassic, northern China (Dubatolova and Shao-Tsze, pl. 1, figs. 18a,b)
5. *Erisocrinus araxensis,* Upper Permian, Dorasham, near Dzhulfa, USSR (Yakovlev and Ivanov, 1956, pl. 19, figs. 2a,b)
6. *?Philocrinus cometa,* Upper Permian, Salt Range, West Pakistan (Waagen, 1885, pl. 95, figs. 20, 20a)
7. *?Philocrinus cometa,* Upper Permian, Salt Range, West Pakistan (Waagen, 1885, pl. 95, figs. 20b,c)
8. *Cyathocrinus kattaensis,* Upper Permian, Salt Range, West Pakistan (Waagen, 1885, pl. 96, fig. 2g)
9. *Parastachyocrinus malaianus* var. *ornata,* Upper Permian, Timor (Wanner, 1949, pl. 3, fig. 19)
10. *Cyathocrinus berkaloffi,* Permian, Tunisia (Valette, 1934, figs. 12, 12a)
11. *Cyathocrinus berkaloffi,* Permian, Tunisia (Valette, 1934, figs. 12b,c)
12. *"Cyathocrinus" goliathus,* Permian, Tunisia (Termier and Termier, 1958, pl. 2, figs. k,l)

nals and the number of culmina is shown in Text–figure 14.

A specimen in the R. C. Moore collection, BA 55 6c (Pennsylvanian, South Bend, Young Co., Texas), probably representing *Cyclocaudex,* resembles specimen KU 73154 in Ci and Ai but has a much larger lumen and smaller columnal height. Measurements and indices for the specimens here discussed are found in Tables 2 and 3.

Occurrence. Loc. 3A, bed 2; Loc. 4, bed 3.

Repository. KU 73119 (Pl. 10, figs. 14a, b), 73149 (Pl. 10, figs. 10a,b), 73154 (Pl. 10, fig. 3), 73165 (Pl. 10, figs. 9a,b), 73166 (Pl. 10, fig. 11). Unfigured specimens KU 73121 and 73152, and possibly 73120 and 73156.

Type 3

Plate 10, figures 2, 4, 6, 8, 12

Description. Stem heteromorphic, appearing homeomorphic in some specimens; of small size; in a few specimens with cirri on adjacent columnals; latera straight or convex; cirrus scars of small width, generally not over one-half the height of columnals; articulation symplectic; articular facet with medium to broad culmina and crenellae; narrow crenularium, areola broad, slightly ornamented; perilumen present, poorly to moderately well differentiated from areola; lumen small and circular, possibly pentagonal in specimen KU 73155. Measurements and indices are given in Table 4.

Discussion. This type generally has 16 to 30 culmina all of equal size and importance. Shape and texture of the perilumen vary: some specimens have a circular perilumen with knoblike culmina, others have loaflike culmina. The relationships between the length of columnals and number of culmina are shown in Text–figure 15.

Illustrated specimens from the literature which resemble Type 3 include *"Cyathocrinus" goliathus* Waagen of Termier and Termier (1958, pl. 2, fig. K) from the Permian of southern Tunisia and *Erisocrinus stefaninii* Yakovlev (1934, pl. 20, figs. 4a,

TABLE 3. MEASUREMENTS (IN mm) AND INDICES FOR CRINOID STEMS IN R. C. MOORE COLLECTION, SIMILAR TO CRINOIDS FROM ALI BASHI FORMATION

SPM	KD	L	Li	P	Pi	A	Ai	C	Ci	KH	KHi	Similar to Type
AK64 (facetal view)	1.6	0.2	1.1	0	0	0.8	47.7	0.4	39.0	—	—	1
(side view)	1.7	—	—	—	—	—	—	—	—	1.4	82.0	
AK65 (facetal view)	2.0	0.3	17.0	0	0	1.0	51.0	0.5	26.0	—	—	1
(side view)	1.9	—	—	—	—	—	—	—	—	2.5	126.0	
*PH105 (v. convex latera) spatium?	6.5	0.7	10.5	0	0	4.2	64.0	1.8	28.0	5.8	89.0	1
BA55 6c (facetal view)	4.7	0.1	21.3	0.6	12.8	0.7	14.8	2.9	62.0	—	—	2
(side view)	4.6	—	—	—	—	—	—	—	—	1.6	29.0	
AK59 5d (facetal view)	3.3	0.5	15.2	0.4	12.1	1.0	30.4	1.3	38.0	—	—	3
(side view)	3.4	—	—	—	—	—	—	—	—	2.6	77.0	
*PH44 (pent. areola)	6.4	0.5	8.0	0.9	14.0	3.7	58.0	1.8	28.0	2.8	44.0	3
PH79	3.6	0.5	13.8	0.5	14.0	1.5	42.0	1.2	36.0	2.5	70.0	3

Localities:

AK	Mingus Shale Member, Garner Formation, Strawn Group, Desmoinesian, Middle Pennsylvanian, Erath Co., Texas
BA	South Bend Shale Member, Graham Formation, Cisco Group, Virgilian, Upper Pennsylvanian, Young Co., Texas
PH	Middle Limestone 2, Word Formation, Guadalupian, Upper Permian, Glass Mountains, Brewster Co., Texas

* These specimens have measurements and indices with closest resemblance to those described in this report.

b) from the Upper Permian of Sicily.

Specimen PH 44 in the R. C. Moore collection, from the Word Formation (Guadalupian), Glass Mountains, Texas, resembles Type 3 in measurements and indices but has a slightly pentagonal areola. Measurements and indices of specimens from the literature and from the R. C. Moore collection are given in Tables 2 and 3.

Occurrence. Loc. 4, beds 2 and 3.

Repository. KU 73147 (Pl. 10, fig. 4), 73150 (Pl. 10, fig. 2), 73155 (Pl. 10, figs. 8a, b), 73159 (Pl. 10, figs. 12a,b), and possibly 73138 (Pl. 10, fig. 6). Unfigured specimens KU 73125, 73134, 73135, 73137, 73142, 73164.

Type 4

Plate 10, figures 7, 16

Description. Stem heteromorphic, circular in transverse section; nodals and internodals present; latera straight; articulation cryptosymplectic; articulum with 36–40 fine culmina including intercalated ones, bifurcating from 15 more or less distinct knobs or intercalating between bifurcating culmina; areola of medium width; perilumen present with knoblike culmina; small, circular lumen. Measurements and indices for specimens KU 73157 and KU 73303 are given in Table 4.

Discussion. Specimens KU 73157 and

Table 4. Measurements (in mm) and Indices for Crinoids from Ali Bashi Formation

SPM	KD	L	Li	P	Pi	A	Ai	C	Ci	KH	KHi	N or IN
Type 1												
1	3.8	0.31	8.1	0	0	2.3	60.0	1.3	34.0	3.5	90.8	IN
41	2.6	0.23	8.0	0	0	1.7	68.0	0.6	43.0	3.7	102.5	IN
Type 2												
2	3.7	0.30	8.4	0.7	18.8	1.0	27.0	1.7	44.5	4.4	119.0	IN
5	3.0	0.35	11.2	0.6	20.0	1.4	46.5	0.7	43.0	3.7	121.5	IN(?)
39A	3.9	0.46	8.4	0.5	11.6	1.7	45.0	1.1	36.5	3.7	95.8	IN
B	3.8	0.26	6.8	0.6	16.8	1.8	47.0	1.1	34.8	4.5	118.0	IN
42A	4.8	0.41	8.6	0.8	17.2	1.8	38.0	1.5	31.1	5.2	109.0	N
B	4.9	0.41	8.6	0.9	18.2	1.5	33.0	1.5	32.5	4.8	98.2	N
44	3.2	0.23	7.1	0.6	17.6	0.4	14.0	2.0	59.0	3.9	121.8	IN
50	4.4	0.40	9.1	1.9	43.5	0.4	9.1	1.8	42.3	5.9	139.8	N
59A	4.0	0.32	7.9	1.3	32.0	0.8	18.9	1.6	39.5	4.4	107.9	N
B	4.0	0.37	9.3	0.9	22.0	1.1	25.5	1.7	42.5	3.5	86.5	IN
Type 2 or 3												
4	3.8	0.35	9.3	0.4	9.2	1.3	33.0	1.8	47.5	5.1	132.0	N(?)
28A	3.3	0.52	6.4	0.8	22.5	1.0	30.0	0.8	41.5	3.9	116.2	N
Type 2 or 4												
46	3.6	0.40	9.1	0.6	16.6	1.8	50.0	1.3	36.1	6.6	182.0	IN
Type 3												
8	3.6	0.40	8.9	0.3	16.8	0.6	36.0	0.8	42.3	3.6	66.1	IN
11B	3.1	0.40	7.7	0.6	19.4	1.0	32.5	1.0	32.0	3.0	97.1	IN
14	3.0	0.25	8.4	0.9	28.4	0.9	33.3	0.8	37.5	5.0	164.5	N
25A	3.0	0.35	8.6	0.8	26.0	1.1	36.6	0.8	36.5	2.1	69.9	IN
37A	2.8	0.20	7.2	0.9	25.0	1.1	39.5	0.5	18.6	4.4	64.5	N
B	2.8	0.30	10.7	0.6	20.5	1.5	54.0	0.4	14.1	3.0	93.5	N
40A	2.8	0.26	9.1	0.6	20.7	1.0	30.0	1.0	35.5	3.2	114.0	IN
D	3.0	0.26	8.8	0.6	20.9	1.3	42.5	0.6	46.0	3.0	100.2	IN
45A	3.9	0.43	9.0	0.7	18.6	1.2	31.6	1.2	31.6	5.2	132.1	N
B	3.8	0.36	9.6	0.6	17.0	0.9	42.0	1.2	32.0	4.7	118.0	N
49A	2.3	0.35	6.5	0.4	15.4	0.6	38.0	0.7	32.5	4.2	183.8	N
C	2.2	0.38	5.9	0.3	15.1	1.0	44.0	0.5	20.5	4.1	182.0	N
55A	4.0	0.30	7.4	0.8	19.6	1.3	31.0	1.3	32.0	3.3	79.9	N
Type 4												
47	4.5	0.47	9.5	0.6	13.4	1.2	27.0	2.3	51.5	4.7	104.3	IN
54A	3.0	0.40	7.6	0.6	18.2	0.7	44.5	1.2	39.0	3.0	99.9	IN

73303 are provisionally separated into a fourth group closely related to Type 2. They differ from Type 2 in their possession of a slightly larger lumen and a perilumen with knoblike culmina rather than loaflike ones. The border between areola and crenularium is less distinct than in some specimens of Type 2, and the culmina are finer. Types 2 and 4 both possess bifurcation from 15 main culmina with others intercalating between them. Specimen KU 73156 appears to be intermediate between Types 2 and 4 in the distinctness of separation of the areola and crenularium and in fineness of the culmina. No specimens from the literature or from the R. C. Moore collection from the Glass Mountains of Texas appear to resemble Type 4.

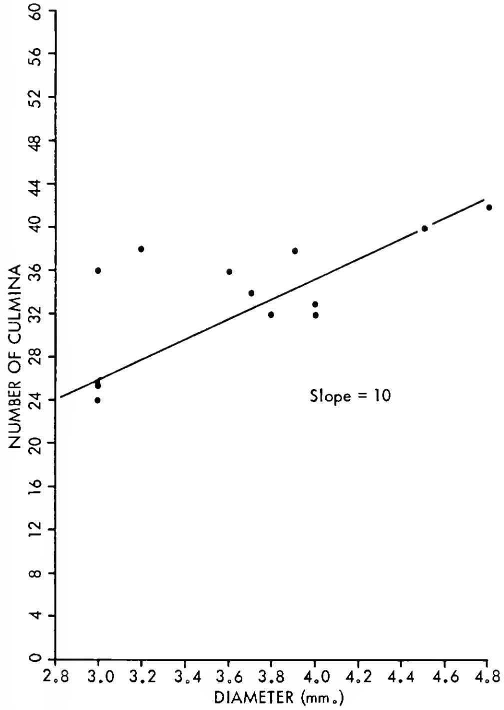
Occurrence. Loc. 4, bed 3; Loc. 3A, bed 2.

Repository. KU 73157, (Pl. 10, figs. 16a, b) and 73303 (Pl. 10, fig. 7), possibly also KU 73146 and 73156.

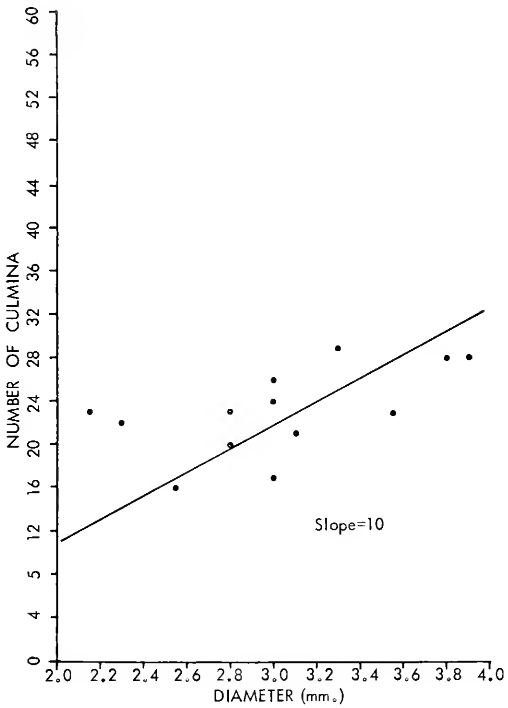
Comments on Growth and Classification

Several lines of evidence suggest that the Ali Bashi crinoids were in an early stage of growth. A plot of columnal diameter versus number of culmina suggests that they are most closely related to Jeffords and Miller's (1968: 11) columnal growth Type 1. The appearance of a specimen of Type 3 sectioned longitudinally also resembles their figure 4A. According to Jeffords and Miller (1968: 6–7), juveniles of columnal growth Type 1 have a diameter of approximately 4–5 mm or less, about 35 culmina, and a lumen 1–2 mm wide. KHi probably decreases with age, so that juveniles would have a greater KHi than adults. The nodals of the Ali Bashi specimens have a KHi of more than 100 except for specimens KU 73164 and KU 73153. Both of these specimens have diameters of more than 4.0 mm. The presence of nodals adjacent to each other or with only two or three internodals in the noditaxis also suggests that the crinoids were young.

The presence of a perilumen seems to be the main feature that distinguishes Type 3 from Type 1. The similarity of the growth-index lines for Type 2 and 3 also suggests a relationship between them (Text–figs. 14, 15). Sufficient data were not available to approximate the growth-index lines of Types 1 and 4.



Text-figure 14. Relationship of diameter of columnals to number of culmina (counted at periphery) in Type 2 specimens.



Text-figure 15. Relationship of columnals to number of culmina (counted at periphery) in Type 3 specimens.

On the basis of similarities between types and with the published illustrations, one or more of the described types may belong to the genus *Erisocrinus*. Similarity to published illustrations and proximity to localities where representatives of this genus were collected suggest relationship to *Erisocrinus araxensis* from the Upper Permian of Dorasham near Dzhulfa, Nakhichevan ASSR, for at least Type 1 specimens (Pl. 10, figs. 1a,b). Some species of *Erisocrinus* have a perilumen, others do not. *E. araxensis* (Yakovlev, 1933, pl. 1, figs. 4, 5a) has none, while *E. stefaninii* (Yakovlev, 1934, pl. 20, fig. 4a) does. Unfortunately, it is not known whether the type material of *E. araxensis* comes from equivalents of the Julfa beds or of the Ali Bashi Formation.

Crinoid Stems from the Julfa Beds

Rather surprisingly, crinoid stems seem to be extremely rare in the Julfa beds that underlie the Ali Bashi Formation. Among hundreds of fossils in our collections from these beds, only five crinoid stems are present. They are, in some respects, similar to the Ali Bashi crinoids but differ in some features.

Type 5

Plate 10, figures 13a, b

Description. Stem heteromorphic; latera strongly convex, some having an incipient equatorial keel; less than three cirrus scars per nodal; diameter of cirrus scars less than one-third of the height of columnal; nodals slightly higher than internodals; lumen circular to slightly elliptical, about one-fifth to one-fourth of facetal diameter (which is larger than in any Ali Bashi crinoids); narrow perilumen present; crenularium of medium width with 22 to 27 medium-width culmina that retain the same width throughout; symplectic articulation; areola rather narrow and concave; border between areola and crenularium distinct. Measurement and indices for the three specimens are given in Table 5.

Discussion. These specimens differ from Type 3 Ali Bashi crinoids in having a larger lumen and a smaller perilumen. The areola is also smaller and better defined. The culmina resemble those of Type 1 more than those of the other three Ali Bashi types but are less square. In facetal view, the Julfa crinoids resemble *Preptopremnum rugosum* Moore and Jeffords (1968, pl. 27, figs. 4, 7a) from the Chaffin limestone member of the Thrifty Formation, Cisco Group, Virgilian, Upper Pennsylvanian of Texas, and *Preptopremnum laeve* (*ibid.*, pl. 27, figs. 11a,b) from the Mingus Shale, Strawn Group, Desmoinesian, Middle Pennsylvanian, Texas. *P. rugosum* has ornamentation not discerned on the latera and areola of the Julfa crinoids, however. A close resemblance to specimen Y1 in the R. C. Moore collection from the Waldrip limestone, no. 3, Wolfcampian, Lower Permian, McColloch County, Texas, is also noted. A jugulum is present in the Texas specimen. No axial canal structures could be identified in the Julfa specimens. Thirty-three culmina were present in the larger diameter Texas specimen, a maximum of 27 in the Julfa crinoids. Measurements and indices for specimens from the literature and from the R. C. Moore collections are given in Tables 2 and 6.

TABLE 5. MEASUREMENTS (IN mm) AND INDICES FOR CRINOIDS FROM JULFA BEDS

SPM		KD	L	Li	P	Pi	A	Ai	C	Ci	KH	KHi	No. of culmina
J17	A	4.6	—	—	—	—	—	—	1.8	—	2.7	59.0	22
	B	4.6	—	—	—	—	—	—	—	—	2.4	52.0	—
(nodal)	C	5.1	—	—	—	—	—	—	—	—	2.9	57.0	—
	D	4.6	—	—	—	—	—	—	—	—	2.5	55.0	22
J16 (larger)													
	A	4.6	0.9	19.6	1.0	22.0	0.8	17.4	1.5	33.0	2.4	52.0	25
(nodal)	B	4.9	—	—	—	—	—	—	—	—	2.8	—	—
	C	4.7	—	—	—	—	—	—	—	—	2.5	—	—
	D	4.8	1.2	25.0	—	—	—	—	—	—	2.6	—	—
J16 (smaller)													
(nodal)	A	4.3	1.2	27.9	0.5	18.0	1.2	27.9	1.5	35.0	2.4	56.0	27
	B	4.4	—	—	—	—	—	—	—	—	2.0	46.0	—
(nodal)	C	4.5	1.2	26.6	0.6	15.0	1.0	22.3	1.5	34.0	2.7	60.0	22

TABLE 6. MEASUREMENTS (IN mm) AND INDICES FOR CRINOID STEMS IN R. C. MOORE COLLECTION SIMILAR TO CRINOIDS FROM JULFA BEDS

SPM	KD	L	Li	P	Pi	A	Ai	C	Ci	KH	KHi	No. of culmina
AK40												
(facetal view)	3.5	1.0	28.6	0.6	7.1	0.4	11.4	1.6	45.7	—	—	28
(internodal view)	3.8	—	—	—	—	—	—	—	—	1.0	26.3	—
(nodal view)	3.8	—	—	—	—	—	—	—	—	2.0	52.6	—
AK43												
(facetal view)	3.7	0.9	24.3	0.7	18.9	0.8	21.6	1.4	37.9	—	—	25
(internodal view)	4.0	—	—	—	—	—	—	—	—	1.0	25.0	—
(nodal view)	4.0	—	—	—	—	—	—	—	—	2.0	50.0	—
AK45 5d[1]												
(facetal view)	3.7	1.1	28.4	0.6	16.2	0.8	21.6	1.0	27.0	—	—	28
(internodal view)	3.9	—	—	—	—	—	—	—	—	1.0	25.6	—
(nodal view)	3.9	—	—	—	—	—	—	—	—	1.8	46.1	—
AW59[2]												
(facetal view)	8.3	2.5	30.3	1.5	18.2	1.8	21.6	2.2	26.5	—	—	40
AW134												
(facetal view)	6.5	2.5	42.3	1.0	15.4	1.3	19.2	1.5	23.1	—	—	58
BA34												
(facetal view)	2.7	0.8	29.6	0.6	22.2	0.4	14.8	0.5	18.5	—	—	23
(side view)	2.8	—	—	—	—	—	—	—	—	1.4	50.0	—
PEG54												
(both views)	5.8	1.8	30.4	1.3	26.1	1.3	26.1	1.0	17.4	1.9	32.6	38
Y1												
(internodal view)	6.2	1.7	27.5	0.6	9.7	1.2	19.4	1.7	27.5	1.9	30.5	33
(nodal view)	6.2	—	—	—	—	—	—	—	—	3.4	55.0	—

AK —Mingus Shale Member, Garner Formation, Strawn Group, Desmoinesian, Middle Pennsylvanian, Erath Co., Texas
AW —Chaffin Limestone Member, Thrifty Formation, Cisco Group, Virgilian, Upper Pennsylvanian, Brown Co., Texas
BA —South Bend Shale Member, Graham Formation, Cisco Group, Virgilian, Upper Pennsylvanian, Young Co., Texas
PEG— Marble Falls Limestone, Atokan, Middle Pennsylvanian, San Saba Co., Texas
Y —Waldrip Shale Member (Waldrip Limestone 3), Pueblo Formation, Wichita Group, Wolfcampian, Lower Permian, McCulloch Co., Texas

For additional information on localities, consult Moore, Jeffords, and Miller (1968b: 2–4).

[1] Moore and Jeffords, 1968, pl. 27, fig. 11a, b

[2] Moore and Jeffords, 1968, pl. 27, fig. 7a

Occurrence. Julfa beds, below Ali Bashi Formation (vicinity of Loc. 4).

Repository. KU 73304 (Pl. 10, figs. 13a, b), unfigured specimen, KU 73305.

Phylum uncertain

CONODONTOPHORIDA Eichenberg, 1930

Although it is believed that the skeletal apparatuses of several of the species described on the following pages consisted entirely of elements of a single morphologic type, taxa recognized are conceived to be "multielement" genera and species. Because all samples came from a limited stratigraphic interval and from a small outcrop area, no statistical evaluation of the collections was attempted. However, data on distribution and frequency given in Tables 7, 8, and 10 should be useful for this purpose when combined with similar information from other regions and sections.

The abbreviation OSU, which precedes catalog designations for types and other figured specimens, refers to the Orton Museum of Geology, at The Ohio State University, where the specimens are housed. The prefixes 69SA, 69SB, and 69SC before sample numbers are Ohio State University section designations that identify samples from Teichert-Kummel field localities 1, 2, and 4 respectively. The sample identified as 67GH-28 was collected by Stepanov *et al.* (1969) and is from bed 67 of their Julfa section. That bed is in the interval 11.3 to 30.8 m above the base of the Elikah Formation.

Genus *Anchignathodus* Sweet, 1970

Type species, *Anchignathodus typicalis* Sweet, 1970

Anchignathodus was established (Sweet, 1970a) to include conodonts with a skeletal apparatus composed solely of bladelike elements having an inconspicuously denticulated anterior crest and a distinctly denticulated posterior process, which surmounts a broad cuplike basal cavity whose lateral extensions may bear one or several denticles. In addition to *A. typicalis*, based on Lower Triassic specimens from Pakistan, Sweet suggested that several previously named conodont species should also be included in *Anchignathodus*, which would then range from Lower Carboniferous into lowermost Triassic. Affinities of many of the Lower Carboniferous forms are uncertain, but inclusion of "*Spathodus*" *minutus* Ellison, 1941, and *Spathognathodus isarcicus* Huckriede, 1958, still seems appropriate. The new species described below is clearly a close morphologic relative of *A. typicalis*.

In Pakistan (Sweet, 1970b), in Kashmir (Sweet, 1970a), and in samples at hand (Table 7), elements of *Anchignathodus* are commonly, but not invariably, associated with those referred to *Ellisonia teicherti* Sweet. There is thus a possibility that all these elements were components of the same skeletal apparatuses, not of the apparatuses of species referable to two conodont genera. At present, however, Sweet prefers to recognize two generic groups, *Anchignathodus* and *Ellisonia*, for no *E. teicherti*-like elements occur with those of *A. isarcicus* in any of his samples from the Werfen Formation of northern Italy, and elements of *Anchignathodus* and *E. teicherti* have little in common either morphologically or structurally.

It should also be noted that Clark (1972) regards *Anchignathodus* as one of the few survivors of an early Permian "crisis" and the probable ancestor of Permian species he refers to the genera *Neostreptognathodus* and *Sweetognathus*. Although there is some question as to whether the latter two names are validly established in Clark's report, they are apparently based on well-known species (*Streptognathodus sulcoplicatus* Youngquist, Hawley and Miller, 1951, and *Spathognathodus whitei* Rhodes, 1963, respectively) and, with *Anchignathodus*, they are referred by Clark (1972) to a new superfamily, the Anchignathodontacea. Kozur (1971), on the other hand, lumps *A. typicalis* Sweet and *A. isarcicus* (Huckriede) together into a single species, *Spathognathodus isarcicus*, the concept of which must be nearly as broad as Clark's Anchignathodontacea.

Anchignathodus isarcicus (Huckriede)

Plate 11, figures 5–7

Spathognathodus isarcicus Huckriede, 1958: 162, 167, pl. 10, figs. 6, 7a–c; Staesche, 1964: 288–289, figs. 6, 60, 61, 62, 63, 64.

Anchignathodus isarcicus (Huckriede), Sweet, 1970b: 223–224, pl. 1, figs. 18, 19.

Staesche's (1964) detailed description and illustrations of the various skeletal ele-

TABLE 7. DISTRIBUTION AND FREQUENCY OF ALI BASHI AND LOWER ELIKAH CONODONTS[1]

Formation	Sample	M above base of formation	Neogondolella orientalis	Neogondolella carinata subcarinata	Neogondolella carinata carinata	Xaniognathus sp. cf. X. elongatus	Anchignathodus julfensis	Anchignathodus typicalis?	Anchignathodus isarcicus	Ellisonia teicherti	Ellisonia gradata	Ellisonia spp.
LOCALITY 1 (OSU SECTION 69SA)												
Elikah Fm.	C8	38.0										
	C7	31.5										
	C6	25.5										5
	C5	21.0										6
	C4	16.5				1						1
	C3	13.5						4		1		
	C2	7.5										
	C1	4.5						3	8	4		
	22U	0–1.0							30	6		
	22M								43	21		
	22L							3				1
Ali Bashi Fm.	21	18.0						1				
	20U	17.4		1	1					2		
	20M	16.4		107	12	9					7	
	20L	15.4		262	26	25					21	
	19U	15.0		4	2	1		1				
	19L	13.6		18	4	1					3	
	18U	12.9		88	14	1					1	
	18L	10.9		350		23					27	
	17	10.6		204		7					12	
	16U	10.2		1								
	16M	9.4		83		1					1	
	16L	8.5		165			20					
	15U	7.9		2			1					
	15M	7.4		3			5			1		1
	14	6.7		159		1						
	12	6.1		198			1					
	10U	5.2		576		2	1				13	
	10M	5.0		765		29					69	
	9	4.3		108		10					8	
	8	4.0					286			87		1
	7	3.4		20		2	22					
	5	2.5		3			52					
	4	2.1		144		2	2				1	
	2	1.5		120		4	178			18		
	1	0.8		2								
	0	-1.0	119			14					3	2
LOCALITY 2 (OSU SECTION 69SB)												
Ali Bashi	3	19.00		30	8	6					5	
	2	18.0		87*		4					5	
	1	17.0		57	30	12					19	
LOCALITY 4 (OSU SECTION 69SC)												
Ali Bashi	7U	16.4		225		10					10	
	7M	14.3		45		9					7	
	7L	13.0		122	4	35		2			16	1
	6	10.4		530		1					1	
	5	4.6		53		3		3		5	3	
	2	2.1		38		6					3	
	1	0.2		29				8		3		
OSU SAMPLE 67GH-28 (From interval 11.3 to 30.8 m above base Elikah Fm.)												
E.					1			1		11		29

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[1] The numbers for units of the Ali Bashi Formation at Locality 1 correspond to those in the measured section on p. 374–381.

* Specimens with corrugated platform margins.

ments of this species cannot be enlarged from study of the 81 specimens at hand. These are clearly typical and are identified with *Anchignathodus isarcicus* without question. It should be noted only that Sweet (1970b) was obviously in error in removing to *A. typicalis* the laterally adenticulate specimens that Staesche (1964) assigned to *A. isarcicus.* Such elements do not occur with the few specimens of *A. isarcicus* known from Pakistan, but they are well represented in the Iranian collections under study (Pl. 11, fig. 5), and they are numerous in both Staesche's and Sweet's collections from the lower Werfen Formation of the southern Alps. These elements are shorter and broader than those of *A. typicalis*; have a high, almost straight posterior terminus; and tips of posterior denticles define a line that is not only normal to the axis of the cusp, but intersects it at midheight. These differences are well illustrated through comparison of figures 5 and 8 on Plate 11.

Kozur (1971) combines *Anchignathodus isarcicus* and *A. typicalis* Sweet into a single species, for which he uses the name *Spathognathodus isarcicus.* He gives no reasons for this combination, which results not only in considerably broadening the scope of a stratigraphically useful species but also seems to ignore distributional data summarized by Sweet (1970b) and increased in this report. Further, because the holotype of *Spathodus primus* Branson and Mehl, 1933, type species of *Spathognathodus,* was almost certainly part of the skeletal apparatus of the Silurian multielement species *Ozarkodina typica,* it seems curiously inexpressive of taxonomic relations to continue use of *Spathognathodus* for this Lower Triassic conodont species.

Occurence. Loc. 1, lower 4.5 m of Elikah Formation (OSU section 69SA), Kuh-e-Ali Bashi (Table 7); Kathwai Member, Mianwali Formation, Pakistan (Sweet, 1970b); lower Werfen Formation, northern Italy (Huckriede, 1958; Staesche, 1964).

Repository. Figured specimens, OSU 29551 (Pl. 11, fig. 5), 29552 (Pl. 11, fig. 6), 29553 (Pl. 11, fig. 7).

Anchignathodus julfensis n. sp.

Plate 11, figures 10–14

Diagnosis. A species of *Anchignathodus* characterized by straight to slightly bowed bladelike skeletal elements, about twice as long as wide, in which denticles in the posterior third of the unit produce a distinctive hump in the lateral profile.

Material. 568 discrete elements.

Description. Elements of *Anchignathodus julfensis* are bladelike units that are straight or slightly bowed and typically about twice as long as wide. At the anterior end of the unit is a laterally compressed cusp that is broadly triangular in lateral view; its axis is outlined by a strip of "white matter" along its posterior edge, which curves anteriorly and upward from the tip of the basal cavity. The anterior one-half to two-thirds of the cusp is a thin, flangelike process that lacks "white matter"; its anterior edge is sharp and smooth in most specimens, but marked by faint serrations anterobasally in a few. In a few large specimens the cusp tip is bifid; in smaller forms, however, it is single and sharply pointed.

Posterior to the cusp are 13 to 18 laterally compressed denticles of subequal width that are fused with adjacent denticles except at their tips, which are sharp in small elements, but bluntly rounded in larger ones. From a level slightly above the basal cavity to their tips, denticles are completely white at all stages in their growth.

The five to seven denticles just behind the cusp decline regularly in length, but in the posterior third of the unit denticle tips form an upwardly convex bulge or hump in the upper edge. In small elements representing early growth stages denticle tips in the "hump" are discrete; but in larger specimens, representing later growth stages, denticle tips fuse or are overgrown in at least the highest part of this segment of the element.

Beneath the posterior two-thirds of the element, the attachment surface is enclosed in a deep, asymmetrically subconical basal cavity, which is widest near its anterior end, tapers to a point at the posterior end of the unit, and is prolonged anteriorly as a low, narrow groove beneath the posterior half of the flangelike anterior extension of the cusp.

Remarks. The upwardly convex bulge or "hump" produced by denticles in the posterior third of the unit readily distinguishes elements of *Anchignathodus julfensis* from those of any previously described species of *Anchignathodus.* Except for this distinctive feature, *A. julfensis* elements are similar to those of both *A. typicalis* Sweet, type species of *Anchignathodus,* and *A. minutus* (Ellison), a common Carboniferous species. The sinuous lateral profile and the absence of lateral denticles, or of any discernible tendency to develop them, distinguish *A. julfensis* elements from those of *A. isarcicus* (Huckriede), a stratigraphically useful lowermost Triassic species.

Occurrence. Loc. 1, 1.5 to 8.5 m above the base of the Ali Bashi Formation, Kuh-e-Ali Bashi. (Samples 69SA-2, 4, 5, 7, 8, 10U, 12, 15M, 15U, and 16L.)

Repository. Syntypes, from sample 69SA-8, OSU 29554 (Pl. 11, fig. 10), 29555 (Pl. 11, fig. 11), 29556 (Pl. 11, fig. 12), 29557 (Pl. 11, fig. 13), 29558 (Pl. 11, fig. 14).

Anchignathodus typicalis Sweet?

Plate 11, figures 8, 9

?*Anchignathodus typicalis* Sweet, 1970a: 7, pl. 1, figs. 13, 22; Sweet, 1970b: 222–223, pl. 1, figs. 13, 20.

Our collections from the Julfa District contain 26 specimens that may represent *Anchignathodus typicalis* Sweet, but cannot be referred to that species with certainty either because they differ in some ways from typical representatives or because they are too fragmentary for positive identification. Two of the better-preserved specimens are illustrated and distribution of the others is given in Table 7.

The most characteristic feature of *Anchignathodus typicalis* elements is the profile of the upper edge of the denticle series, which forms a more or less straight line that declines regularly from the cusp tip to a point two or three denticles anterior of the posterior end of the unit. In addition, the posterior end of the unit curves abruptly downward, so that in the holotype it is essentially normal to the plane of the base. Elements here tentatively included in *A. typicalis* exhibit the profile distinctive of the holotype and lack the "hump" in the posterior part of that profile that is taken to be characteristic of *A. julfensis* elements. However, in a number of specimens, including the ones illustrated, abrupt rounding of posterior ends begins at a much higher level than in typical *A. typicalis* elements, with the result that the entire unit is somewhat shorter relative to its width than is true of the type material.

With respect to the morphology of its elements, *Anchignathodus typicalis* was undoubtedly a generalized form and it now seems likely that it was the stock from which several species having more distinctive elements developed. Our tentative identifications here may thus be susceptible of improvement in the future, when we have seen more material and can understand the phylogeny of *Anchignathodus* more fully.

Occurrence. Distribution of elements tentatively identified with *Anchignathodus typicalis* in Kuh-e-Ali Bashi is given in Table 7. The species is known from the uppermost Chhidru and lowermost Mianwali Formation of the Salt Range, West Pakistan (Sweet, 1970b); from the upper Zewan series and the lower few meters of the superjacent Lower Triassic beds at Guryul Ravine, Kashmir (Sweet, 1970a); from the *Otoceras-Ophiceras* beds of the Spiti District, western Himalayas (Sweet, unpublished MS); from Upper Permian and Lower Triassic strata in the Kap Stosch area of East Greenland (Sweet, unpublished MS); from the lower part of the Dinwoody Formation in Idaho and Wyoming (Sweet, 1970b and unpublished information); and from the lowest few meters of the Werfen Formation in the southern Alps of northern Italy (Sweet, 1970b).

Repository. Figured specimens, OSU 29559 (Pl. 11, fig. 8), 29560 (Pl. 11, fig. 9).

Genus *Ellisonia* Müller, 1956

Type species, *Ellisonia triassica* Müller, 1956

In a report on latest Permian and Early Triassic conodonts from Pakistan, Sweet (1970b) referred seven species based on recurrent groups of morphologically different elements to *Ellisonia* Müller. By referring these multielement species to *Ellisonia,* he indirectly expanded the scope of a genus originally erected to include only hibbardelliform conodont elements. No revised diagnosis was presented, however, for it was noted that a large number of conodont species, ranging in age from Ordovician through Triassic, had skeletal apparatuses composed of combinations of the forms that distinguish the multielement groups he assigned to *Ellisonia.* It is still not known how most of those species should be assembled into genera or what the names for those genera should be. *Ellisonia* was chosen primarily because the type of the form genus is Early Triassic in age and was probably a skeletal component of one of the species described. This essentially conservative procedure has drawn critical comment from Kozur and Mostler (1972a), however, and their views merit analysis.

On page 10 of their 1972a paper, Kozur and Mostler write:

> "In der sehr gewissenhaften und vorbildlichen Arbeit von HUDDLE 1968 wurde die Gattung *Ellisonia* als Synonym zu *Diplododella* gestellt. Die Typusart von *Ellisonia* und viele der dreiästigen Conodonten der Trias gehören zu *Diplododella.* Ein jüngeres Synonym muss aber verworfen werden; der Name *Ellisonia* kann also nicht verwendet werden."

This is a puzzling statement. The first sentence of it is correct; the second is a subjective assertion; and the last could be correct only if it were established that (1) Müller's original proposal of *Ellisonia* was defective in terms of the *International Code of Zoological Nomenclature*, and hence was invalid from the start; or that (2) the type species of *Diplododella* Bassler and *Ellisonia* Müller are founded on the same type specimen(s), and hence are objective synonyms.

In our opinion, *Ellisonia* is valid because Müller (1956) satisfied all of the provisions of the *International Code* in establishing it. That is, the name was published in the meaning of Chapters III and IV of the Code; it can be treated as a Latin word and as a noun in the nominative singular; Müller consistently applied binominal nomenclature in his paper; and proposal of the name was accompanied by a statement giving characters differentiating the taxon for which it was proposed. Further, Müller's original diagnosis of *Ellisonia* is accompanied by definite fixation of a type species, *Ellisonia triassica* Müller, 1956, which is founded on a discrete holotype from the Lower Triassic cephalopod bed, Dinner Springs Canyon, Nevada (Dept. Geol. Univ. Iowa, SUI 2257), that was also diagnosed and illustrated in Müller's 1956 report (p. 822, pl. 96, figs. 12–14).

By the same reasoning, *Diplododella* Bassler, 1925, is also valid. Its type species is *D. bilateralis* Bassler, 1925, which is based on a shale-embedded holotype (U. S. National Museum 11306 VP) from the Gassaway Member of the Chattanooga Shale of Alabama. Holotypes of *Ellisonia triassica* Müller, 1956, and *Diplododella bilateralis* Bassler, 1925, are clearly different specimens, of different ages, and from geographic localities more than 2,500 kilometers apart. There is not the remotest possibility that the two species, hence the genera of which they are types, are based on the same specimen, and Huddle (1968) makes no such claim.

In short, *Diplododella* Bassler, 1925, and *Ellisonia* Müller, 1956, are both valid generic names and they can not possibly be *objective* synonyms. All that Huddle did in his 1968 report was state the opinion that *Diplododella, Elsonella,* and *Ellisonia* are names for the same conodont form genus. In doing this, he proposed a *subjective* synonymy and chose *Diplododella* as the name for the combined form genus because it has obvious priority. Article 17(1) of the *International Code*, however, states that ". . . a name is or remains available even though . . . it becomes a junior synonym; such a name may be re-employed if the synonymy is judged to be erroneous, or if the senior synonym is found to be invalid or unavailable . . ." Thus, despite Huddle's action, *Ellisonia* is still available, and it will continue to be so until we either abandon binominal nomenclature or rewrite the *International Code.* Objectively and incontrovertibly, the name will always be available for use with the holotype of *E. triassica* Müller, 1956, which is type species of *Ellisonia.* Subjectively, the name is available for (but need not be used for) (1) any specimen identified as a representative of the same form species as the holotype of *E. triassica;* (2) any collection of specimens deemed to represent the multielement species of which the holotype of *E. triassica* is thought to have been a part; or (3) any form or multielement species thought to be part of the same genus as *E. triassica.*

Sweet (1970b) expressed the opinion that the holotype of *Ellisonia triassica* was part of a skeletal apparatus that also included the type specimens of *Hibbardella subsymmetrica* Müller, 1956; *Lonchodina triassica* Müller, 1956; *Hindeodella nevadensis* Müller, 1956, *H. triassica* Müller, 1956; *H. raridenticulata* Müller, 1956; *Neoprioniodus unicornis* Müller, 1956; and possibly the specimen Müller (1956) identified as *Ozarkodina*? sp. Because this array of elements includes one (*E. triassica*) that is type specimen of the type species of a genus (*Ellisonia*), Sweet chose, as first reviser, to use the name *Ellisonia triassica* for the species he thought was represented by the entire assembly just enumerated. Sweet's opinion may be unacceptable, but his procedures are permissible within the framework of the *International Code.* Actually, the only nomenclatural constraint introduced is upon those who agree with the Sweet opinion, for they must now use the trivial name *triassica* (rather than *subsymmetrica, nevadensis, raridenticulata,* or *unicornis*) for this multielement species.

The seven multielement species included in *Ellisonia* by Sweet (1970b) are similar in many ways, but they are by no means identical. In fact, three subgroups can be recognized. In one, including *E. triassica,* the hibbardelliform (or U-) element has a long, denticulated posterior process but there was apparently no enantiognathiform (or LC-) element; in another, including *E. teicherti,* the U-element lacks a posterior process and no enantiognathiform (or LC-) elements have been recognized; and in a third, including *E. clarki, E. delicatula, E. gradata,* and *E. torta,* enantiognathiform (=LC-) elements are prominent skeletal components and hibbardelliform (or U-) elements have denticulated posterior processes. If these differences are substantiated through study of additional material, they are probably sufficient to merit recognition of three genera. The name *Ellisonia* can be used appropriately for multielement species like the first one mentioned, but it is still not certain what names could (or should) be used for the other two groups. A likely candidate for the third group is *Cypridodella* Mosher, 1968, which is based on *C. conflexa* Mosher, 1968, a probable LA-element of a multielement apparatus generally like that of *Ellisonia gradata* Sweet, 1970a, 1970b. In this report, however, we continue to use *Ellisonia* for species of all three groups because their components are currently isolated from better-known Paleozoic faunas, interspecies relations are not clear, and there is some controversy as to the makeup of the apparatuses themselves.

Ellisonia gradata Sweet

Plate 12, figures 6–10

Ellisonia gradata Sweet, 1970a: 8, pl. 1, figs. 1, 5, 6, 9; Sweet, 1970b: 229–231, pl. 4, figs. 1–8.

Lonchodina latidentata (Tatge),-Huckriede, 1958: 151, pl. 10, figs. 32, 38, 39.

Roundya n. sp. A. Huckriede, 1958: 161, pl. 10, fig. 20.

Gen. et spec. indet. A. Huckriede, 1958: 163, pl. 10, fig. 28.

Collections from the Ali Bashi Formation in three sections in Kuh-e-Ali Bashi include 235 discrete elements that compare favorably with the syntypes of *Ellisonia gradata* Sweet and are assigned to that species without question. Sample-by-sample distribution and frequency of the five morphologically distinct components of *E. gradata* in Kuh-e-Ali Bashi collections are given in Table 8.

Except to extend the range of *Ellisonia gradata* downward into the uppermost Permian, and its geographic distribution to northwestern Iran, the material at hand adds little to the concept of the species as given by Sweet (1970a, 1970b), which was derived from a study of more than 1,000 discrete elements from Lower Triassic rocks in Kashmir and West Pakistan. Nevertheless, an extended discussion of *E. gradata* and its skeletal components is appropriate because questions about the species have been raised by Kozur and Mostler (1972a).

Kozur and Mostler (1972a: 10) have recorded their views as to identity of the syntypes of *E. gradata* (Sweet, 1970b, pl. 4, figs. 1–8) and those views are summarized and contrasted with Sweet's view in Table 9 of this report. After listing their views about *E. gradata,* Kozur and Mostler ask: "Why has a 'new species' been created here?" Moreover, they seem to be incredulous that "*Ellisonia gradata,*" which is common in, and ranges through, the entire Scythian, has not been encountered by conodont workers before 1970 and that no individual element had been named before Sweet's (1970b) report appeared. Their conclusion, referring to views summarized in Table 9 but omitting mention of the U-element (OSU 28030), is that we here deal with no new form species but just with forms that were apparently unknown to Sweet even though they are among the commonest in the Triassic. That is, it is apparently their view that all the components of *E. gradata* (except its U-element) had already been named before 1970, but that Sweet was ignorant of this fact.

TABLE 8. DISTRIBUTION AND FREQUENCY OF ELEMENTS OF *Ellisonia gradata* SWEET

Sample number	Frequency of element types				
	U	LA	LB1	LB2	LC
69SC-7U	3		2	1	4
69SC-7M	2	2			3
69SC-7L	3				13
69SC-6					1
69SC-5	1			2	
69SC-2	1				2
69SB-3	1		2		2
69SB-2	1		1		3
69SB-1	7	1	4	3	4
69SA-20M	3		1		3
69SA-20L	3	2	4	5	7
69SA-19L			1	1	1
69SA-18U			1		
69SA-18L		6	9	1	11
69SA-17	4	1	1	1	5
69SA-16M					1
69SA-10U	5			1	7
69SA-10M	11	7	16	4	31
69SA-9	3	1		1	3
69SA-4					1

Contrary to this opinion, all the form species mentioned by Kozur and Mostler as senior synonyms for the various skeletal components of *Ellisonia gradata* were well known to Sweet before he proposed names for any of the multielement species in his reports on conodonts from Kashmir and Pakistan. In June 1966, Sweet compared all components of *E. gradata* directly with type and other relevant specimens in the Tatge and Huckriede collections in Marburg, and in the Staesche collections in Tübingen. He has not seen the type material of *Apatognathus ziegleri* Diebel, which is housed in Berlin. From those comparisons, Sweet concluded that, in spite of obvious similarities in overall organization and structure, material from Pakistan differed systematically from, and therefore did not represent any of, the form species founded on type material housed in the Marburg or Tübingen collections. He also concluded, as stated in the synonymy on page 229 of his 1970b report, that U-elements of *E. gradata* are the same as the Salt Range Triassic specimens Huckriede (1958) described as *Roundya* n. sp. A; and that LB2-elements of *E. gradata* were clearly the same as the Salt Range specimens assigned to *Lonchodina latiden-*

TABLE 9. IDENTITY OF SYNTYPES OF *Ellisonia gradata* ACCORDING TO SWEET (1970b) AND KOZUR AND MOSTLER (1972a)

Syntypes	Identified by Sweet as	by Kozur and Mostler as
OSU 28027	LC-element, *E. gradata*	Fragment of an undoubted *Enantiognathus ziegleri* (Diebel, 1956).
OSU 28028	LB1-element, *E. gradata*	*Hindeodella (Metaprioniodus) suevica* (Tatge, 1956) emend. Kozur & Mostler (=*Hindeodella (Metaprioniodus) latidentata latidentata* (Tatge) *sensu* Kozur, 1968).
OSU 28029	LA-element, *E. gradata*	*Prioniodina (Cypridodella) muelleri* (Tatge, 1956); anterior process fragmentary; of the type of *Prioniodina mediocris* (Tatge) of Huckriede (1958).
OSU 28030	U-element, *E. gradata*	*Hibbardella* sp.; probably a new form species; preservation too bad to permit statements about it; probably identical with *Roundya* n. sp. A. Huckriede, 1958 and *Hibbardella nevadensis* (Müller) of Igo and Koike, *in* Igo, Koike, and Yin, 1965.
OSU 28031	LA-element, *E. gradata*	*Prioniodina (Cypridodella) muelleri* (Tatge, 1956); anterior process fragmentarily preserved.
OSU 28032	LB1-element, *E. gradata*	So fragmentary that no assignment to a certain form species is possible (possibly *Hindeodella (Metaprioniodus) suevica*).
OSU 28033	LB2-element, *E. gradata*	*Hindeodella (Metaprioniodus) suevica*; very fragmentary; posterior process broken off; form with forked anterior end.

tata (Tatge) by Huckriede (1958)—but not the same as the type specimen of *Prioniodina latidentata* Tatge, 1956. Kozur and Mostler seem to have overlooked this, and in forming their conclusions about Sweet's lack of familiarity with the form species they cite, they also contradict one of their own dicta (1972a: 9–10), which states: ". . . wir möchten nicht in den Fehler einiger Autoren verfallen, die nicht aufgeführte Untersuchungen als nicht vorhandene Untersuchungen werten . . ."

What then, is the problem with *Ellisonia gradata?* Apparently there are two problems. First, Sweet has adopted multielement taxonomy as a *modus operandi* in conodont studies; and second, he apparently permitted considerably less variation from the stratigraphic and morphologic norms set by type specimens than did Kozur and Mostler. As to the first problem, Sweet notes that he is far more concerned with identifying and determining the distributions of recurrent groups of conodont elements that exhibit similarities in structural and secondary morphologic details than with establishing either the distribution or morphologic limits of the form species to which components of these groups might be assigned by practitioners of form taxonomy. In brief, Sweet regards the recurrent group as the basis for founding a conodont species, not the components (= form species) of that group, for at least some of the latter may be generalized forms that occur in several groups. Trivial names for these multielement species must be those of their oldest-named components only if it can be established that types of those form species were also parts of the recurrent groups for which their names are to be used.

But Kozur and Mostler are not inexperienced in multielement taxonomy. Indeed, in their 1971 paper they provide a good answer to the question they posed later (Kozur and Mostler, 1972a) about the need to name *Ellisonia gradata*. That is, in the former paper they established a "multielement" named *"Enantiognathus ziegleri,"* which includes components previously referred to the form species *Hibbardella magnidentata* (including *"Prioniodella" prioniodellides*) (= U-element), *Prioniodina muelleri* (= LA-element), *Hindeodella* (*Metaprioniodus*) *suevica* (= LB1- and LB2-elements), *Enantiognathus ziegleri* (= LC-element), and *Ozarkodina tortilis* (= ?-element). Except for *O. tortilis*, whose association with the *"E. ziegleri"* multielement is questioned by Kozur and Mostler themselves, this is the same array of element types assigned by Sweet (1970b) to the multielement species *Ellisonia gradata, E. clarki, E. delicatula, E. robusta*, and *E. torta*. Indeed, except for *Ozarkodina tortilis* and the U-element, this is the same list of form species to which Kozur and Mostler (1972a) assign the components of multielement *E. gradata* Sweet (cf. Table 9).

Sweet agrees that *"Enantiognathus ziegleri" sensu* Kozur and Mostler, 1971, (minus the problematic *Ozarkodina tortilis*) is a likely multielement species and comments only that it probably belongs in the same genus as *Ellisonia gradata*. Whether the Kozur-Mostler multielement species should be named *"Enantiognathus ziegleri"* or not is quite a different matter. That is, until it is known what other elements are associated with the type specimen of *Apatognathus ziegleri* Diebel, 1956, it would seem far safer to choose a name for the Kozur-Mostler multielement species from among the form species Tatge (1956) named *Roundya magnidentata, Lonchodina muelleri, Apatognathus longidentatus*, and *Prioniodina latidentata*, for the holotypes of all these are from the same sample and there can be little doubt about their co-occurrence or identity in age.

What is especially significant to this discussion is the fact, admitted by Kozur and Mostler (1972a), that the U-elements of *Ellisonia gradata* and *"Enantiognathus ziegleri"* are different. In all of the 156 U-elements of *E. gradata in* Sweet's collections from the Salt Range, West Pakistan, and from Kuh-e-Ali Bashi, Iran, the cusp is at the crest of the anterior arch, is several times longer than any preserved denticle posterior of it, and is not preceded in any specimen by anterior denticles of any size. On the holotype of *Roundya magnidentata*, the U-element of *"Enantiognathus ziegleri,"* however, there is a denticle anterior of the cusp, and Kozur and Mostler (1972b) state that in this form species there are generally one to two small denticles between the cusp and the crest of the anterior arch. Other differences, perhaps of lesser importance, are readily discernible by comparing Sweet's (1970b) description and illustration of the syntype U-element of *E. gradata* with Tatge's (1956) illustration and description of the holotype of *Roundya magnidentata* and Kozur and Mostler's (1972b) description and illustrations of specimens they identify with the form species.

According to Kozur and Mostler (1972a; Table 9 of this report), all the syntype LB1- and LB2-elements of *Ellisonia gradata* are fragmentary representatives of *Hindeodella* (*Metaprioniodus*) *suevica* (Tatge), in which they also include *Prioniodina latidentata* Tatge and the conodonts distributed by 12 previous authors among some 18 different form species (Kozur and Mostler, 1972b). Sweet has re-examined the 268 questioned specimens from the Lower Triassic of Pakistan and has given careful attention to 57 additional ones from Kuh-e-Ali Bashi collections. All these specimens are fragmentary in one way or another. Most lack a denticle- or cusp-tip here and there and all lack an unknown length of the posterior process. Nevertheless, in a substantial number enough of that process is preserved to show that its lower margin is quite straight in lateral view, not bowed downward a short distance behind the cusp as in the holotype of *Lonchodina suevica* Tatge and in all the complete representatives of this form species illustrated by Kozur and Mostler (1972b, pl. 9, figs. 20, 22, 23). On a few tiny specimens, the posterior process, although truncated by breakage, is so low at its distal end that it is difficult to believe it could ever have been as long as, to as much as three times as long as, the anterior process. Further, denticles on both anterior and posterior processes are distinctly compressed and bladelike, not of circular cross section as are the denticles and cusp of the holotype; and the cusp of elements representing late growth stages is broadly triangular in lateral view and can be seen to have incorporated in its basal portion denticles that were adjacent to it laterally at earlier stages in growth. None of these features was mentioned by Tatge (1956) as a character of the two specimens on which she based her concept of *Lonchodina suevica* and none was apparent to Sweet when he examined those specimens in Marburg. Finally, LB- elements of *Ellisonia gradata,* like other skeletal components of this species, are distinguished from the holotype of *L. suevica* by a cloudy distribution of "white matter." Kozur and Mostler (1972a) minimize the taxonomic significance of "white-matter" by appeal to an unsupported assertion that this feature (and others such as robustness and, to some extent, the degree of fusion and the number and development of the denticles) is dependent on facies conditions such as water depth and water movement. This may well be so, but the fact remains that all the features mentioned, including "white-matter" distribution, are objective characters and, as such, they are commonly used to distinguish one specimen from another.

What about *Ellisonia gradata,* then? As conceived by Sweet (1970a, 1970b), it is a multielement species, based on an assemblage of conodont elements, which forms a recurrent group with an average Index of Affinity of 0.77 in collections from Lower Triassic rocks in West Pakistan. Based on the 24 Pakistan samples that contain all the elements of this recurrent group, the coefficient of rank concordance is 0.41, and this value is statistically significant at the 0.05 level. Further, components of this group are intergradational morphologically and similar in style of denticulation, conformation of attachment surface, size, and distribution of "white matter." In fact, the group meets all the criteria Sweet and his colleagues have set for themselves in recognizing multielement species (Webers, Schopf and Sweet, 1966; Bergström and Sweet, 1966; Kohut and Sweet, 1968; Sweet and Bergström, 1970; Sweet, 1970b; etc.). Kozur and Mostler (1972a) do not question the concept of *E. gradata,* which closely matches that of their "*Enantiognathus ziegleri,*" so they must be worried about the name proposed for *E. gradata,* not about the species itself.

Sweet has tried to show that there are objective differences between the U- and LB-elements of *Ellisonia gradata* and the holotypes of *Roundya magnidentata* Tatge and *Lonchodina suevica* Tatge. Comparable differences could be cited if additional space were devoted to comparing the LA-elements of *E. gradata* with the type of *Lonchodina muelleri* Tatge. However, even if one were to accept all the synonymies suggested by Kozur and Mostler for the components of *E. gradata,* the hibbardelliform U-element would still be unassociated with a previously named form species. And this, in Sweet's opinion, is sufficient to distinguish the recurrent group he named *Ellisonia gradata* from "*Enantiognathus ziegleri*" of Kozur and Mostler (1971), which may well include the type specimens of all the form species but *Apatognathus ziegleri* to which those authors referred the syntypes of *E. gradata.*

Occurrence. Loc. 1, 1.0 m below base of Ali Bashi Formation, and Ali Bashi Formation, Kuh-e-Ali Bashi, Iran (Table 7); base to top of Mianwali Formation (Lower Triassic), Salt Range, West Pakistan (Sweet, 1970b); Lower Triassic strata, Guryul Ravine, Kashmir (Sweet, 1970a).

Repository. Figured hypotypes, OSU 29561 (Pl. 12, fig. 8), 29562 (Pl. 12, fig. 10), 29563 (Pl. 12, fig. 9), 29564 (Pl. 12, fig. 6), 29565 (Pl. 12, fig. 7).

Ellisonia teicherti Sweet

Plate 12, figures 1–5

Ellisonia teicherti Sweet, 1970a: 8, pl. 1, figs. 3, 4, 7, 8, 12; Sweet, 1970b: 232–234, pl. 4, figs. 20–28.

This distinctive multielement species is represented in the collections at hand by the 159 discrete elements whose distribution and frequency are given in Tables 7 and 10. In general, representatives of *Ellisonia teicherti* in Kuh-e-Ali Bashi collections are somewhat smaller than the syntypes of the species, which are from Lower Triassic rocks in Pakistan. In all other respects, however, they are comparable and are assigned to the species without question.

As noted in the original diagnosis of *Ellisonia teicherti* (Sweet, 1970a, 1970b) the uniform distribution of "white matter" throughout all elements is a distinctive character of the syntypes of this species, and it is equally evident in the specimens at hand. We also have pointed out in the discussion of *Ellisonia* earlier in this report that U-elements of multielement *E. teicherti* lack a posterior process and that the species thus differs from multielement *E. triassica,* whose hibbardelliform U-elements have a long, denticulated posterior process. This difference may ultimately be judged to be of generic significance when more is known of the distribution of *E. teicherti* and related species.

Occurrence. Ali Bashi and lower Elikah formations, Kuh-e-Ali Bashi, Iran (Tables 7, 10); uppermost Chhidru and lowermost Mianwali Formation, Salt Range, West Pakistan (Sweet, 1970b); uppermost Zewan series and lower part of superjacent Lower Triassic strata, Guryul Ravine, Kashmir (Sweet, 1970a); Upper Permian and Lower Triassic strata, Kap Stosch area, East Greenland (Sweet, unpublished MS); lower Dinwoody Formation at Teton Pass, Wyoming (Sweet, unpublished MS).

TABLE 10. DISTRIBUTION AND FREQUENCY OF ELEMENTS OF *Ellisonia teicherti*

	Frequency of Element Types				
Sample No.	U	LA	LB	LD	LE
Loc. 4					
69SC-5		1	2	1	1
69SC-1			1		2
Loc. 1					
69SA-C3		1			
69SA-C1		3			1
69SA-22U		3	3		
69SA-22M	1	1	10	4	5
69SA-20U				2	
69SA-15M				1	
69SA-8	2	14	39	12	20
69SA-2	4	2	5	4	3
67GH-28	1	4	4	1	1

Repository. Figured hypotypes, OSU 29566 (Pl. 12, fig. 5), 29567 (Pl. 12, fig. 2), 29568 (Pl. 12, fig. 1), 29569 (Pl. 12, fig. 3), 29570 (Pl. 12, fig. 4).

Ellisonia spp.

Our collections from Kuh-e-Ali Bashi include 47 specimens that almost certainly represent skeletal components of some species of *Ellisonia* as that genus is defined in this report. A majority of the specimens are fragmentary and most of them are substantially larger than the ones assigned to either *E. gradata* or *E. teicherti.* It is likely that many, if not all, of these specimens are assignable to *E. triassica,* but we make no such assignment because the few identifiable specimens we have occur in different samples, not in association.

Occurrence. Distribution and frequency of specimens identified as *Ellisonia* spp. are given in Table 7.

Genus *Neogondolella* Bender and Stoppel, 1965

Type species, *Gondolella mombergensis* Tatge, 1956

The concept of this conodont genus employed here is the same as that outlined by Sweet (1970b). Clark and Mosher (1966) have described features that distinguish groups of Pennsylvanian, Permian, and Triassic species referred by most previous authors to *Gondolella,* and Sweet (1970b) has noted that *Neogondolella* elements differ from those of typical *Gondolella* in being finely to coarsely pitted (rather than smooth and glassy) on their upper sides; and in having a platform that is continued around the posterior side of the cusp as a more or less pronounced brim, whereas in typical

Gondolella elements, lateral platform elements are continuous with well-defined costae on the sides of the terminal cusp. Because relationships between Carboniferous and Permian-Triassic conodonts with gondolelliform elements are still obscure, it seems better to emphasize differences by referring the two types to separate genera than to unite all these forms in a single genus, *Gondolella*.

Gondolelliform elements dominate our collections from 1 m below the Ali Bashi Formation and from the superjacent Ali Bashi Formation. *Ellisonia gradata* Sweet and *Xaniognathus* cf. *X. elongatus* Sweet are common associates, but there is little in the way of morphologic similarity or frequency-ratios to suggest that all these elements were once parts of the same skeletal apparatus. Instead, we regard the gondolelliform elements at hand as representatives of two single-element species, *Neogondolella orientalis* (Barskov and Koroleva) and *N. carinata* (Clark). Among elements assigned to the latter, we recognize three intergradational subgroups, which are described formally as two subspecies of *N. carinata*.

Neogondolella carinata (Clark)

Gondolella carinata Clark, 1959: 309, pl. 44, figs. 15–19.

Neogondolella carinata (Clark),–Sweet, 1970b: 240, pl. 3, figs. 1–17, 24, 26, 27.

More than 75 percent of the conodont elements in collections from the Ali Bashi Formation are referable to *Neogondolella*. A few of these (102) are clearly identifiable with *N. carinata* (Clark), but the majority are intermediate morphologically between typical *N. carinata* and *N. orientalis* (Barskov and Koroleva), which are abundantly represented in the beds immediately below the Ali Bashi Formation. Because characters that distinguish most specimens of the Ali Bashi *Neogondolella* are constant through the formation, we believe the taxon merits separate recognition. However, because the elements at hand exhibit posterior characters more like those of *N. carinata* than of *N. orientalis*, we describe them here as representatives of a new subspecies of *N. carinata*, *N. carinata subcarinata*. A third group of gondolelliform elements, all from sample 69SB-2, is apparently related to the one we describe as *N. carinata subcarinata*, but platform margins are distinctly corrugated. We include these tentatively in *N. carinata subcarinata*, although in the future they may deserve separate identity as a subspecies of *N. carinata* or as an independent species of *Neogondolella*.

Neogondolella carinata carinata (Clark)

Plate 11, figures 1–4; Text-figure 16, I–L

(See synonymy for the species)

Elements of the typical subspecies of *Neogondolella carinata* (Clark) are distinguished by a spoutlike buttress at the posterior end which develops ontogenetically as the posterior ends of lateral platform segments grow around the cusp. Straight elements are essentially bilaterally symmetrical and, in superior view, the posterior platform buttress is set off by distinct notches in the platform margin just anterior to the cusp. Bowed elements lack an obvious notch on their convex side, particularly if they represent late growth stages, but retain a deep invagination in the platform margin on the concave side. In very large specimens the diagnostic platform notches tend to disappear or to be greatly subdued by continued growth of the posterior platform segment.

Occurrence. Locs. 1, 2, and 4, upper part of Ali Bashi Formation (at or near base of that part of the Ali Bashi Formation termed Paratirolites limestone by Stepanov *et al.*, 1969), and in sample 67GH-28 from between 11.3 and 30.8 m above the base of the Elikah Formation, Kuh-e-Ali Bashi, Iran (Table 7); uppermost part of Chhidru Formation (Permian) and lower part of superjacent Mianwali Formation (Lower Triassic), Pakistan (Sweet, 1970b); 33 to 55 feet above base of Triassic, Guryul Ravine, Kashmir (Sweet, 1970a); pre-*Meekoceras* Zone Triassic beds, Nevada (Clark and Mosher, 1966); uppermost Permian and

Lower Triassic strata, Kap Stosch region, East Greenland (Sweet, unpublished MS).

Repository. Figured specimens, OSU 29571 (Pl. 11, figs. 1, 3), 29572 (Pl. 11, figs. 2, 4).

Neogondolella carinata subcarinata Sweet n. subsp.

Plate 13, figures 12–17; Text-figure 16E–H

Diagnosis. A subspecies of *Neogondolella carinata* (Clark) with elements distinguished from those of the typical subspecies by a somewhat broader platform; a shorter, wider keel; and a less distinctly set-off buttress beneath the posterior platform brim.

Description. Elements of *Neogondolella carinata subcarinata* are symmetrical to slightly asymmetrical, 2.2 to somewhat less than 3 times as long as wide, and lachrymiform in outline. The carina is laterally compressed, straight or slightly bowed, and composed of seven to as many as 18 denticles, which are discrete in small specimens but fused, except at their tips, in larger ones. In elements representing intermediate and late growth stages, denticles in the middle third of the carina tend to form a low ridge, or are overgrown almost to their apexes by the platform. At both ends of the carina are distinctive crests of denticles: a posterior set of two or three includes the cusp, which is strongly inclined posteriorly; an anterior set of four to six surmounts a fragile bladelike extension of the carina.

Even in the smallest specimens available (Text-fig. 16, E), the carina is completely surrounded by a platform. The posterior extension of the platform is continuous with the posterior margin of the cusp and can be seen from below to be the upper edge of a faint spoutlike buttress, which, in small specimens, is more distinctly set-off from the remainder of the platform than in larger ones.

The under surface bears a narrow median groove, which is continuous with a slightly expanded, elongate pit beneath the cusp. Bordering the groove and pit and forming a very narrow band around the posterior end of the pit, is a well-marked keel, the under surface of which is flat or slightly convex. In none of our specimens is the keel more than half as wide as the unit; in most it is no wider than a fourth to a third the width of the platform.

Discussion. Elements of *Neogondolella carinata subcarinata* are readily distinguished from those of *N. orientalis* (Barskov and Koroleva) by presence of a distinct cusp at the posterior end of the unit at all stages of growth, by the very narrow posterior platform brim, and by the relatively narrow keel. Elements of this new subspecies are distinguished from those of *N. carinata carinata* by the indistinct posterior platform buttress and by lack of the distinct notches that mark the points in *N. carinata carinata* elements where lateral and posterior platform brims join around the cusp.

Occurrence. Ali Bashi Formation, Locs. 1, 2, 4, Kuh-e-Ali Bashi, Iran (see Table 7 for distribution and frequency).

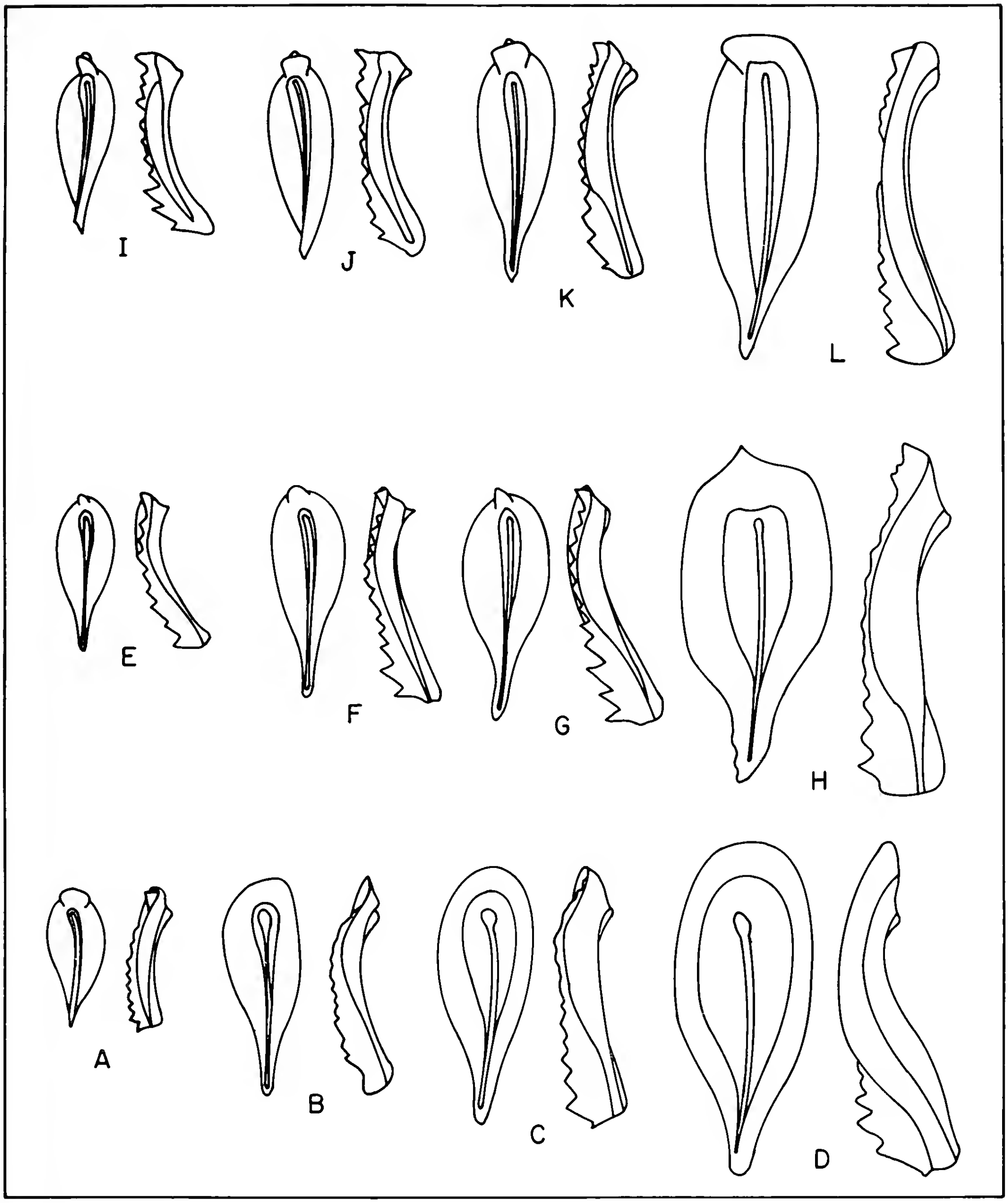
Repository. Syntypes, OSU 29573 (Pl. 13, figs. 12, 13), 29574 (Pl. 13, figs. 14, 15), 29575 (Pl. 13, figs. 16, 17).

Neogondolella carinata subcarinata Sweet, n. subsp. ?

Plate 13, figures 1–3

From a single sample (69SB-2) taken from about 1 m above the base of the Paratirolites limestone in the upper part of the Ali Bashi Formation, we have 87 gondolelliform elements that may be variants of *Neogondolella carinata subcarinata* or may represent a taxon that merits separate identity. We associate these specimens tentatively with *N. carinata subcarinata* because they exhibit some of the characters of elements of that subspecies, occur within the upper part of its range, and are known from just a single sample.

The elements in question are similar to those of *Neogondolella carinata subcarinata* in features of the lower surface and are in possession of a distinct posterior cusp, which is enclosed by an indistinct platform buttress. At the same time, they differ from those of *N. carinata subcarinata* in develop-



Text-figure 16. Outline of under and lateral views, ×50, of 12 specimens representing successive growth stages of (A–D) *Neogondolella orientalis* (Barskov and Koroleva), (E–H), *Neogondolella carinata subcarinata*, n. subsp., and (I–L) *Neogondolella carinata carinata* (Clark). Originals of views A–D are from *Vedioceras* beds, Dorasham 2 section, Nakhichevan ASSR; views E–H represent four of the syntypes of *N. carinata subcarinata;* and views I–L are of specimens from the Kathwai Member of the Mianwali Formation, Salt Range, Pakistan.

ment of transverse corrugations or crenulations along the lateral platform margins. These corrugations are only faintly discernible in small elements (Pl. 13, fig. 2), but increase in prominence in larger ones (Pl. 13, figs. 1, 3).

Occurrence. Sample 69SB-2, Loc. 2, 18 m above base of Ali Bashi Formation, Kuh-e-Ali Bashi, Iran.

Repository. Figured specimens, OSU 29585 (Pl. 13, fig. 1), 29586 (Pl. 13, fig. 2), 29587 (Pl. 13, fig. 3).

Neogondolella *orientalis* (Barskov and Koroleva)

Plate 13, figures 4–11; Text-figure 16A–D

Gondolella orientalis Barskov and Koroleva, 1970: 933, fig. 1, 1–4.

Barskov and Koroleva (1970) assigned some 150 specimens from the middle part of the Dzhulfian *Vedioceras* beds of the Dorasham 2 section in Transcaucasia to this distinctive species, and we have an additional 119 specimens from a stratigraphically comparable level in Kuh-e-Ali Bashi that are clearly conspecific. Although all of the specimens illustrated by Barskov and Koroleva lack part or all of the anterior end, the diagnosis and description prepared from a study of these specimens are thorough and more than adequate for recognition of the species.

Elements of *Neogondolella orientalis* are bilaterally symmetrical to weakly asymmetrical, lachrymiform in outline, and prominently arched in the posterior third of their length. In elements representing the earliest growth stages recognized in our collections, the carina is laterally compressed and consists of seven to nine apically discrete denticles of essentially the same length. In elements representing successively later stages of growth, the anterior three to five denticles become progressively more prominent, whereas those in the middle third of the carina fuse laterally to form a ridge that declines in height posteriorly and loses its identity at a point well anterior of the posterior margin of the element.

In elements representing all of the growth stages available to us, the carina is completely surrounded by a scoop-shaped platform having a finely pitted upper surface, which is broadly concave transversely, rounded posteriorly, widest at element midlength, and gradually tapered to the extremity of the element in the anterior third of its length. In the smallest element in our collection (Text-fig. 16, A), a prominent denticle at the posterior end of the carina, the cusp, is separated from the posterior margin of the element by a narrow platform brim, which can be seen from the under side to be the upper edge of a rounded buttress at the posterior end of the platform. In successively larger elements, the buttress disappears and the posterior platform brim broadens, in part through incorporation of the cusp, which is not a prominent feature, or may even be completely overgrown, in elements representing later growth stages.

The undersurface is distinguished by a narrow median furrow that terminates posteriorly in an elongate pit beneath the cusp. In elements representing early growth stages, the pit and furrow are enclosed laterally by a thin-walled sheath, which forms a median ridge on the under surface. In successively larger elements the pit and furrow come to be surrounded by a progressively wider and longer keel, the flat to faintly concave undersurface of which is marked by closely spaced longitudinal striae that represent the edges of growth lamellae. In specimens representing intermediate and late growth stages, the keel occupies one-half to as much as two-thirds the width of the undersurface.

Discussion. Elements of *Neogondolella orientalis* are distinguished from those of *N. carinata carinata* (Clark) by the lack of a prominent cusp except in early growth-stage elements, by the broad posterior platform brim, and by a keel that is one-half to two-thirds as wide as the unit in elements that represent intermediate and late growth stages. However, elements typical of *N. orientalis* grade through elements here assigned to *N. carinata subcarinata* Sweet, n. subsp., into elements referable to *N. carinata carinata* in all of the features just mentioned. Indeed, it appears from evidence now available that features seen only in early growth-stage elements of *N. orientalis* are prolonged into successively later growth stages in *N. carinata subcarinata* and *N.*

carinata carinata. From this we conclude that *N. carinata* evolved from *N. orientalis* in the latest Permian, and that linkage in this suggested series is provided by forms from the Ali Bashi Formation of Iran that we refer to *N. carinata subcarinata.*

Occurrence. Sample 69SA–0, Loc. 1, from beds 1 m below the base of the Ali Bashi Formation, Kuh-e-Ali Bashi, Iran; mid-portion of *Vedioceras* beds, Dorasham 2 area, Nakhichevan ASSR (Barskov and Koroleva, 1970).

Repository. Figured hypotypes, OSU 29576 (Pl. 13, figs. 10, 11), 29577 (Pl. 13, figs. 4, 5), 29578 (Pl. 13, figs. 8, 9), 29579 (Pl. 13, figs. 6, 7).

Genus *Xaniognathus* Sweet, 1970

Type species, *Xaniognathus curvatus* Sweet, 1970

Xaniognathus was erected (Sweet, 1970b) to include conodont species with skeletal apparatuses consisting of elements of a single morphologic type. In conventional parlance, these are ozarkodiniform elements with a long, denticulated anterior process that is longitudinally ribbed at mid-height, and a shorter posterior process that bears no midlateral rib.

Xaniognathus sp. cf. *X. elongatus* Sweet

Plate 12, figures 11–15

cf. *Xaniognathus elongatus* Sweet, 1970b: 266, 268, pl. 3, fig. 19.

Our collections from Kuh-e-Ali Bashi contain 219 representatives of *Xaniognathus* that are closely similar in a majority of their comparable characters to elements from the upper part of the Lower Triassic on which Sweet (1970b) based *Xaniognathus elongatus.* The elements at hand are largely from Permian rocks, however, and collectively they differ in at least two ways from the holotype and its companions on which the concept of *X. elongatus* was based. We do not know at this time whether greatest taxonomic weight should be placed on the many similarities, or on the differences between the Iranian Permian specimens and typical *X. elongatus* elements. Hence we describe the specimens at hand in open nomenclature, but indicate their close morphologic relationship to *X. elongatus* by comparing them with that species.

Iranian specimens compared with *Xaniognathus elongatus* are all arched and bowed ozarkodiniform elements, with a long, straight posterior process that is stout but not distinctly ribbed longitudinally; a steeply reclined, laterally compressed, sharp-edged cusp; and a short posterior process, which is thin, fragile, and no more than half as long as the anterior process. The eight to ten denticles of the anterior process, and the three to five of the posterior process, are sharply pointed, compressed, discrete for at least half their length, and steeply and uniformly reclined with respect to the axes of their respective processes. In lateral profile, the lower edge of the unit is almost straight in some elements (Pl. 12, fig. 15), but distinctly arched in others (Pl. 12, figs. 11–14); in elements of both types, however, there is a short downwardly convex segment in the lower margin just behind the posterior edge of the basal pit. Beneath the cusp is a sharp-pointed basal pit, which projects upward into the blade for about half its height but does not flare noticeably laterally. The pit is prolonged as a shallow groove beneath the proximal third of both processes; the underedge of the balance of the processes is sharp or faintly rounded. In elements that apparently represent later stages of growth, the attachment surface is distinctly "inverted" for essentially its entire length and, in a number of specimens, a narrow, sharp-edged ridge parallel to, but somewhat above, the lower margin, marks the upper edge of the "inverted" base.

In most specimens, the blade is clear and transparent below the level of denticle bases, and denticles and cusp are uniformly, but not densely, white. A few specimens, however, exhibit a slightly irregular distribution of "white matter" in denticles and cusp, and in this respect they somewhat resemble elements of *Ellisonia gradata.*

Remarks. The elements here compared

with *Xaniognathus elongatus* differ from typical representatives of that species in lacking a distinct midlateral rib on the stout anterior process and in having an attachment surface that is "inverted" for essentially its full length (rather than just posteriorly) in late growth-stage forms. It should be noted, however, that Iranian specimens are mostly much larger than typical *X. elongatus* elements from Pakistan and the differences just mentioned could well be associated with size and stage of growth represented.

The elements at hand, like the type material of *Xaniognathus elongatus*, are also similar in many ways to elements of "*Ozarkodina*" *tortilis* Tatge, but the posterior process of the latter is prominently twisted and nearly as long as the anterior process. Furthermore, in none of the descriptions of "*Ozarkodina*" *tortilis* elements is "inversion" of the attachment surface mentioned as a distinctive character.

Occurrence. Distribution and frequency in the Kuh-e-Ali Bashi samples are summarized in Table 7.

Repository. Figured specimens, OSU 29580 (Pl. 12, fig. 11), 29581 (Pl. 12, fig. 12), 29582 (Pl. 12, fig. 13), 29583 (Pl. 12, fig. 14), 29584 (Pl. 12, fig. 15).

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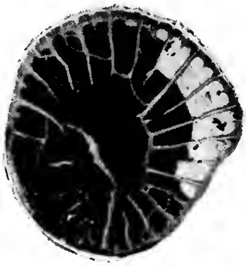
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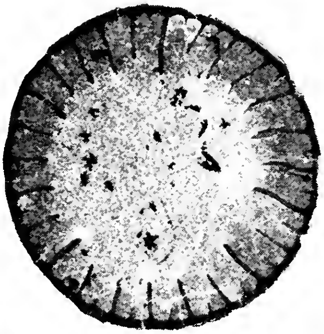
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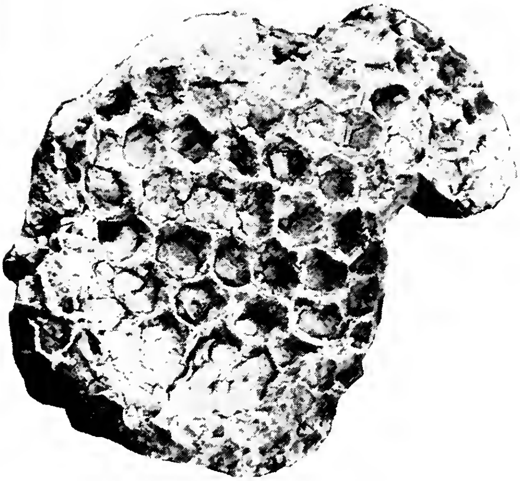
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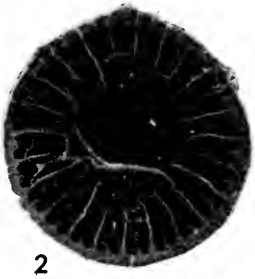
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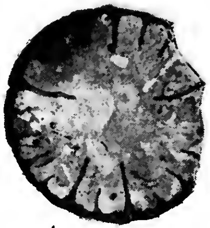
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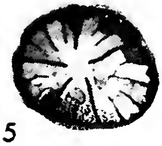
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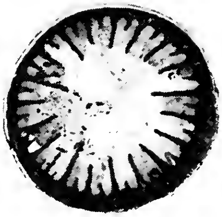
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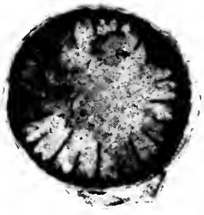
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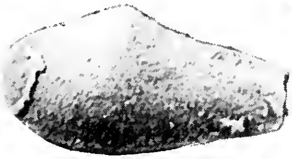
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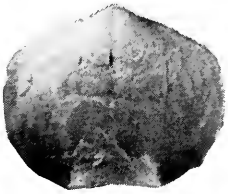
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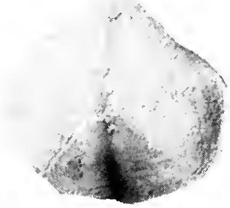
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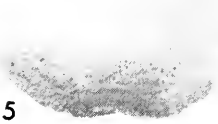
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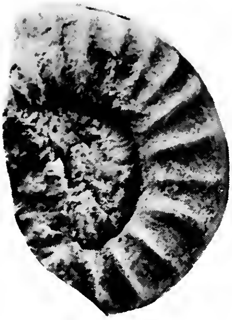
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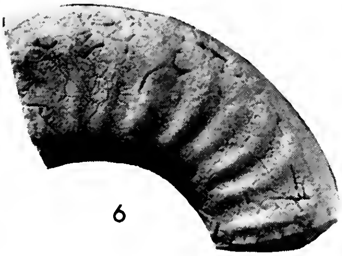
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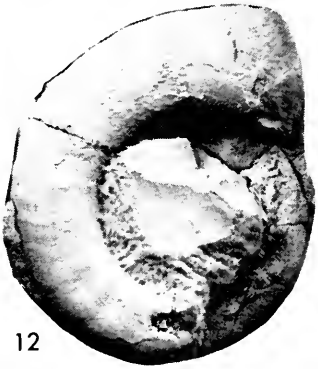
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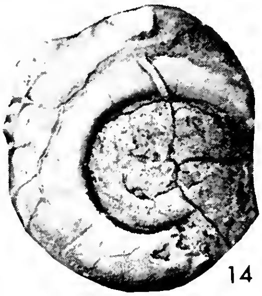
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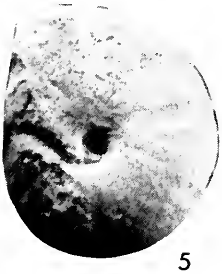
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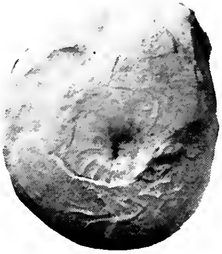
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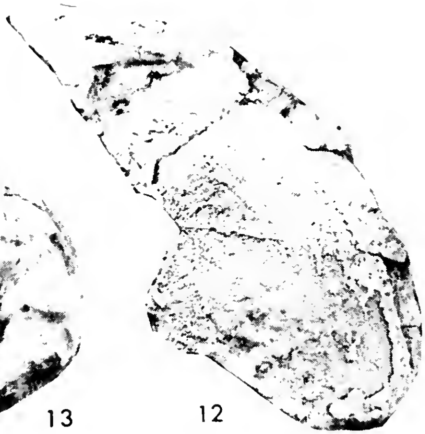
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5, 6	*Iranites transcaucasius* (Shevyrev) Specimen in place from Loc. 1, 10 m above base of formation. MCZ 9701. ×2.	408
7, 8	*Iranites transcaucasius* (Shevyrev) Float from undetermined horizon. MCZ 9702. ×1.5.	408
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10	*Iranites transcaucasius* (Shevyrev) Float from Loc. 2, 3.5 m above base of formation. MCZ 9704. ×1.5.	408
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18, 19	"*Pseudotirolites*" sp. indet. Float from Loc. 2, 2.1 m above base of formation. MCZ 9710. ×1.5.	405


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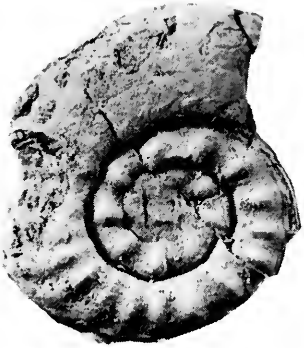
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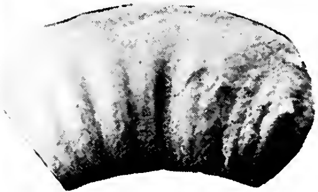
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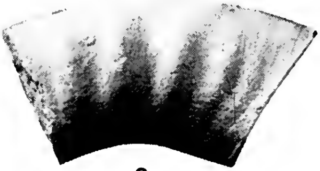
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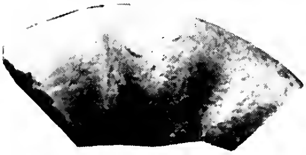
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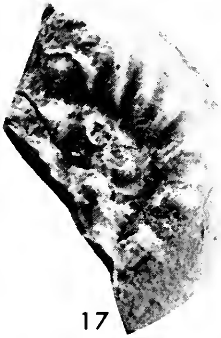
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3, 4	*Paratirolites kittli* Stoyanow Float from undetermined horizon. MCZ 9730. ×1.	408
5	*Paratirolites kittli* Stoyanow Floot from 20 cm above base of Paratirolites beds, Loc. 2. MCZ 9731. ×1.	408
6	*Paratiralites spinosus* (Shevyrev) Float from undetermined horizon. MCZ 9732. ×1.	413
7	*Paratirolites kittli* Stoyanow Float from 20 cm above base of Paratirolites beds, Loc. 2. MCZ 9733. ×1.	408
8, 9	*Paratirolites mojsisovicsi* (Stoyanow) Float from 1 m above base of unit 19, Loc. 1. MCZ 9734. ×1.	414
10, 11	*Paratiralites kittli* Stoyanow Float from undetermined horizon. MCZ 9735. ×1.5.	408


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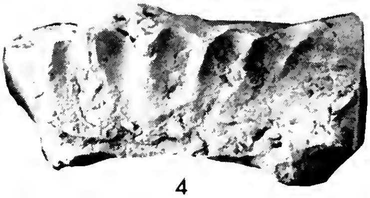
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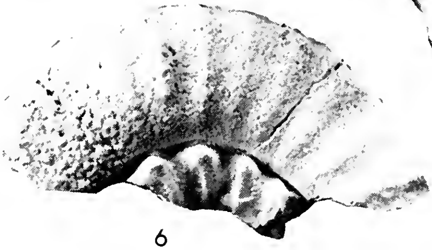
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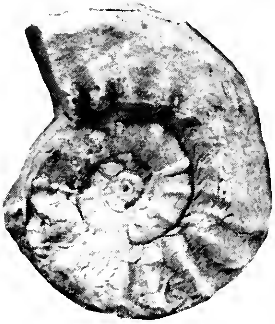
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Plate 7. PARATIROLITES

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1, 2	*Paratirolites mojsisovicsi* (Stoyanow) Float from Loc. 2, 9 m above base of formation. MCZ 9736. ×1.	414
3	*Paratirolites kittli* Stoyanow Float from undetermined horizon. MCZ 9737. ×1.	408
4, 5	*Paratirolites spinosus* (Shevyrev) Float from undetermined horizon. MCZ 9738. ×1.	413
6	*Paratirolites mojsisovicsi* (Stoyanow) Float from Loc. 3, 3 m above base of formation. MCZ 9739. ×1.	414
7	*Paratirolites kittli* Stoyanow Float from undetermined horizon. MCZ 9740. ×1.	408
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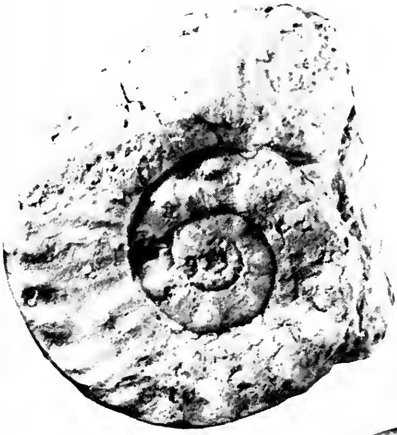
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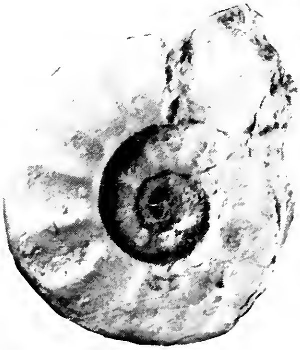
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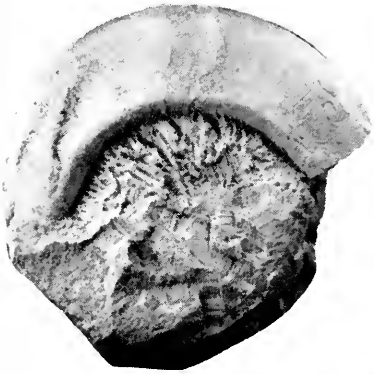

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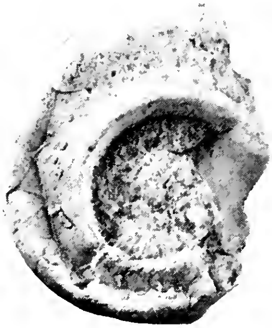

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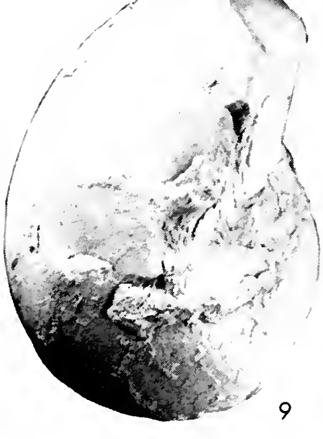

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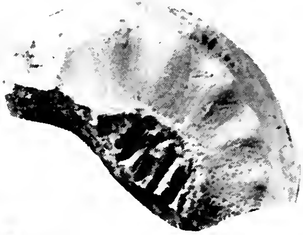
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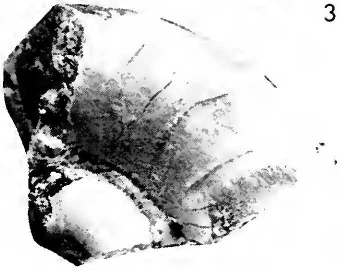
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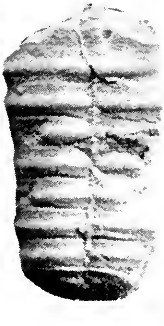
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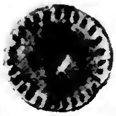
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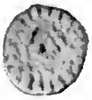
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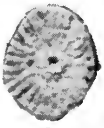
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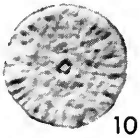
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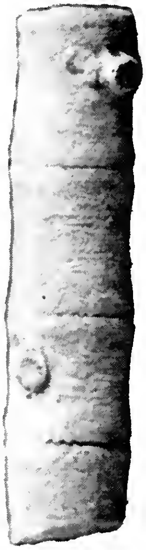
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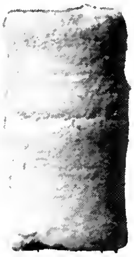
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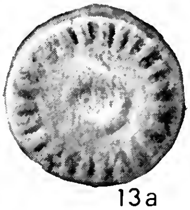
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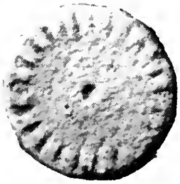
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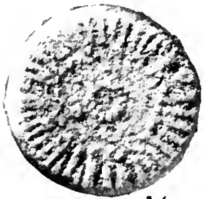
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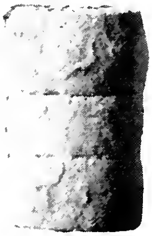
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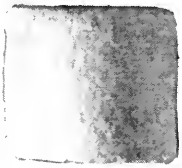
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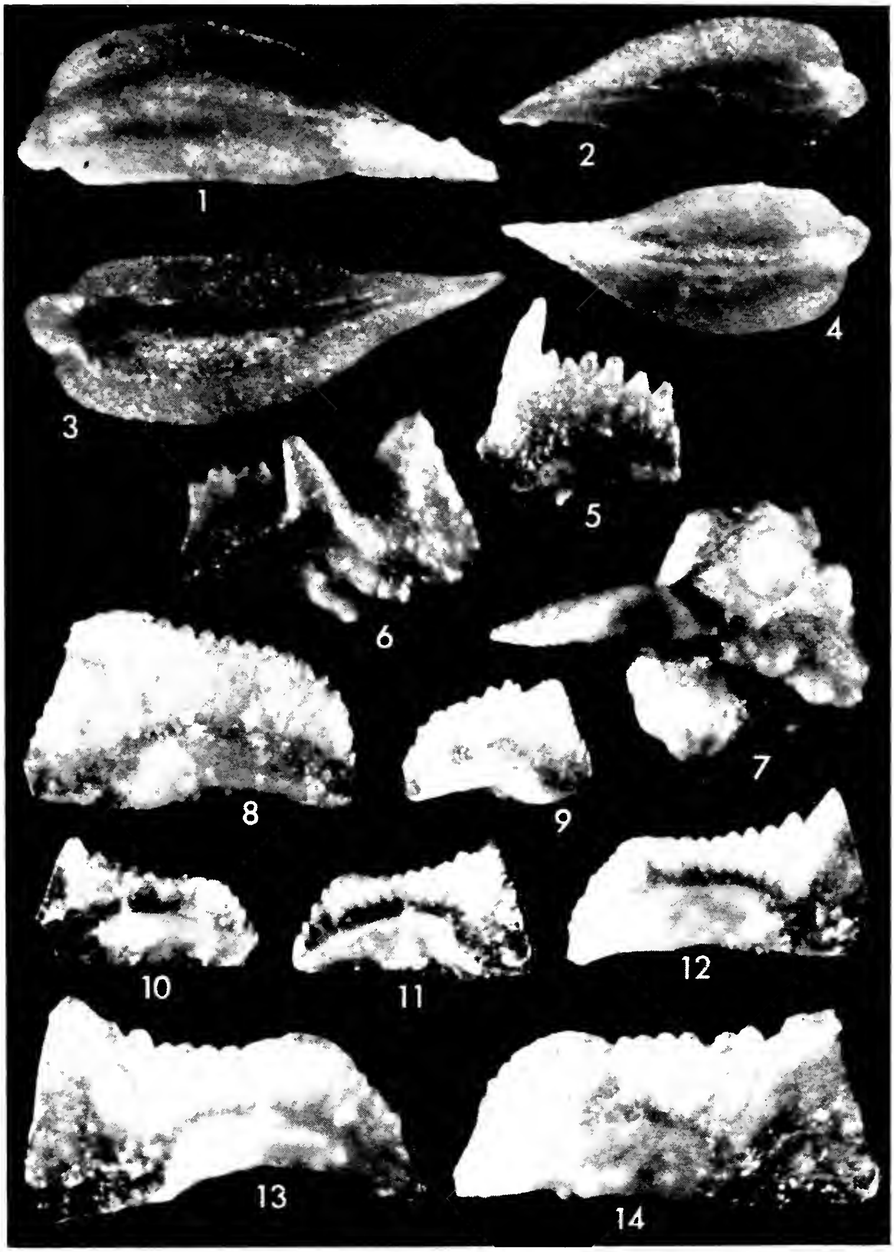
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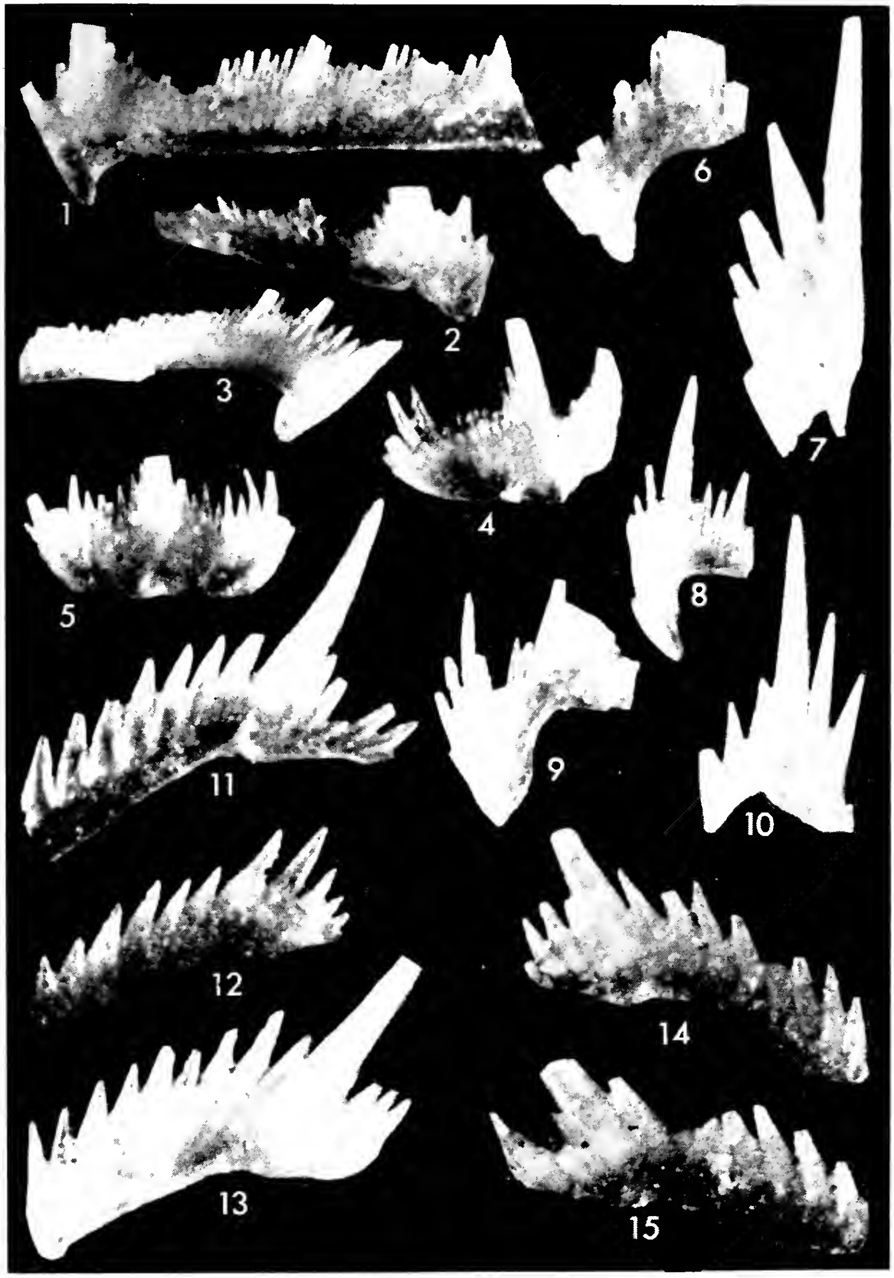
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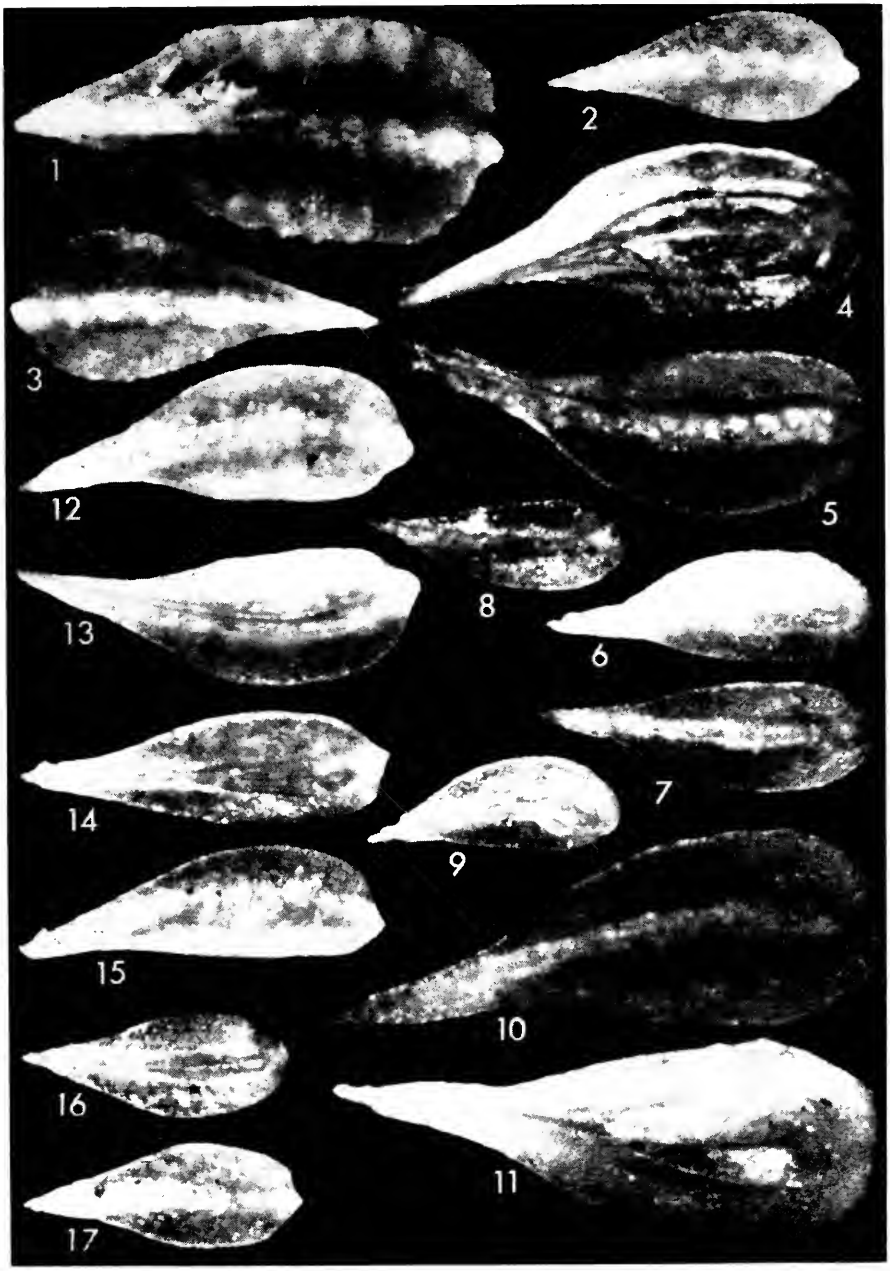
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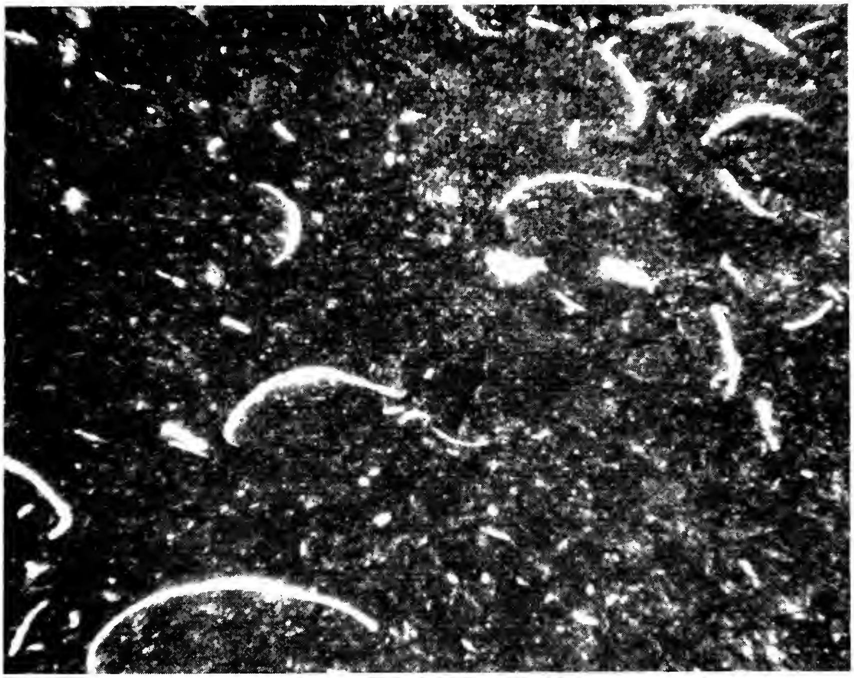

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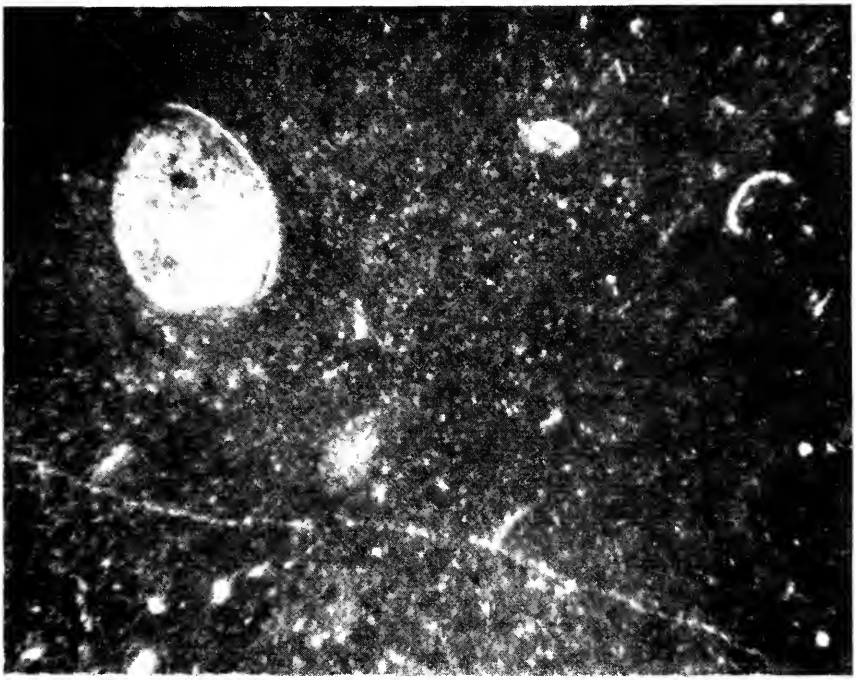

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Bulletin OF THE
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Small Orb-Weavers of the Genus *Araneus* North of Mexico (Araneae: Araneidae)

HERBERT W. LEVI

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CAMBRIDGE, MASSACHUSETTS 02138 U.S.A.

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CONTENTS

SMALL ORB-WEAVERS OF THE GENUS *ARANEUS* NORTH OF MEXICO (ARANEAE: ARANEIDAE)

HERBERT W. LEVI

Abstract. The small species of *Araneus* include the genera and subgenera *Amamrotypus, Cambridgepeira, Conaranea, Mimaranea* and *Conepeira* of Archer. There are altogether 31 species north of Mexico. Many of the species are rare in collections, presumably because they are forest species that make their webs in tree-crowns. Most larger collections come from mud dauber wasp nests. The distribution of the small species in general is eastern and southern North America, in contrast to the northern distribution of the larger species. Many species, as in theridiids, show a cline with the largest specimens in the North, the smallest in Florida. A correction is made to the previous study on the genus *Neoscona* and additional information presented on several large species of *Araneus*.

While meadows, "old field communities," shrubs, herbaceous layers of forests, and leaf litter have been well collected in many parts of North America, the spider fauna of the forest canopy remains largely unknown. Foliage of forest tree-crowns probably is the habitat of numerous small species of *Araneus*. Despite the possible economic importance of predators high up in trees, the scant knowledge we have of this habitat appears mostly in the European literature. This probably explains why the number of specimens available for this revision has been small.

I gratefully acknowledge the cooperation of my colleagues in entomology, Howard E. Evans and Robert W. Matthews, whose helpful wasps did most of the collecting, presumably high up, and delivered the spiders to the nest traps from which they were conveniently harvested. Without their assistance, insufficient material would have been available to sort out the species. Other collections were made available by J. Beatty, D. Bixler, W. J. Gertsch, J. A. L. Cooke and V. D. Roth of the American Museum of Natural History (AMNH[*]), Cornell University, and Utah University collections. J. E. Carico, R. E. Crabill of the U.S. National Museum, C. Dondale of the Canadian National Collections, Ottawa, R. Leech, B. J. Kaston, K. V. Krombein, F. E. Kurczewski, P. Miliotis, W. Wayne Moss of the Academy of Natural Sciences, Philadelphia, W. Peck of the Exline-Peck collection, Miss Susan Riechert, W. A. Shear, J. A. Sheals, D. Clark and F. R. Wanless of the British Museum (Natural History), Karl Stone, B. Vogel, H. K. Wallace (HKW) and H. W. Weems of the Florida State Collection of Arthropods (FSC). Next to the American Museum, the Museum of Comparative Zoology (MCZ) has the largest collections of these small *Araneus* species. Peter van Helsdingen and W. Shear contributed ideas throughout; E. Mayr advised on complicated nomenclatural matters. Also, I would like to thank Ann Moreton for living specimens and photographs. This investigation was supported in part by Public Health Service Research Grant AI-01944 and by a grant from the National Science Foundation GB-36161.

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[*] For rare species I have given the initials of the collection in the text.

INTRODUCTION

Unlike most groups of spiders, this group of *Araneus* has been previously revised. Archer's work (1951b) is unsatisfactory at present, as mine may be 20 years hence. I cannot agree with Archer's establishment of numerous genera (further discussion below) and with his delimitation of species. Many of his generic names are unnecessary and obscure the relationship of the included species. I have found this group of spiders extremely difficult to study; it took me a year to figure out the species. Neither the descriptions nor the illustrations of Archer give useful diagnostic characters. But Archer was handicapped by having few specimens to work with; only 25 years ago types were not readily available, and museum curators thought it more important to protect these name-bearing specimens than to make them available for study. Archer assumed that collections he borrowed were correctly identified, and that the specimens in each vial belonged to a single species. On the contrary, most specimens of the difficult *A. juniperi* subgroup were collected by wasps, which do not differentiate the species. Also, Archer seemed unaware that many old localities of Marx were in error. Perhaps Archer's most serious mistake was his use of only one character to differentiate species, the median apophysis of the palpus (Figs. 440–474) and the outline of the epigynum. One-character taxonomy is not the best way to study animals, and as it turns out, the median apophysis alone is a poor character for separating males of different species (Levi, 1971), as is the outline of the epigynum for separating females. As second revisor, I have learned much from the mistakes of my predecessor, just as my successors will learn much from mine.

The size of genera. If I were to follow Archer and split this group of *Araneus* I would end up having to place each of the relatively few tropical American *Araneus* in its own genus. Although there are not many *Araneus* species in the American tropics, they are quite distinct. Unnecessarily splitting genera just leads to further splitting, as new species found do not fit into the previously established genera. This eventually leads to having almost each species in its own genus. As most araneologists are aware, the large number of genera in the families Salticidae and Linyphiidae has not only impeded their study, but also has made it difficult for museum curators to file incoming collections and make specimens available. Worse, particularly in the Linyphiidae, the large number of genera has led to a most undesirable instability of names. The species, especially of Europe, are constantly being shifted from one genus to another. Instability and proliferation of names results in a nomenclature incomprehensible to anyone other than the specialist. Of course in small spiders, such as Linyphiidae, there is much greater diversity and many more species than in larger spiders (see below). When differentiating species one looks for consistent differences. It is thus easier to see differences than to see the similarities that are the basis for definition of a genus. If there is a choice, a large, monophyletic genus, though unwieldy, is preferable. The splitting of monophyletic groups into smaller and smaller units does not add to knowledge. While it is easy to make new generic names, synonymizing excess names (whose types are often unknown species) is one of the most difficult tasks for the taxonomist.

Diversity and size of spiders. It appears to be a general rule in spiders that the smaller the physical size, the larger the number of species within a group. Thus, in theridiids, the large-bodied genera *Steatoda* and *Latrodectus* have relatively fewer species in a given area than the small-bodied *Theridion* or still smaller *Thymoites* in the American tropics. The numerous generic name synonyms for *Thymoites* indicates, perhaps, a greater degree of diversity. Similarly, larger Linyphiidae have fewer species than the smaller Linyphiidae (Erigoninae). The majority of generic names in the Linyphiidae refer to the more diverse small species. Again, in *Araneus* in North America, there are only about 20 species in the well-known, large-sized *diadematus* group, but over 30 poorly known small species.

The reason for the greater speciation and diversity in smaller spiders is not known. The ranges of small-sized spiders do not seem smaller than the ranges of large ones. But perhaps the distributions of small species are less continuous, permitting geographic speciation, and perhaps there is less gene exchange among populations. One might expect that small species balloon more effectively, but little is known of ballooning. Recent Dutch studies on two related species of *Pardosa* indicate that the young of the species with a specialized habitat balloon, the young of the species with a more generalized habitat do not (Richter, 1970). Unfortunately, we know little that is accurate of the geographic distribution of these *Pardosa* species. As in the well-studied Dutch *Pardosa* species there is reason to believe that many of the small *Araneus* are specialized in their habitats [*e.g.*, *Araneus gadus* on pitch pine (*Pinus rigida*) in the Northeast].

European relatives of small-sized American species tend to be larger than their American relatives. I was made aware of this by P. van Helsdingen, who is studying the linyphiid spiders. The two European species *Araneus sturmi* and *A. triguttatus* are larger in size than their many American relatives. This size difference probably does not hold for the large-sized species. In North America there is often a cline in size, the largest individuals of a species in the North, the smallest in Florida, West Indies and Texas. This is true of the small species of *Araneus* as well as of many theridiid species. The reason for this and for the comparatively larger size of European relatives might be the competition of larger-sized species belonging to tropical genera that find it easier to spread north in the Americas but that might be blocked in Europe by the deserts of North Africa and the Mediterranean.

Names. Names of animals, including spiders, are not provided in order to be changed, anymore than are the names of chemicals, geological strata, or minerals. The object of the Code of Nomenclature (1961) is to "promote stability and universality in the scientific names of animals and to ensure that each name is unique and distinct. All its provisions are subservient to these ends. . . ." Unfortunately, some taxonomists take articles from the Code out of context, to rationalize their changing names, digging up older names, or finding better spellings. Such activities generally have an inverse correlation with the amount of research that has been done. Changes in names should only be made when biologically necessary, or when an older name is discovered for a recently established (or little-used name), and in cases of synonymy or homonymy.

Among the most complex nomenclatural problems is the treatment of homonyms of specific names, identical names applied to two species. I have been inconsistent from the point of nomenclatural rules in the discarding of junior homonyms of specific names (which are at present in different genera). However, I have been consistent from the point of view of spider names, making the least possible number of changes of names in use.

Among the working tools handed down through successive spider workers at the Museum of Comparative Zoology, there was included a list of about 30 common Latin adjectives to be used as new species names. Unfortunately, the use of common Latin adjectives in large families and in large genera such as *Araneus* results in name changes, when, in revision, the names are found to be homonyms. It is better to avoid trite Latin adjectives and use instead arbitrary combinations of letters, the names of American Indian tribes as nouns in apposition, or place names, even though they might be difficult to pronounce by Chinese or Greek colleagues. Also, I personally object to naming a new species after a living colleague (unless he collected the specimen, or his homonym needs renaming), as it would ask for a return of such a "favor."

Abbot, in the latter part of the 18th century, made colored illustrations of Georgia spiders. He indicated that many of his *Araneus* specimens were harvested from wasp nests. In the 1830's, Walckenaer gave names to the illustrations of Abbot's manuscript. In the 19th century, on rediscovering the Abbot manuscript, McCook used those Walckenaer names that he could identify with the illustrations (Chamberlin and Ivie, 1944; Levi and Levi, 1961). Since these species have no other names (except some very recent ones by Archer) and can readily be recognized by color pattern of specimens freshly collected by wasps, it would be capricious to ignore these Walckenaer names of Abbot illustrations.

However, Chamberlin and Ivie (1944) took a black-and-white film of these Abbot illustrations, which are kept in the British Museum (Natural History), and on the basis of subjective interpretation, substituted many of these Walckenaer names in place of the accepted Hentz names that had been in use for common spiders for almost 100 years. The procedure is generally unacceptable and is not permitted by the present Code of Nomenclature. Chamberlin's film, to judge by his 1944 reproductions, was of poor quality (perhaps high contrast film) and numerous obvious errors were made (Levi and Levi, 1961), including substituting Walckenaer 1841 names for older names in use at the time [*e.g.*, for *Peucetia viridans* (Hentz, 1832)]. Kodachrome and xerox copies of Abbot's pictures and accompanying notes are now available at the Museum of Comparative Zoology.

Chamberlin and Ivie's (1944) interpretation of Walckenaerian names and descriptions and Abbot's illustrations for the small species of *Araneus* are erroneous, despite the fact that the pattern on the abdomen in this group may be diagnostic. The Chamberlin collection, now kept in the American Museum of Natural History, was available to me. Some published names in this paper were applied to juvenile specimens collected by W. Ivie (*Epeira juniperi, E. guttulata*) which I cannot place. Archer examined only one of these Georgia specimens in the Chamberlin collection, marked by Ivie *guttulata,* and left a note in the vial correctly indicating that this cannot be the correct name.

Methods. All drawings in this paper were made with an American Optical dissecting microscope, Greenough type, or a comparable Greenough-type Leitz microscope. A reticle in the eyepiece is divided, 20 by 20, into 400 squares. The drawings are made on tracing paper with a grid of squares underneath to match the grid of the reticle. The drawings are then traced on sculptured Coquille paper, drawn with Rapidograph pens and lithographic pencils nos. 3, 4, and 5, and touched up with opaque white paint. For drawing, the specimens are completely submerged in a dish of alcohol, the bottom of which has a layer of paraffin with various sized depressions and holes. Usually black paraffin is preferable; a white background causes reflections that make structures hard to see. However, to see some black peripheral structures, a white background may be useful. I have found it unsatisfactory to keep structures in place with petroleum jelly (Vaseline) as it is difficult to clean off. Placing the structure in sand may also cause disturbing reflections not present with a dark background. Lighting is provided by several microscope lights used together (American Optical Model 651), and a fiberglass light. Left palpi and sometimes epigyna have to be cut off for study. These are stored with the spider in a separate, tiny, cotton-plugged vial. If necessary, the palpi and the epigyna are cleaned with ultrasonic cleaner, an E/MC Corp. Model LP2 (Shear and Levi, 1970). Placing the whole spider in the ultrasonic cleaner is inadvisable as it disturbs the pigment pattern. For clearing to see internal structures, the alcohol is blotted off and the structure or the whole spider is immersed in clove oil. The clove oil can be blotted off and the specimen returned to 80 percent ethanol (Levi, 1965).

An attempt was made to photograph species live (or recently preserved) on high-speed Ektachrome film to record the color pattern, which washes out in the alcohol preserving fluid. In the difficult *A. juniperi* subgroup the diagnostic color pattern may be helpful, especially for an amateur or an ecologist who is not a spider specialist.

Procedure of study. When I started the study of small species of the *A. juniperi* subgroup of *Araneus,* I followed Archer (1951b) and used his characters, the median apophysis and outline of the epigynum, to differentiate the species. As the median apophysis hooks into the scape in mating, I studied the scape. This led me completely astray, as I took for granted that Archer matched males and females correctly. Some specimens that Archer studied appeared lost. Archer's habit of sometimes taking off one palpus of a type and putting it into another vial with a paratype (often of a different species) adds to the confusion. Only later did I examine the heavily sclerotized structures, the embolus (partly hidden within the palpus), the tooth of the conductor, and the terminal apophysis of the palpus, and in the female, the openings of the epigynum as well as the coloration (washed out in old specimens). I made numerous drawings (unpublished). In the meanwhile, a statistical study was started trying to differentiate the species by proportions. It was a complete waste of time. All of the *A. juniperi* subgroup turned out to have similar proportions. Finally I had some success in sorting the specimens into species by structures. Matching males and females proved especially difficult. A clue came when recently collected specimens from Georgia revealed that different species have different patterns. But most old alcoholic collections had lost their color and patterns except for black pigment. Collections that presumably included *A. cingulatus* and *A. niveus* males were carefully sorted out according to black pigment on the abdomen. Further study showed that *Araneus niveus* with a black patch on the abdomen also had the conductor spine at a different angle from that of *A. cingulatus,* but the embolus length was variable. New questions were raised when I examined old collections of nonpigmented *niveus*-like males from New Hampshire, an area from which I had no females of *A. niveus.* It occurred to me then that these might be the missing males of *A. guttulatus.* Later, a wasp trap in eastern Massachusetts yielded a female of *A. guttulatus* which had the same abdominal pattern as that of a male collected with it; the male had a palpus similar to that of males from New Hampshire. On reexamining males determined as *A. niveus,* I found that I had confused two species (*A. guttulatus* and *A. niveus*). *Araneus niveus* always has black pigment on the abdomen, *A. guttulatus* may or may not; but both have an otherwise unique character, the conductor spine behind or near the tegulum margin.

While to a nonsystematist taxonomic work appears mysterious and, if names are changed, annoying, the difficulties in sorting out populations by morphology are not appreciated. Published studies give only the final result in which all appears dogmatic, simple and obvious, without showing the numerous false leads and fumbling errors.

The species concept. While I cannot agree with what Archer (1951b) called a species in this group, I still consider that there are numerous poorly known species (rather than a single variable one) in the *A. juniperi* subgroup. The reason is that the shape of the scape of the epigynum, though somewhat variable, is correlated with a certain shape of the base of the epigynum, which has characteristic openings. In addition the shape and color pattern of the abdomen correspond to the character of the epigynum. The specimens thus segregated, though much alike, are quite distinct and without intermediates, indicating sympatric populations. Nevertheless, the species are surprisingly similar and hardly any differences could be found in size and none in proportions. Those who work with measurements only may be misled into considering all to be one species.

My friend and mentor Willis Gertsch has at various times strongly disagreed with me on the definition of a species (in correspondence, and Gertsch, 1960). One of his strong objections (in correspondence) was to my figures 2 and 3, 5 and 6, of *Enoplognatha ovata* (Levi, 1957), which, according to Gertsch, could not possibly be one species. This species has now been reared, and the illustrated variation is found to occur within siblings from the same egg sac (V. Seligy in correspondence, and 1971).

I make the assumption, of course, that we can tell natural species readily by their morphology, an assumption that may not always be correct. I also assume that species are variable and might on occasion hybridize, as has recently been shown by den Hollander (1970, and 1973) in *Pardosa*. A further assumption is that sibling species do have biological differences other than morphology, *e.g.*, the differences in habits of *Latrodectus mactans* and *L. variolus*. While I disagree with those who believe species should not be described on the basis of a single available specimen, I also disagree with those who consider every collection of specimens a different species without taking account of geographical or possible individual variation. After all, taxonomy is a branch of biology.

Neoscona Correction

When we revised the genus *Neoscona* in North America (Berman and Levi, 1971) the type of *Neoscona naiba* Chamberlin and Gertsch could not be found. On the basis of measurements given by the authors, the name was synonymized with *N. arabesca* Walckenaer. When the collection of the University of Utah was recently transferred from the University of Utah to the American Museum, the type and paratypes were found. They had been overlooked because they were marked *Neoscona oaxacensis naiba* Chamberlin and Gertsch. The holotype is a poorly preserved specimen of *N. oaxacensis.* While the pattern could not be checked, the epigynum is characteristic for this species. The male and female paratypes are in worse condition. The male lacks all appendages, including most coxae; the female is also a specimen of *N. oaxacensis.* Perhaps the specimens were the remnants found in the web of another spider, or the prey of a wasp or other predator. The name is not a synonym of *N. arabesca.* It is, as Chamberlin already recognized (judging by the label and its place in the collection), a synonym of *N. oaxacensis.*

Araneus Clerck, 1757

Araneus Clerck, 1757, Svenska Spindlar, p. 15. Type species *A. angulatus* Clerck. (For details and additional synonymy see Levi, 1971, Bull. Mus. Comp. Zool., 141: 131–179.)

Atea C. L. Koch, 1837, Übersicht des Arachniden Systems 1: 3. Type species *Epeira sturmi* (Hahn) designated by Bonnet, 1955, Bibliographia Araneorum, 2: 769.*

Neosconella F. P.-Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 474. Type species *Neosconella styligera* F. P.-Cambridge 1904, by original designation.

Amamrotypus Archer, 1951, Amer. Mus. Novitates, No. 1487: 17. Type species *Amamrotypus mammatus* Archer 1951, by original designation. NEW SYNONYMY.

Cambridgepeira Archer, 1951, Amer. Mus. Novitates, No. 1502: 2. Type species *Epeira detrimentosa* O. P.-Cambridge, by original designation. NEW SYNONYMY.

Conaranea Archer, 1951, Amer. Mus. Novitates, No. 1502: 5. Type species *Epeira excelsa* Banks [= *A. bispinosus* (Keyserling)], by original designation. NEW SYNONYMY.

Mimaranea Archer, 1951, Amer. Mus. Novitates, No. 1502: 7. Type species *Epeira triguttata* Fabricius, by original designation. Described as a subgenus. NEW SYNONYMY.

Conepeira Archer, 1951, Amer. Mus. Novitates,

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* Bonnet designated *Atea agalena* the type of the genus; this is not one of the three originally included names (*sturmi, vulpina, sclopetaria*); however, on the same page Bonnet gives a synonymy of *Atea agalena* = *Araneus sturmi.*

No. 1502: 12. Type species *Epeira miniata* Walckenaer, by original designation. NEW SYNONYMY.

Note. Neosconella was separated from *Araneus* by F. P.-Cambridge, who indicated that no species close to *Aranea diadema* [= *Araneus diadematus*] and *Epeira cornuta* are found in Central America. He described the female as lacking macrosetae, and the male "clavis [median apophysis] biforked." The lack of macrosetae is a characteristic of small *Araneus* species. Archer took the simple hook-shaped median apophysis of *A. pegnia* and *A. thaddeus* as a character to separate the genus. The type species *Neosconella styligera* F. P.-Cambridge, although close to *A. pegnia* and *A. thaddeus,* has quite a different median apophysis (Fig. 439). *Neosconella styligera* characters are intermediate between *A. thaddeus* and the other small species and illustrate well the difficulties of splitting up the genus *Araneus.*

It is difficult to make a key to the groups within the genus *Araneus,* since the divisions are somewhat arbitrary.

Diagnosis. I am forced to wait with a differential diagnosis of *Araneus* until I have studied species of related genera including *Metepeira, Araniella, Aculepeira* and the common widespread species "*Araneus*" *cornutus,* "*A.*" *patagiatus* and "*A.*" *sericatus.*

NATURAL KEY TO SPECIES GROUPS OF *Araneus*

1 First leg coxa of males with a hook on distal margin fitting into a groove on second femur 2

— First leg coxa of males without a hook on distal margin 3

2(1) Median apophysis almost circular in mesal view with 2 to 3 distally (on palpus) directed teeth (Figs. 422, 434) .... *A. pegnia* group

— Median apophysis longer than wide .... (Levi, 1971) .... *A. diadematus* group,* *A. diadematus* subgroup

3(1) Embolus with a cap covering only its tip (Levi, 1971), total length of males except *A. illaudatus* more than 5 mm .... *A. diadematus* group,* *A. cavaticus* subgroup

— Embolus with a cap having a tail along length of embolus (Figs. 100, 102); total length of males less than 5 mm, except *A. mammatus* .... *A. sturmi* group

KEY TO GROUPS OF *Araneus* FEMALES

1 Total length more than 8.5 mm; if less, then epigynum with sclerotized posterior lamellae (Levi, 1971, figs. 3, 78, 117, 125) 2

— Total length less than 8.0 mm and without sclerotized posterior lamellae on epigynum 3

2(1) With openings of epigynum anterodorsally (Figs. 77, 78); southwestern states .... *mammatus*

— Openings ventral or posterior .... *A. diadematus* group*

3(1) Epigynum with a long straight scape extending almost as much anteriorly of base as posteriorly (Levi, 1971, figs. 34–36); abdomen with dorsal folium and white spots arranged in shape of a cross (fig. 37); Newfoundland to Great Lakes, Pacific coast from British Columbia to Oregon .... *diadematus*

— Epigynum and abdomen otherwise; most species less than 6 mm total length .... *detrimentosus,* *A. sturmi* group and *A. pegnia* group, p. 487.

KEY TO GROUPS OF *Araneus* MALES

1 First leg coxa with a hook on distal margin 2

— First leg coxa without a hook on distal margin 3

2(1) Terminal apophysis a sclerotized prong (Figs. 411, 412); median apophysis elongate with spines on both ends or one end (Fig. 412) .... *diadematus* group*

— Terminal apophysis a wide pointed piece (Figs. 422, 423, 434, 435); median apophysis short, rounded in mesal view with hooks or teeth directed to tip of bulb (Figs. 422, 434) .... *pegnia* group, p. 489.

3(1) Terminal apophysis a flat, wide hard sclerite (Figs. 13, 18, 68) .... *sturmi* group, p. 489.

— Terminal apophysis tip not sclerotized or if sclerotized, prong-shaped (*yukon, groenlandicola, iviei, cavaticus, gemmoides, gemma, pima, illaudatus*) .... *diadematus* group*

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* Key, Levi, 1971: 139. Although *A. detrimentosus* is included in this paper and key with small *Araneus* it is probably closer to the *A. diadematus*

The Diadematus Group

This group, except for one additional species, *A. detrimentosus* (p. 00), has been revised (1971).

Correction, p. 140 (Levi, 1971). In the key 12b leads to 15 (not 14) and 13b to 14 (not 15).

The specific name has to be *Araneus groenlandicola* (not *groenlandicolus*).**

Araneus andrewsi (Archer)
Plates 1, 2

A series collected in Monterey Peninsula, California, in pine and oak woods; all were found on the trunks of pine trees and except for two were greenish in color (R. Johnson, Jr., personal communication). The spiders were hard to find because of their protective coloration.

A female collected and sent to me from Santa Cruz, California, by Mr. Mark Stowe had "made a web from a lichen covered tree. Others made webs along the edge of pine forests." The color matched the lichens. Surprisingly, the specimen had a delicate velvety green background color on the dorsum of the abdomen and legs (Plate 2). The darker parts of the folium and posterior part of the humps were brown. In coloration and habits it is similar to the eastern *A. bicentenarius.* It readily built a web in the window frame of my study (Plate 1) and fed on moths.

Araneus washingtoni Levi
Plate 2

A female collected at the foot of Mt. Washington, New Hampshire, by Mr. Mark Stowe, was kept alive and photographed (Plate 2). Females can readily be recognized when alive by the shape of the abdomen and its pattern. The color is brown. An additional record, extending the distribution of this species, is from Lake Nipigon, Ontario.

Plate 1. *Araneus andrewsi* web made by adult female in window frame. The spider made its retreat in the begonias on right.

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group. In the key to my 1971 paper (p. 140) on the *diadematus* group, it would key out to 4a of the key to females, to 5b in the key to males.

** B. J. Kaston and the late Father Chysanthus made me aware of the errors.

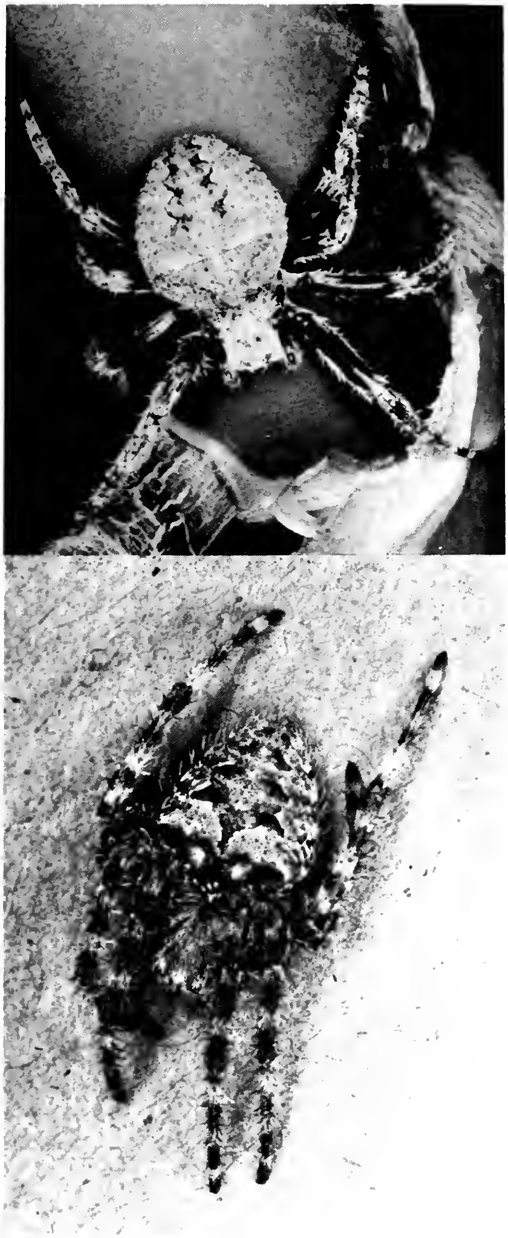

Plate 2. Top Fig. *Araneus andrewsi* female from California. The specimen was a soft velvety green with dark brown marks. Bottom Fig. *Araneus washingtoni* female from New Hampshire.

Araneus gemma (McCook)

Little was known of the habits of this Pacific coast species (Levi, 1971) except that it was often found together with *A. gemmoides* on houses and that there is considerable evidence of crossing and introgression. Of interest are numerous individuals of this species which were recently collected from dense woods by Roy Johnson, Jr. in the Monterey Peninsula, California, and which have webs among shrubs close to the ground. Unlike specimens collected on houses with *A. gemmoides,* there was little variation in genitalia in a habitat excluding *A. gemmoides.*

Araneus iviei (Archer)

An additional record extending the range of the species is from Matanuska, Alaska.

Small ARANEUS: the STURMI and PEGNIA Groups

The *A. pegnia* group includes only two species north of Mexico, *A. pegnia* and *A. thaddeus;* others are Central American and Mexican. The remaining species described in this paper, except for *A. detrimentosus,* belong to the *A. sturmi* group. *Araneus detrimentosus* is closest to the *A. diadematus* group. The *sturmi* and *pegnia* groups include the smaller species of *Araneus.* Many species of the *A. sturmi* group have similar eye size and proportions, a similar palpus and epigynum. They differ from each other in the shape of the abdomen, the covering of setae, and the often bright color of the abdomen as well as in the details of the palpus and epigynum. The relatives of *A. juniperi* have especially bright colors, usually green to red, which unfortunately wash out in alcohol. Presumably the colors are ommochromes. There is little or no black on the venter; *A. pegnia* and *A. thaddeus* have transverse ventral bars (Figs. 420, 432). In all, the carapace is longer than wide without any thoracic mark in the female, or with a longitudinal line.

Eyes. The posterior median eyes are subequal in size to slightly larger than anterior medians, the laterals are of the same size or slightly smaller than the anterior median eyes. Only *Araneus miniatus* and

A. niveus may have the posterior median eyes slightly smaller than the anterior medians. Only *A. nashoba* may have the laterals very slightly larger than the anterior median eyes. The ocular quadrangle is about as long as wide in front, slightly narrower behind, slightly wider only in *A. pratensis.* The clypeus is equal to the diameter of the anterior median eyes or slightly higher.

The anterior median eyes are slightly more than their diameter to two and one-half diameters apart, the posterior median eyes are slightly less than one to slightly less than two diameters apart. The distance of median eyes from lateral eyes depends on size of the spider; it is least in the smallest. The anterior median eyes are from slightly more than one to three diameters from laterals; the posterior median eyes are two to four anterior median eye diameters from the posterior laterals. Only in *A. bispinosus* and *A. mariposa* females are the anterior median eyes three diameters apart, two in males. Only in the largest, *A. mammatus,* are the lateral eyes more than three anterior median eye diameters from the median eyes.

The eyes of some appear to have the lens slightly smaller than the eye. The eyes of *A. pratensis* have black rings (Fig. 29); the posterior median eyes of the *A. juniperi* subgroup have white pigment rings, which in living specimens may be colored yellow (Diagram 1). The eyes grow allometrically with other parts of the spider. In general small *Araneus* species, like early instars of large species, have relatively large eyes closely spaced. Also the smaller *Araneus* species have much less pigment in the eyes (as well as on their bodies) and there seem to be all intergradations in these characters. I do not think that they differ from those of the large species (Homann, 1952: 352) in gross structure, but there is some knowledge I lack especially in regard to early instars of large species. All have a canoe-shaped tapetum in the center only (Diagram 1), with grate-shaped arrangement of the rods on one side. The eye structure will be an extremely useful character in *Meta* and *Leucauge,* which have the canoe-shaped together with the grate-shaped tapetum (Homann, 1971), despite genitalia closer to *Tetragnatha.*

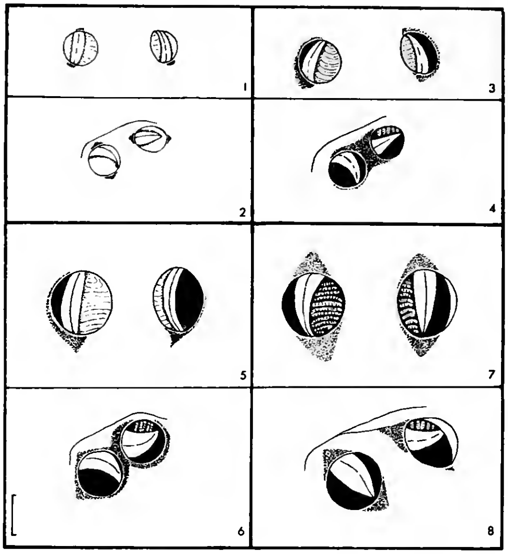

Diagram 1. Eyes showing canoe-shaped tapetum traversing center of eye only, reflecting light. 1–2. *Araneus miniatus.* 3–4. *Araneus detrimentosus.* 5–6. *Araneus pegnia.* 7–8. *Araneus diadematus.* 1, 3, 5, 7. Posterior median eyes with the left eye in focus. 2, 4, 6, 8. Left lateral eyes.

(Size indicator 0.1 mm. All eyes in same proportion)

Chelicerae. The chelicerae of all have four teeth on the anterior margin, the first and third usually large, the others small.

Legs. The leg length of all females is similar. The first patella and tibia of females are 1.2 to 1.5 times the carapace length. In the shortest, *A. pratensis* and *A. cochise,* they are equal to the length of the carapace. They are 1.7 times carapace length in *A. miniatus* and *A. carroll.* The second patella and tibia are 0.8 to 1.2 carapace length, or as long as to 1.5, in *A. mammatus, A. montereyensis, A. carroll.* The third, 0.5 to 1.2 and the fourth, 0.8 to 1.1 carapace length, 1.4 in *A. bivittatus.*

Males have the first patella and tibia 1.4 to 1.8 times the carapace length, 1.2 in *A. pratensis,* the second patella and tibia

1.2 to 1.7, the third 0.6 to 0.8 and the fourth 0.9 to 1.3.

Setation. As in juvenile stages of large species, the smaller species of *Araneus* have fewer setae and females may lack macrosetae.

Males. Males are generally the same size as females or slightly smaller. The color is also the same except that the legs may be banded with red. They have two patellar setae on the palpus; one may be stronger than the other. The carapace has a median thoracic line, a narrow depression. The palpal femur has a ventral tooth on the proximal end. From the *A. sturmi* group, none have the coxae modified. *Araneus pegnia* and *A. thaddeus* have a hook on the distal margin of the first coxae. The second tibia of males rarely has slightly stronger setae; however, in the two European species the first tibia is modified. There appear to be greater differences in the second leg length in males of different species than in the other legs. *Araneus pegnia* has strong macrosetae on the prolateral surface of the second tibia (Fig. 438); they are less pronounced in *A. thaddeus*, absent in related species from Central America.

The palpal structure (Figs. 1–6) is like that of the *A. diadematus* group. There are two macrosetae on the cymbium of *A. juniperi* subgroup (except *alboventris, tuscarora* and *texanus*). However, the cap of the embolus is of a different shape than in the *diadematus* group; it has a huge tail and barely covers the tip of the embolus if at all. It does break off in mating, and mated females have it hanging out of the epigynum. The cap is large in *A. detrimentosus* but relatively small in *A. pegnia* and *A. thaddeus*. Apparently the cap in most is intermediate between the *Hypsosinga* scale and the cap of *A. diadematus* group. I do not know whether *A. sturmi* and *A. triguttatus* have a cap on the embolus; too few specimens were available and the embolus is even more hidden than in other species. Also I do not know about the cap of *A. pratensis* as the embolus is completely hidden. After mating, the scape of the epigynum is torn off in *A. pratensis* as in *A. corticarius, A. groenlandicola* and some *Eriophora* species.

It is impossible to say at present which cap is primitive and which is derived. But it is clear that those species having a cap, males as well as females, can mate only twice (Gerhardt, 1924–1933), once with each palpus in males, or once with each side of the epigynum in females.

The embolus in this group (as also in *A. bicentenarius*) is exceedingly difficult to study, most difficult in *A. pegnia* and *A. thaddeus*. It is partly hidden and its attachment on a soft sclerite makes it vary its position. In virgin males it is cloaked by the cap. In those that have mated, the cap may in part remain attached, giving the embolus a different profile.

Variation. In the Florida peninsula, all species have a much smaller size and less black pigment. There also are small differences in the genitalia such as a shorter scape. Unfortunately, no recently collected specimens of the *A. juniperi* subgroup were available from Florida. The largest specimens of widespread species generally come from Illinois, Missouri, and Arkansas. Perhaps the competition from generally larger-sized tropical species favors smaller sizes in widespread temperate ones.

The *A. juniperi* subgroup contains numerous closely related, brightly colored species. The color is lost in alcohol and the species are difficult to separate. The subgroup includes *alboventris, bivittatus, bonsallae, carroll, gadus, guttulatus, juniperi, nashoba, niveus, cingulatus, prunus, raui, texanus, tuscarora.*

Diagnostic features. Females of the difficult *A. juniperi* group differ in the dorsal pattern of the abdomen (Plates 6–10). Even though there is variation, absence or presence of paired red spots within a species (*juniperi*), there are generally characteristic markings, such as a white pigment spot in the center anteriorly with branches going posteriorly down the sides in *guttulatus*, while black pigment may be present or not (Plate 8). *Araneus bivittatus* has stripes that are either red or green (Plate 6). But since both red and green color washes out, this is not a useful character in specimens that have been in alcohol for a century. The shape of the abdomen is useful. In *A. bivittatus* there is an anterior median hump; *A. juniperi* has a spherical abdomen.

The epigynum is the best character, especially in colorless females kept in alcohol. The epigynal scape is long and winding, or in some straight and short. The openings have a distinct border on the outside and often a still more diagnostic inner margin (*A. niveus, A. guttulatus;* Figs. 315, 318, 333, 335, 338, 339).

Males of the *A. juniperi* subgroup are unusually difficult to separate. The median apophysis, the single character used by Archer to separate males, cannot be used as the only diagnostic feature (Figs. 440–474). Even though different in different species, in most it is not very distinct. The conductor of the palpus has a tooth at the base which may be drawn out into a spine* in *A. alboventris* (Fig. 201) or very small in *A. juniperi* (Figs. 258, 259) or parallel to the axis of the conductor near its base in *A. niveus* (Figs. 326–328). The tip of the terminal apophysis is relatively wide in *A. juniperi* (Fig. 257), quite narrow in *A. niveus* and *A. guttulatus* (Figs. 325, 355). The lobe of the unsclerotized median apophysis is variable in shape in all species (Figs. 447–474). The cymbium has two macrosetae, absent in males of *A. alboventris* and sometimes in individual males (a male *A. guttulatus* from Texas). But I have also examined a male of *A. cingulatus* from Florida having three macrosetae. No doubt the best genital character is in the embolus. However, the embolus is wrapped in its cap in virgin males. In mated males it has a different appearance (Figs. 261, 262) but there may be remnants of the cap. Only the pattern on the dorsum of the abdomen permits matching males with females. I could not use broken-off embolus tips, or embolus shape, and female ducts, or the median apophysis and scape to match sexes.

The next step in the studies would have been to decapitate the bulb, that is, cut the terminal apophysis off, and study the embolus in detail. This was not done because there were not enough specimens of most species.

Natural history and collecting. Collecting members of the *A. juniperi* group of species is difficult. Most of the *A. juniperi* relatives are forest foliage species and are believed to make their webs high up under the foliage of forest trees, and there is circumstantial evidence that they specialize in particular kinds of trees. For example, *Araneus gadus* seems to make its webs only in pitch pine (*Pinus rigida*) in New England and some other pines in the South, but not white pine (*Pinus strobus*); *A. juniperus* inhabits only coniferous trees. Certain sphecid wasps, however, provision their nests with tree top spiders, and Abbot, being a good naturalist, made use of this source of specimens in the 18th century, and illustrated several species. Later collectors largely overlooked the possibility of harvesting spiders from wasp nests; despite enormous amounts of collecting in New England by Hentz, Emerton, Bryant, Banks and others, very few specimens from tree tops or wasp nests are in collections. (To judge from the labels in vials, Emerton appeared puzzled. The *A. juniperi* specimens were labelled correctly, others had *juniperi* written on the label at a later date or had a question mark connected with the determination.)

The European species *A. sturmi* and *A. triguttatus* are also often found in tree foliage, low as well as high up in trees, and there are several papers on tree top spiders [Wipfelspinnen] of Europe (Engelhardt, 1958). Engelhardt, to study spider predation on the tussock moth, *Lymantria mona-*

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* I am using spine here in its general sense: "a sharp rigid process on an animal" (Webster's Seventh New Collegiate Dictionary, 1967, G. and C. Merriam Co., Springfield); "sharp ridge or projection" (The Concise Oxford Dictionary of Current English, 1934, Clarendon Press, Oxford), not as in older spider literature for a heavy movable seta. The latter would better be called a macroseta or bristle. The older usage is confusing.

Figures 1–6. Structure of *Araneus* left palpus, expanded. 1. *A. sturmi* (Hahn), subventral. 2. *A. pratensis* (Emerton), subventral. 3. *A. guttulatus* (Walckenaer), subventral. 4. *A. thaddeus* (Walckenaer). 5–6. *A. pegnia* (Hentz). 5. Subventral. 6. Lateral.

Abbreviations. A, terminal apophysis; C, conductor; DH, distal hematodocha; E, embolus; H, basal hematodocha; I, stipes; M, median apophysis; P, paracymbium; R, radix; S, subtegulum; T, tegulum; Y, cymbium.

(Size indicators 0.1 mm)

Plate 3. *Araneus pratensis* female in web. The web was dusted with corn starch to increase its visibility.

cha, examined the crowns of 15 spruce trees and one pine, 35 to 80 years old. The trees were felled so that their crowns dropped on a previously spread tent cloth and the spiders were collected by 8 to 10 assistants who separated branches from the trunk and beat them above the cloth. Engelhardt himself watched the edge of the cloth to prevent ground spiders from running onto it. Of the 2,000 spiders collected, 40 percent were thomisids. Among the araneids there were 71 specimens of *Araneus omoedus* (Thorell) and 36 of *Araneus sturmi* (Hahn); otherwise only *Cyclosa conica* (Pallas) was more abundant than *A. sturmi.*

Plate 4. Web of *Araneus nashoba* female in *Forsythia* bush.

To obtain collections of American species, one can make traps for the sphecid wasps of the genera *Trypoxylon* and *Trypargilum.* The traps are made by drilling a 3–4-mm diameter hole into a block of wood 20 × 20 × 150 mm. Straight-grained pine wood is preferable. The traps are placed near the edge of woods. As traps are capped with mud by a wasp, they are opened with a chisel (Plate 5). From 10 to 50 spiders can be found in the trap, the lumen of which the wasp will have divided by mud walls into cells. In each cell the wasp lays an egg on one of the spiders. The traps are inspected

Plate 5. Wasp traps opened with a chisel contain numerous specimens of several small *Araneus* species.

weekly. I did not attempt to fell trees or collect in tree crowns by other means.

The evidence for the tree-crown habitat is circumstantial, because these spiders are rarely collected other than by raiding wasp nests.

Distribution. While the large species of the *A. diadematus* group are mostly northern North American and Eurasian, with species even found in Alaska, Greenland and Siberia, the smaller species belong to the fauna of the southern United States and also Mexico and Central America. Large species of other genera of Araneidae (*e.g., Eriophora*) have taken their place in the tropical and subtropical Americas.

Life history. The smaller species of *Araneus* are mature in spring, an adaptation of small orb-weavers as a result of competition and availability of prey (Bristowe, 1958: 247), the larger species being mature in fall when larger insects are available as prey. The medium-sized *A. pegnia* and *A. thaddeus* mature in late summer to early fall. An interesting discussion of this is in F. Enders (1972).

Misplaced species. Neosconella devia Gertsch and Mulaik, 1936, Amer. Mus. Novitates, No. 863: 16, fig. 38 ♀ belongs to *Eustala* (Gertsch, personal communication). The type is lost at the present time.

KEY TO FEMALES OF SMALL *Araneus* SPECIES

1	Abdomen oval, wider than long from above and without humps; either with dorsal transverse white marks framed by black lines (Fig. 433) or sides of dorsum with distinctly delineated (toward dorsum) black to brown marks (Figs. 408, 421)	2
—	Abdomen of various shapes, but with different dorsal pattern	4
2(1)	Venter of abdomen with transverse white mark behind epigynum followed by a transverse black mark in front of spinnerets (Figs. 420, 432)	3
—	Venter as in Fig. 409 without transverse white and black marks; epigy-	

num in posterior view with ventral concavity and dorsal notch (Figs. 401, 403, 405) .... *detrimentosus*

3(2) Dorsum of abdomen with transverse white patch framed by black, sometimes reddish or greenish (Fig. 433); epigynum in posterior view rounded on sides and with a dark curved mark on each side (Figs. 429, 431) ...... *pegnia*

— Dorsum of abdomen framed by black sides (Fig. 421); epigynum in posterior view appearing as a transverse rectangle (Fig. 418) .... *thaddeus*

4(1) Eastern United States and Canada (Nebraska, Kansas, Texas to Atlantic) 13

— Western United States (Wyoming, Colorado, New Mexico to Pacific) ... 5

5(4) Scape of epigynum straight in ventral view or torn off (Figs. 32, 35, 73, 123, 139) 6

— Scape of epigynum coiled, or with lateral kinks in ventral view (Figs. 45, 56, 61, 87) 9

6(5) Opening of epigynum visible anteriorly 139) .... *montereyensis*

— Openings of epigynum not visible in ventral view, or openings posterior on in base, on each side of scape (Fig. base (Figs. 38, 73, 123) 7

7(6) Base with a median posterior notch (Figs. 34, 35); scape much wider anteriorly than posteriorly (Figs. 35, 38) .... *allani*

— Base more or less evenly rounded posteriorly (Fig. 73); scape widest posteriorly or of equal width anteriorly and posteriorly (Figs. 73, 123) 8

8(7) Base with black on each side (Fig. 73); abdomen longer than wide (Fig. 79) .... *mammatus*

— Base without black marks along lateral edges (Fig. 123); abdomen much wider than long (Fig. 131) .... *mariposa*

9(5) Openings a slit on venter of base with a posterior lip, one on each side of scape (Fig. 45) .... *chiricahua*

— Openings otherwise 10

10(9) Openings on posterior part of base (Figs. 58, 63) 11

— Openings not visible in ventral view, placed anteriorly on base (Figs. 91, 115) 12

11(10) Openings in center of a subspherical lobe on each side of scape (Figs. 56, 58) .... *cochise*

— Openings in a posterior depression (Figs. 61, 63) .... *arizonensis*

12(10) Openings facing anteriorly in base (Figs. 87, 91) .... *bispinosus*

— Openings facing dorsally in base (Figs. 111, 115) .... *monica*

13(4) Scape of epigynum coiled (Figs. 302, 318, 333) 14

— Scape of epigynum straight or at most with one kink or angle, or torn off (Figs. 22, 161, 249, 381) 17

14(13) Lip of opening mesal (Fig. 376) .. *prunus*

— Lip of opening lateral (Figs. 315, 333) 15

15(14) Scape very long; base of epigynum appearing about three times as wide as long; secondary openings, curved oval and visible on each side below lip (Figs. 315, 318), abdomen 1.2 times as long as wide with dorsal black spot (Figs. 320, 321) .... *niveus*

— Scape shorter; base of epigynum at most 2.5 times as wide as long; secondary openings otherwise; abdomen almost as wide as long, sometimes with a black dorsal patch 16

16(15) Lateral lips of epigynum convex in slightly posterior view (Figs. 333, 336), or with very narrow lips in slightly anterior view (Fig. 339); in posterior view area under scape raised (Figs. 335, 338); abdomen often with black pigment .... *guttulatus*

— Lips otherwise (Figs. 302, 305); base underneath scape a depression as seen in posterior view (Figs. 304, 306); abdomen usually without black pigment .... *cingulatus*

17(13) Abdomen wider than long (Figs. 164, 183, 208), as wide as long and widest anteriorly or with humps (Fig. 157) .. 18

— Abdomen if as wide as long, subspherical (Fig. 252), usually longer than wide 24

18(17) Openings of epigynum on ventral face of base (Figs. 153, 363) 19

— Openings on anterior margin of base (Figs. 159, 179) 23

19(18) Lips toward median, openings toward scape (Figs. 153, 156) .... *calusa*

— Lips and openings otherwise (Fig. 363) 20

20(19) Openings with a lateral outer lip, and an anterior and median inner lip (Figs. 362, 363) .... *texanus*

— Openings otherwise 21

21(20) Openings large, more or less parallel to scape (Figs. 193, 205) 22

— Openings small, diagonal, posteriorly on base (Fig. 173) .... *miami*

22(21) Abdomen with a black spot on dorsum surrounded by red on golden yellow (Figs. 196, 197) .... *alboventris*

— Abdomen without black spot on dorsum (Fig. 208) .... *tuscarora*

23(18) Scape with a kink and having transverse grooves (Figs. 159, 161) .. *miniatus*

— Scape very short, straight, attached to center of base, lacking transverse grooves (Figs. 179, 180) ...... *partitus*

24(17) Openings underneath scape (which may be torn off), base with a deep notch posteriorly (Figs. 22, 24, 27 28); eyes on black spots; abdomen widest in middle, smooth and glossy (Fig. 29) .... *pratensis*

— Openings to side of scape; base without posterior notch; no black around eyes; abdomen if widest in middle then not smooth and glossy (Fig. 225) 25

25(24) Openings with lip only mesally on each side of scape (Fig. 381); abdomen with indistinct anterior white spots on green .... *nashoba*

— Openings with lip laterally, anteriorly or posteriorly (Fig. 222); abdomen marked otherwise 26

26(25) Scape rather narrow, openings very large, about twice diameter of scape and distinctly bordered on three sides (Fig. 222); abdomen with two distinct crimson or green bands separated by white (Fig. 225) .... *bivittatus*

— Epigynum otherwise, abdominal markings sometimes with green bands, rarely red 27

27(26) Abdomen with a black patch surrounded by red on yellow (Fig. 197), scape rather short and wide (Fig. 193) .... *alboventris*

— Abdomen and scape otherwise 28

28(27) Openings longer than wide (Figs. 219, 296) 29

— Openings as long as wide or wider than long, a posterior slit (Fig. 232) or a round depression (Fig. 277) ... 31

29(28) Openings with narrow rims; secondary openings relatively small (Figs. 296, 297) .... *raui*

— Openings with wide rims; secondary openings larger (Fig. 219) 30

30(29) Epigynum as in Fig. 219; ducts short in ventral view, opening anteriorly (Fig. 215); abdomen narrow (Fig. 220) .... *carroll*

— Epigynum as in Fig. 363; ducts long, opening laterally (Fig. 362); abdomen wide (Fig. 374) .... *texanus*

31(28) Dorsum of abdomen with paired black spots surrounded by a light halo (Fig. 239); openings a posterior slit, slit most anterior toward median (Fig. 232) .... *gadus*

— Abdomen without black pigment spots; if openings a posterior slit, then slit most anterior laterally (Fig. 249) ... 32

32(31) Abdomen with indistinct longitudinal green bands, rarely red (Fig. 352); scape often with a slight kink, anterior lip of depression indistinct (Fig. 349) .... *juniperi*

— Abdomen with transverse green or white markings in anterior half (Figs. 283, 286); scape without a kink, anterior rim of depression distinct (Figs. 266, 277) .... *bonsallae*

KEY TO MALES OF SMALL *Araneus* SPECIES

(Males of *calusa, carroll, cochise, miami, monica, prunus, raui* are unknown.)

1 Coxae of first legs with a hook on distal margin 2

— Coxae of first legs without hook on distal margin 4

2(1) Embolus large, curved and visible on mesal side as in Fig. 411 .. *detrimentosus*

— Embolus small and hidden behind conductor 3

3(2) Median apophysis with two apical prongs as in Fig. 434 .... *pegnia*

— Median apophysis with three apical teeth as in Fig. 422 .... *thaddeus*

4(1) Western United States (Wyoming, Colorado, New Mexico to Pacific coast) 5

— Eastern United States and Canada (Nebraska, Kansas, Texas, Atlantic coast) 11

5(4) Median apophysis of palpus with two tips (Figs. 80, 81, 442); conductor very long with a distinctly swollen end and stalk (Fig. 81) .... *mammatus*

— Median apophysis with three tips (Fig. 66) or one tip and denticles on other end (Fig. 49, 96); conductor otherwise 6

6(5) Median apophysis with three tips, one "upper" one and a double "lower" one (Figs. 66, 67, 69) .... *arizonensis*

— Median apophysis with a tip on one end, denticles or numerous teeth on other (Figs. 49, 96) 7

7(6) Terminal apophysis about twice as long as wide (Figs. 96, 98); conductor with a sclerotized lateral edge bearing a short tooth as in Fig. 97; California .... *bispinosus*

— Terminal apophysis about as long as wide (Figs. 52, 134, 147) or if narrower, conductor otherwise 8

8(7) Conductor bottle-shaped, narrower distally with a constricted neck (Fig. 146); California .... *montereyensis*

— Conductor without constricted neck (Figs. 50, 133) 9

9(8) Conductor with a notch and tooth on middle of lateral side (Fig. 133); California .... *mariposa*

— Conductor without notch and tooth on lateral side (Figs. 40, 50); Arizona . . . 10

10(9) Conductor with a notch on distal margin near lateral side (Fig. 40) . . *allani*

— Conductor without such notch (Fig. 50) . . . . *chiricahua*

11(4) Median apophysis positioned parallel to margin of cymbium (Fig. 30); eyes on black spots (Fig. 29) . . . . . . *pratensis*

— Median apophysis never parallel to margin of cymbium (Figs. 185, 310); eyes not on black spots 12

12(11) Embolus straight or slightly curved with a parallel lobe almost hiding it, in mesal view (Figs. 165, 189); abdomen subtriangular with two anterior humps (Fig. 191) 13

— Embolus otherwise, no parallel lobe from its base in mesal view (Figs. 209, 309, 387); abdomen rarely subtriangular 14

13(12) Embolus curved, pointed (Fig. 170); median apophysis with two tips (Fig. 168) . . . . *miniatus*

— Embolus truncate (Figs. 189, 190); median apophysis with only one tip (Fig. 188) . . . . *partitus*

14(12) Conductor spine longer than width of conductor (Figs. 199, 201); embolus a distinct coil (Figs. 202, 203); abdomen with a red-fringed black spot on yellow (Fig. 196) . . . . *alboventris*

— Conductor spine shorter than width of conductor (Fig. 212); embolus otherwise (Fig. 209); abdomen if with black spot then spot not red-fringed . . 15

15(14) Abdomen with three pairs of black spots having a light halo (Fig. 239); embolus as in Figs. 244–246 . . . . . *gadus*

— Abdomen spots red or absent, never black 16

16(15) Embolus a projection almost parallel to and above lamella as in Fig. 387; abdomen green with anterior white spots (Fig. 386) . . . . *nashoba*

— Embolus not as in Fig. 387, and abdomen usually not as in Fig. 386 17

17(16) Abdomen with longitudinal green or red bands (Figs. 225, 252) 18

— Abdomen not with longitudinal bands 19

18(17) Abdomen bands indistinct (Fig. 252); embolus very slender (Figs. 261–263), conductor tooth minute (Figs. 258, 259) . . . . *juniperi*

— Abdomen bands distinct (Fig. 225); embolus heavier, though of same shape (Fig. 230); conductor tooth larger (Fig. 229) . . . . *bivittatus*

19(17) Conductor tooth small, touching or underneath transparent tegulum margin (Figs. 326–328, 348–351) 20

— Conductor tooth at some distance from tegulum margin 21

20(19) Distal bent tip of embolus very short (Figs. 329–331); terminal apophysis wide (Fig. 325) . . . . *niveus*

— Distal bent tip of embolus longer (Figs. 356–361); terminal apophysis noticeably narrow (Figs. 352–355) . . . . *guttulatus*

21(19) Abdomen brownish, white along anterior margin, triangular, as wide as long (Fig. 208); end piece of terminal apophysis wider than long, short and blunt (Fig. 211); total length less than 3 mm . . . . *tuscarora*

— Abdomen usually with at least some white pigment on dorsum, longer than wide; terminal apophysis longer than wide (Fig. 369) 22

22(21) Embolus as in Fig. 370; tooth of conductor on a long sclerotized edge (Fig. 373) . . . . *texanus*

— Embolus not as in Fig. 370 (Figs. 392, 313); tooth of conductor sometimes on sclerotized edge (Figs. 291, 312) . . . 23

23(22) Embolus as in Figs. 292–294; median apophysis with a notch (Figs. 453–454) . . . . *bonsallae*

— Embolus as in Fig. 313 with a long tip; similar to *bivittatus;* median apophysis without notch (Figs. 455–458) . . . . *cingulatus*

Araneus sturmi (Hahn)

Figures 1, 7–13

Epeira sturmi Hahn, 1831, Die Arachniden, 1: 12, pl. 3, fig. 8, ♀, ♂. The specimens came from Nürnberg, Germany, and are believed lost.

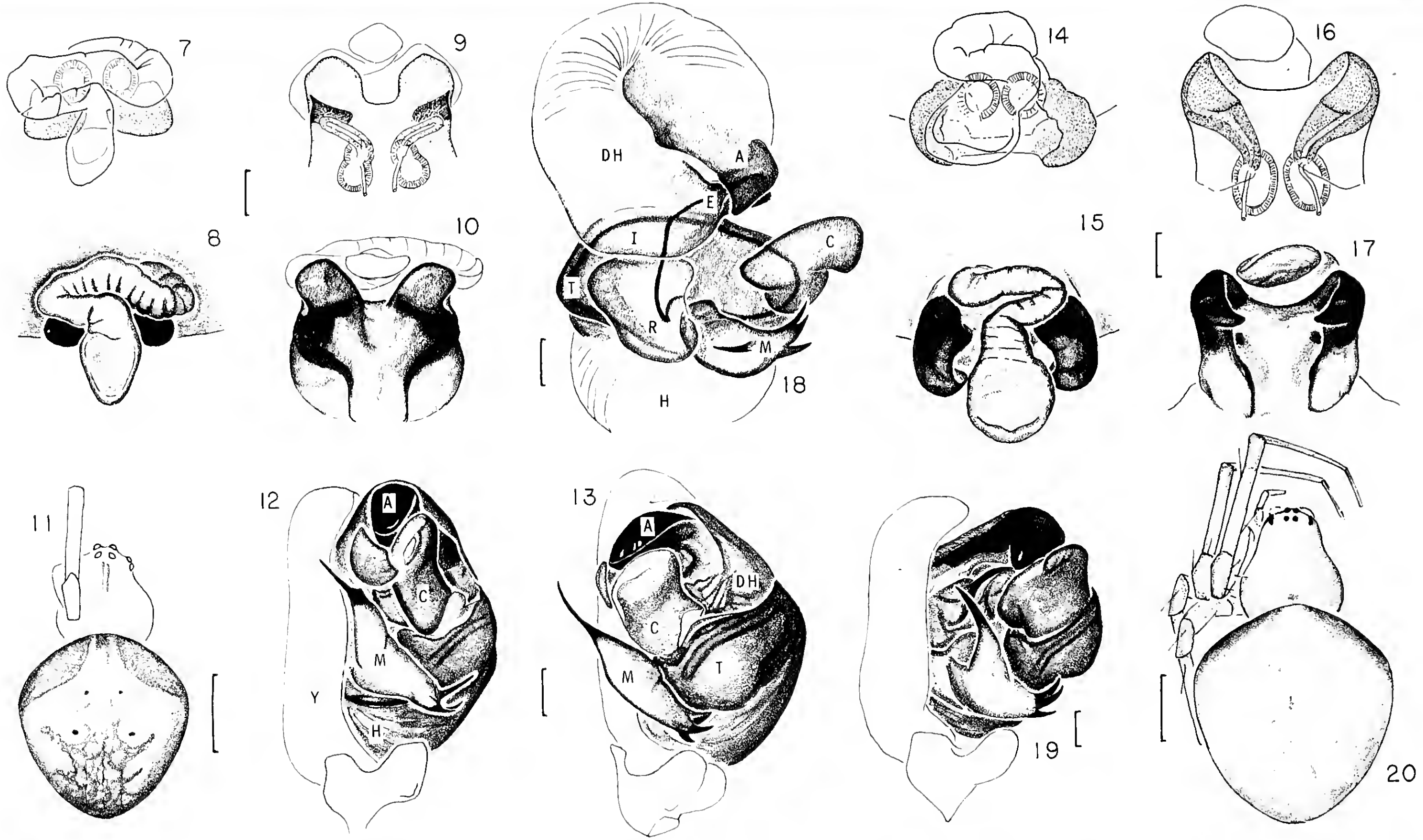
Aranea sturmi,—Wiehle, 1931, *in* Dahl, Die Tierwelt Deutschlands, 23(6): 113, figs. 177–182, ♀, ♂. Roewer, 1942, Katalog der Araneae, 1: 792.

Araneus sturmi,—Locket and Millidge, 1953, British Spiders, 2: 141, figs. 94 a,b; 95 a,b, ♀, ♂. Bonnet, 1955, Bibliographia Araneorum, 2: 605.

Unlike most other species of *Araneus,* the first tibia of the male is slightly curved and has stronger spines than the second.

Natural history. According to Wiehle (1931) the species is found exclusively in pines, spruce and juniper, only rarely on deciduous trees nearby. The web is like that of other *Araneus* species. There are usually fewer than 20 radii in the small web.

Distribution. Europe.



Figures 7–13. *Araneus sturmi* (Hahn) of Europe. 7–10. Epigynum. 7. Ventral, cleared. 8. Ventral. 9. Posterior, cleared. 10. Posterior. 11. Female with first patella-tibia. 12–13. Left palpus. 12. Mesal. 13. Ventral.

Figures 14–20. *Araneus triguttatus* (Fabricius) of Europe. 14–17. Epigynum. 14. Ventral, cleared. 15. Ventral. 16. Posterior, cleared. 17. Posterior. 18–19. Palpus. 18. Expanded, submesal. 19. Mesal. 20. Female.

Abbreviations. A, terminal apophysis; C, conductor; DH, distal hematodocha; E, embolus; H, basal hematodocha; I, stipes; M, median apophysis; R, radix; T, tegulum; Y, cymbium.

(Size indicators 0.1 mm, except for females 1 mm)

Araneus triguttatus (Fabricius)
Figures 14–20

Aranea triguttatus Fabricius, 1793, Ent. Syst. 2: 419. Fabricius' collection was kept at Copenhagen and was destroyed. Wiehle, 1931, *in* Dahl, Die Tierwelt Deutschlands, 23(6): 115, figs. 183–187, ♀, ♂. Roewer, 1942, Katalog der Araneae, 1: 794.

Epeira mayo McCook, 1894, American Spiders, 3: 179, pl. 8, fig. 11, ♀. Female holotype labeled as coming from Biscayne Bay, Florida (G. Marx), in the U.S. National Museum, examined. But McCook published that he had specimens from Wisconsin and one in the Marx collection from Minnesota.* NEW SYNONYMY.

Araneus triguttatus,—Locket and Millidge, 1953, British Spiders, 2: 143, figs. 94 c,d, 95 c, ♀, ♂. Bonnet, 1955, Bibliographia Araneorum, 2: 616.

The first legs of the male, rather than the second as in most *Araneus* species, are curved and have large setae.

Note. There is no evidence that this species occurs in America. The Marx specimen given a name by McCook appears to have had an error in locality, as do most Marx specimens. I have no doubt that McCook made his drawings from the Marx specimen examined.

Natural history. According to Wiehle (1931) *A. triguttatus* is found on deciduous trees.

Distribution. Eurasia.

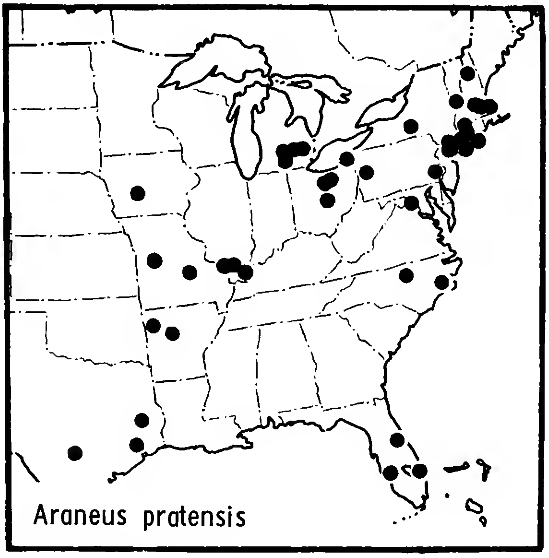
Araneus pratensis (Emerton)
Plate 3; Figures 2, 21–31; Map 1

Singa pratensis Emerton, 1884, Trans. Connecticut Acad. Sci., 6: 322, pl. 34, fig. 15, pl. 37, figs. 14–15, ♀, ♂. One male and three female syntypes from wet fields, New Haven, Connecticut, in the Museum of Comparative Zoology, examined. Comstock, 1912, Spider Book, p. 462, fig. 475, ♀; 1940, Spider Book, rev. ed., p. 476, fig. 475, ♀. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 240, figs. 745, 758–759, ♀, ♂.

Epeira reptilis Keyserling, 1893, Spinnen Amerikas, 4: 244, pl. 12, fig. 182, ♂. Male holotype from Crescent City, Florida (Marx collection, locality in doubt), in the U.S. National Museum, examined. NEW SYNONYMY.

Singa listerii McCook, 1894, American Spiders 3: 231, pl. 19, figs. 3, 4, ♀, ♂. Two female, three male syntypes from Georgia in the Academy of Natural Sciences, Philadelphia, examined and labeled as type. Name first synonymized by Banks, 1910, Bull. U.S. Natl. Mus. 72: 40.

Araneus praticola Simon, 1895, Histoire Naturelle des Araignées, 1: 807. New name for *Singa pratensis* Emerton, because thought preoccupied by *Epeira pratensis* Hentz, 1847 (= *Neoscona pratensis*). Bonnet, 1955, Bibliographia Araneorum, 2: 568.



Map 1. Distributions of *Araneus pratensis* (Emerton).

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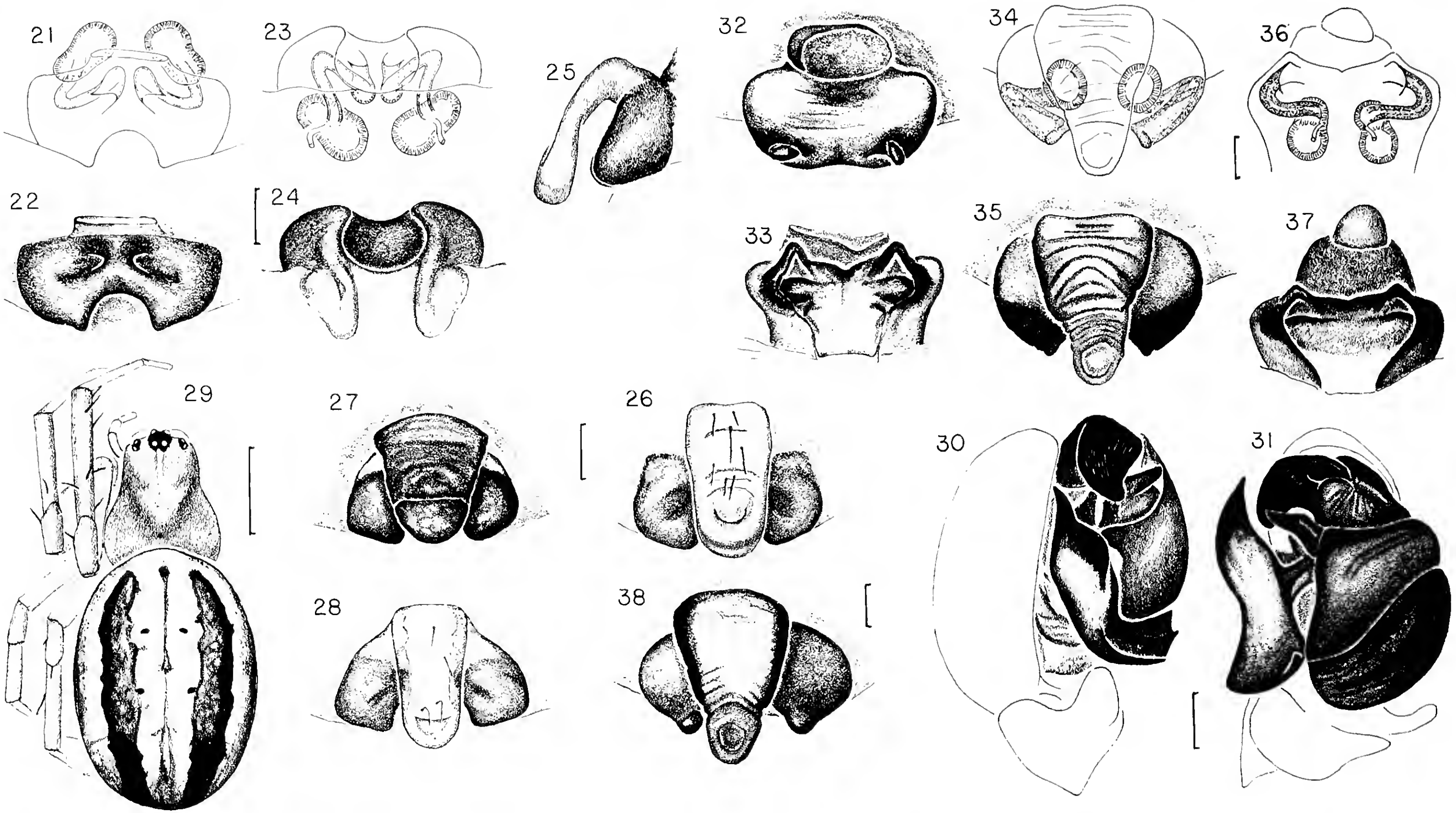
[*] McCook's next sentence is "The known patria is thus the Northwestern United States."



Figures 21–31. *Araneus pratensis* (Emerton). 21–28. Epigynum. 21. Ventral, cleared. 22. Ventral, scape torn off. 23. Posterior, cleared. 24. Posterior. 25. Lateral. 26–28. Ventral with scape. 29. Female. 30–31. Left palpus. 30. Mesal. 31. Ventral.

Figures 32–38. *Araneus allani*, new name, epigynum. 32. Ventral, scape torn off. 33. Posterior. 34. Ventral, cleared. 35, 38. Ventral. 36. Posterior, cleared. 37. Posterior.

(Size indicators 0.1 mm, for Fig. 29, 1 mm)

Description. Female. Carapace yellow-brown with median ocular quadrangle black, smooth; lateral eyes on black spots (Fig. 29). Sternum dark brown. Legs, including coxae, light yellowish. Dorsum of abdomen white with two longitudinal brown bands and a median dark line (Fig. 29); sides brownish; venter with a median square brown spot between epigynum and spinnerets bordered by a white line on each side; spinnerets dark brown. Abdomen without setae, smooth. Posterior median eyes 1.3 diameters of anterior medians, laterals same diameter as anterior medians. Anterior median eyes 1.5 diameters apart, 1.7 diameters from laterals. Posterior median eyes less than one diameter apart, two diameters from laterals. The abdomen is suboval, longer than wide, slightly overhanging spinnerets. Total length 4.3 mm. Carapace 2.0 mm long, 1.4 mm wide. First femur, 1.8 mm; patella and tibia, 2.1 mm; metatarsus, 1.4 mm; tarsus, 0.7 mm. Second patella and tibia, 1.8 mm; third, 1.2 mm; fourth, 1.9 mm.

Male. Coloration like that of female. Carapace with a short longitudinal line in thoracic region, also lacking setae. Eye sizes like those of female. Anterior median eyes 1.5 diameters apart, slightly more than one diameter from laterals. Posterior median eyes slightly less than one diameter apart, two diameters from laterals. Total length 3.6 mm. Carapace 1.7 mm long, 1.4 mm wide. First femur, 1.7 mm; patella and tibia, 2.1 mm; metatarsus, 1.5 mm; tarsus, 0.7 mm. Second patella and tibia, 1.9 mm; third, 1.2 mm; fourth, 1.8 mm.

Variation. *Araneus pratensis* varies little in color. No two median apophyses (Fig. 30) of the palpus are exactly alike. Also the scape of the epigynum when not torn off may be wide and wrinkled or narrow and smooth (Figs. 26–28). Females varied from 3.8 to 5.0 mm total length, 1.2 to 1.7 mm carapace width, males 3.0 to 3.5 mm total length, 1.2 to 1.4 mm carapace width.

Diagnosis. *Araneus pratensis* differs from other *Araneus* species by the *Hypsosinga*-like smooth carapace and smooth, long oval abdomen having two longitudinal bands (Fig. 29). The openings of the epigynum are hidden in a posterior depression of the base behind the scape (Figs. 21, 22); the scape in mated specimens is torn off (Fig. 22). The shape and position of the median apophysis (Fig. 30), parallel to the cymbial margin, separates *A. pratensis* from other *Araneus.* (The epigynal scape and large median apophysis preclude placing the species in *Hypsosinga.*)

Natural history. Virgin males are believed to have a small cap over the embolus. But since the embolus of virgin males is well hidden between sclerotized terminal apophysis and conductor, I am not certain of this. Males are mature in May and June. Mature females are found until August, in Florida until September. The species is found in moist meadows in the open, on alfalfa, and has been swept from fields with mixed vegetation. The orb of the web is about 20 cm in diameter; one observed in Massachusetts lacked a retreat and the spider, hanging in the center, dropped when approached only to climb back minutes later (Plate 3).

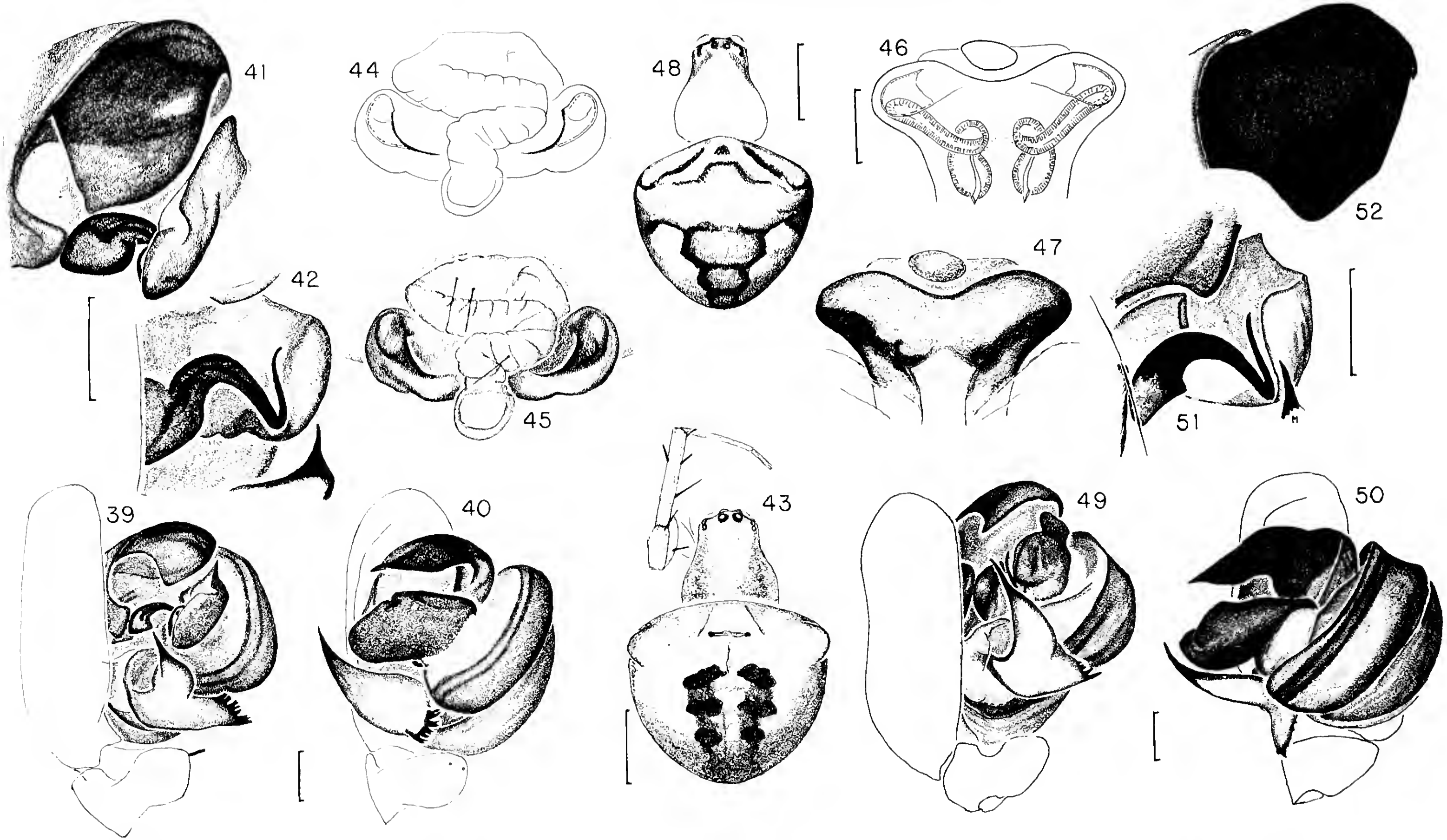
Distribution. From the northernmost record, Woodstock, New Hampshire, the species ranges to Florida; and the westernmost record is San Antonio, Texas (Map 1).

Araneus allani, new name

Figures 32–43, 440; Map 2

Amamrotypus miniatus Archer, 1951, Amer. Mus. Novitates, No. 1487: 18, fig. 23, ♀. Female holotype in poor condition from White House Canyon, Santa Rita Mountains, Arizona, in the American Museum of Natural History, examined. The specific name is preoccupied by *Araneus miniatus* (Walckenaer, 1841); it is now named after the original author, Allan Archer.

Description. Female. Carapace brown, much darker on sides, posterior median eyes on black spots. Sternum brown with some dark pigment. Legs brown with narrow bands. Dorsum of abdomen spotted brown with a pair of darker marks anteriorly (Fig. 43); most have folium less distinct than in illustration. Venter between epigynum and spinnerets white, enclosing a dark center. Carapace hairy, with a deep longitudinal



Figures 39–43. *Araneus allani,* new name. 39–42. Left palpus. 39 Mesal. 40. Ventral. 41. Terminal apophysis. 42. Embalus, mesal. 43. Female with first leg.
Figures 44–52. *Araneus chiricahua* n. sp. 44–47. Epigynum. 44. Ventral, cleared. 45. Ventral. 46. Posterior, cleared. 47. Posterior. 48. Female. 49–52. Palpus. 49. Mesal. 50. Ventral. 51. Embolus, mesal. 52. Terminal apophysis.
(Size indicators 0.1 mm, for females 1 mm)

thoracic groove. The abdomen has two large humps. Total length 3.5–4 mm. Carapace 1.7–1.8 mm long, 1.3–1.4 mm wide.

Male with carapace yellow-white with some white pigment in center of thorax; eyes on black pigment spots; sides slightly gray. Sternum, legs yellowish white. Dorsum of abdomen white with indistinct brown folium. Venter white; in the center the pigment is broken by a longitudinal pigmentless line; epigastric area and spinneret area with gray pigment. The abdomen is suboval, longer than wide, without humps. Total length 2.7 mm. Carapace 1.3 mm long, 1.2 mm wide.

Diagnosis. Female *Araneus allani* differ from other small western *Araneus* species whose epigynum does not show openings on the ventral face by having the openings posterior (Figs. 32–37) rather than anterior or dorsal, by having the base notched posteriorly, in the middle, and pointed on each side of the scape, and by having the scape much wider anteriorly than behind (Figs. 35, 38). There is a resemblance to the epigynum of *A. pratensis,* but the shape and color of the abdomen are different. Male *Araneus allani* have a wider terminal apophysis (Fig. 41) than the related California species, a longer embolus (Fig. 42), and a differently shaped conductor (Fig. 40). *Araneus allani* is much smaller than related sympatric species of *Araneus.*

Records. Arizona. Cochise Co.: Cave Creek Canyon, Chiricahua Mts., 15–31 August 1956, ♀, ♂ (A. F. Archer). Santa Cruz Co.: Madera Can., Big Rock Camp, "9–10–41," ♀ (W. Ivie) (Map 2).

Araneus chiricahua n. sp.

Figures 44–54, 441; Map 2

Conaranea pacifica,—Archer, 1951, Amer. Mus. Novitates, No. 1502: 10, fig. 26, ♀. Not *Epeira pacifica* McCook.

Conaranea anguinifera,—Archer, 1951, Amer. Mus. Novitates, No. 1502: 11, in part; not *Aranea anguinifera* F. O. P.-Cambridge.

Type. Female holotype, female and male paratypes from Southwestern Research Station, 5 mi. (8 km) west of Portal, Cochise County, Arizona, 5,600 ft. (1,800 m) elev., Chiricahua Mountains, 15 August 1972 (N. Platnick) in the Museum of Comparative Zoology. The name is a noun in apposition after the type locality.

Note. Specimens of this species have been labeled as *Atea gertschi, Conaranea pacifica* and *Conaranea anguinifera* by Archer.

Description. (Specimen 10 days in alcohol; the reddish color washes out in time.) Female carapace with central white patch, darker on each side, more so in head region, and margin gray; eyes on dark spots. Sternum gray, darker on margin. Legs yellowish. Dorsum of abdomen with an indistinct folium bordered by black marks. Anterior of folium a white A-shaped mark bordered red (Figs. 48, 53, 54). A red line passes down side from anterior of folium to venter. Venter with a median longitudinal reddish black band, on each side of which is a white band of equal width; spinnerets brown. Carapace quite narrow. Posterior median eyes 1.3 diameters of anterior. Anterior lateral eyes equal in diameter to anterior medians. Posterior laterals 0.9 diameters of anterior median eyes. The median ocular area is square. The abdomen is slightly longer than wide, widest in anterior half with humps almost always present. It barely covers the carapace. Total length 3 mm. Carapace 1.2 mm long, 1.0 mm wide. First femur, 1.4 mm; patella and tibia, 1.5 mm; metatarsus, 0.8 mm; tarsus, 0.5 mm. Second patella and tibia, 1.2 mm; third, 0.7 mm; fourth, 1.1 mm.

Male coloration like female, except for legs which are indistinctly banded. Total length 2.8 mm. Carapace 1.4 mm long, 1.2 mm wide. First femur, 1.8 mm; patella and tibia, 1.9 mm; metatarsus, 1.3 mm; tarsus, 0.5 mm. Second patella and tibia, 1.7 mm; third, 1.0 mm; fourth, 1.4 mm.

Variation. Mexican females have the abdomen with humps more distinct (Fig. 54). Females varied from 3.0 to 3.9 mm total length, carapace 1.2 to 2.0 mm long, 1.0 to 1.5 mm wide. Males varied from 2.8 to 3.5 mm total length, carapace 1.4 to 1.7 mm long, 1.2 to 1.5 mm wide.

Diagnosis. Unlike other western female *Araneus, A. chiricahua* has the openings of epigynum on the venter (Fig. 45) easily visible, bordered posteriorly and laterally. Like *A. arizonense* and *A. cochise,* but unlike *A. allani* and *A. mammatus,* in *A. chiricahua* the scape is long and coiled. But the base of the epigynum is wider than long (Figs. 45, 47); in the larger *A. arizonense* and *A. cochise* it is about as long as wide. The shape of the wide terminal apophysis (Fig. 52), the conductor (Fig. 50) and the long median apophysis (Fig. 441) separate males from related species.

Natural history. The holotypes and paratypes were collected by sweeping low vegetation and pines. Males are mature in late summer.

Records. Arizona. Cochise Co.: Southwestern Research Station, Portal, August 1956, 3 ♀ (A. F. Archer); Cienega Lake, 5 mi. north of Portal, 6 August 1968, ♀, ♂. *Hidalgo.* Apulco, 6 October 1947, ♀, ♂. *Distrito Federal.* Chapultepec, ♀ (Map 2).

Araneus cochise n. sp.

Figures 55–59; Map 2

Type. Female holotype from Southwest Research Station, 5,400 ft. (1,800 m), Chiricahua Mts., Cochise Co., Arizona, 1 July 1968 (V. Roth) in the American Museum of Natural History. The name is a noun in apposition after the type locality.

Description. Carapace yellow-white with a median white patch in thoracic region. Eyes on black spots. An indistinct brown patch on each side of head region, radiating posteriorly to a black mark on each side of a white thoracic patch. Thorax yellowish white on sides and posteriorly. Clypeus brown with black around margin. Sternum yellowish white, brown on sides. Coxae and proximal part of femora whitish. Distal segments with narrow rings. Abdomen with two humps, dorsum with an indistinct folium, darkest posteriorly, outlined by black marks, bordered laterally by white spots (Fig. 59). Anteriorly the abdomen is reddish; a white spot lies above spinnerets. There is a white patch on each side below the hump, with black below and posteriorly on the side. Between epigynum and spinnerets, the venter is gray with a white patch on each side. Posterior median eyes 1.3 diameters of anterior medians, laterals 0.8 diameters of anterior median eyes. Anterior median eyes one diameter apart, 1.8 from laterals. Posterior median eyes 1.3 diameters apart, 2.5 from laterals. The height of the clypeus equals the diameter of the anterior median eyes. Total length 3.7 mm. Carapace 1.9 mm long, 1.5 mm wide. First femur, 1.6 mm; patella and tibia, 2.0 mm; metatarsus, 1.2 mm; tarsus, 0.6 mm. Second patella and tibia, 1.5 mm; third, 1.0 mm; fourth, 1.5 mm.

Diagnosis. The epigynum of this species (Fig. 56) is surprisingly similar to that of *A. sturmi.* Female *Araneus cochise* has a long folded scape (Fig. 56), unlike other small western *Araneus,* except *chiricahua, arizonensis,* and *bispinosus;* it differs from the three species and also from *A. sturmi* in having an indistinct opening at the tip of each posterior, lateral, spherical projection of the base (Figs. 55–57).

Araneus arizonensis (Banks)

Figures 60–71; Map 2

Epeira arizonensis Banks, 1900, Canadian Entomole., 32: 100. Female holotype from Arizona* [no locality], Townsend collector, in the Museum of Comparative Zoology, examined. Banks, 1901, Proc. U.S. Natl. Mus., 23: 585, pl. 22, fig. 5, ♂.

Neosconella arizonensis,—Archer, 1951, Amer. Mus. Novitates, No. 1487: 38.

Conaranea gertschi,—Archer, 1951, Amer. Mus. Novitates, No. 1502: 7, figs. 17, 30, ♀. Not male holotype of *Conaranea gertschi* Archer.

Description. Female. Carapace, sternum, legs yellow. Dorsum of abdomen white without any marks or some specimens

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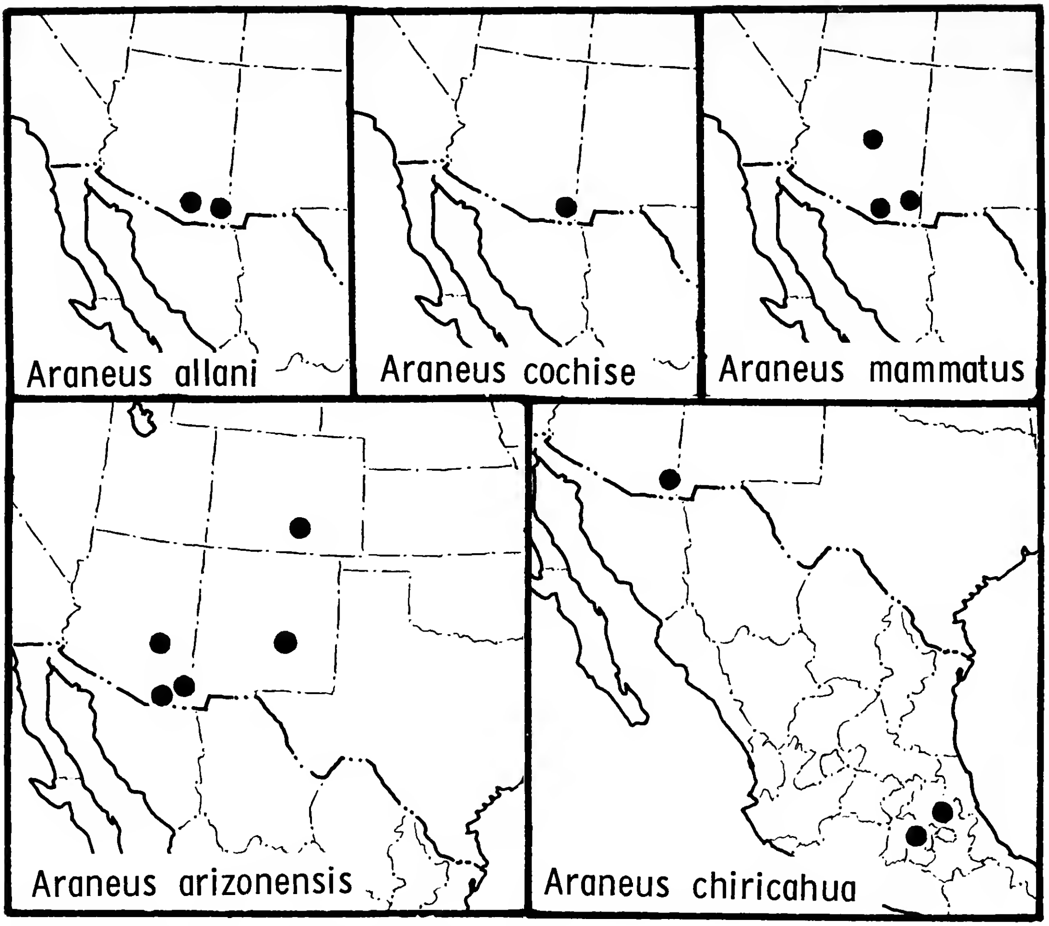
* Nathan Banks traversed the country by railway. Wherever the train stopped in the west to take on water for the steam locomotive, Banks dashed out to collect and as soon as the train started, he jumped back on board. His localities thus may have the forgotten names of water storage tanks which have long since disappeared, or just the name of the state. This specimen, however, had a collector, probably C. H. T. Townsend, a wasp specialist.



Map 2. Distributions of small southwestern species of *Araneus*.

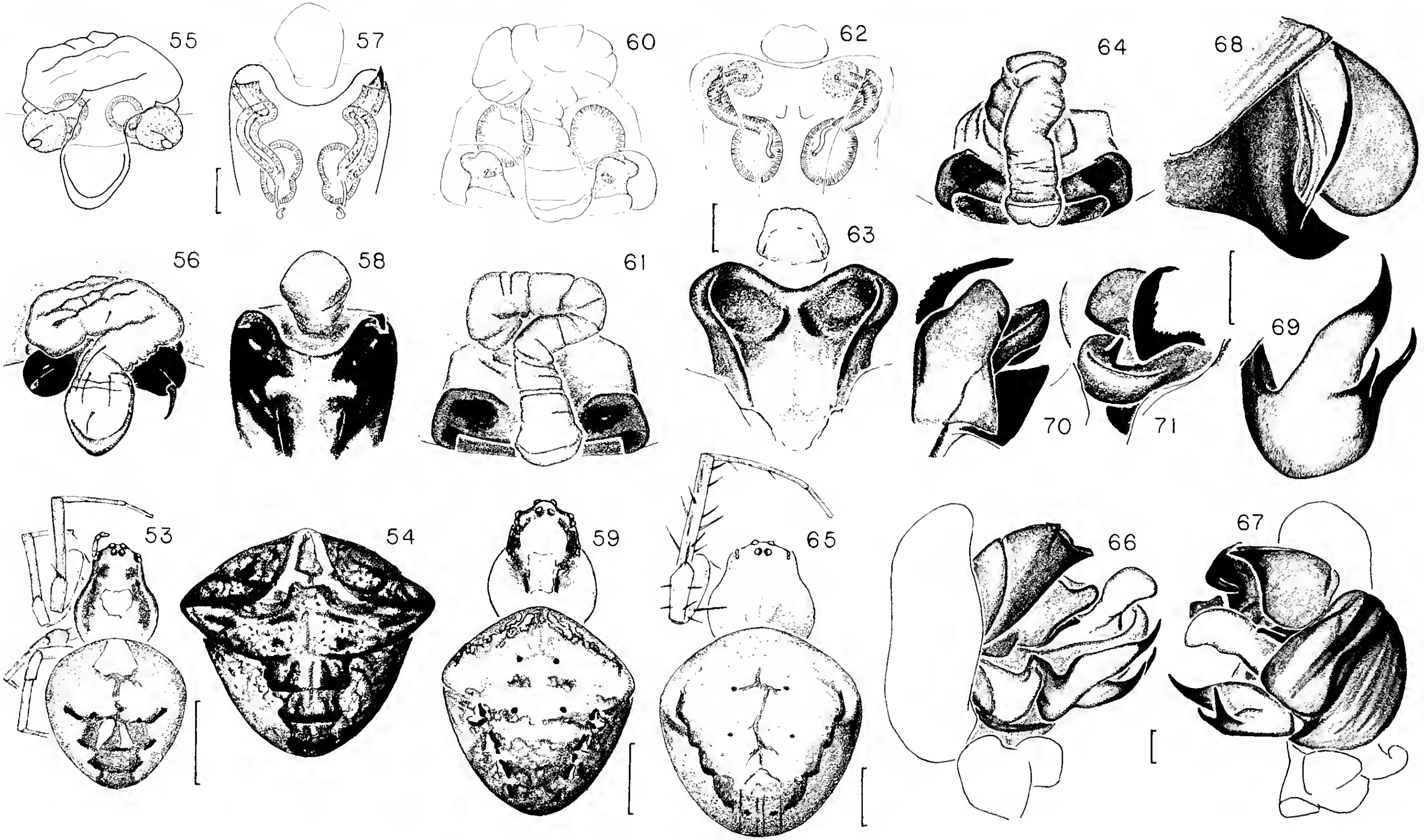
with a folium enclosing a field of fine black stipples (Fig. 65). Venter of abdomen white. The abdomen is suboval with two slight humps anterior dorsally (Fig. 65). Total length 4.2–6.1 mm. Carapace 2.0–2.4 mm long, 1.7–2.1 mm wide.

Male. Coloration like that of female, but legs indistinctly banded. Abdomen subtriangular with two slight humps anteriorly. Total length 4.3–4.8 mm. Carapace 2.2 mm long, 1.9 mm wide.

Variation. Araneus arizonensis seems more variable in genitalic structure than other species, perhaps because suitable habitats and populations are far apart and isolated. The holotype of *A. arizonensis* has a shorter scape, specimens from the Huachuca Mountains have the lip on the epigynum shaped slightly differently (under the tip of the scape). Not enough males are in collections to permit study of the variation.

Diagnosis. Araneus arizonensis females, like those of *A. chiricahua*, *A. cochise* and *A. bispinosus*, have a long coiled scape, but differ by having the openings on each side of a posterior transverse groove on the base of the epigynum (Figs. 61, 63, 64). Unlike other species the median apophysis of the male palpus is tipped by three prongs facing the same direction (Fig. 69).

Natural history. One male was found as



Figures 53–54. *Araneus chiricahua* n. sp. 53. Female (Arizona). 54. Female abdomen (Hidalgo).
Figures 55–59. *Araneus cochise* n. sp. 55–58. Epigynum. 55. Ventral, cleared. 56. Ventral. 57. Posterior, cleared. 58. Posterior. 59. Female.
Figures 60–71. *Araneus arizonensis* (Banks). 60–64. Epigynum. 60. Ventral, cleared. 61. Ventral. 62. Posterior, cleared. 63. Posterior. 64. Ventral. 65. Female. 66–71. Left palpus. 66. Mesal. 67. Ventral. 68. Terminal apophysis. 69. Median apophysis. 70–71. Embolus. 70. Mesal. 71. Apical.
(Size indicators 0.1 mm, for females 1 mm)

prey of the wasp *Stenopogon* at Portal, Arizona, another in a can trap in a recent lava bed in New Mexico. The species, according to S. Riechert, is moderately abundant on the lava flow, with webs in crevices.

Records. Colorado. Fremont Co.: Canon City, ♂. *New Mexico.* Lincoln Co.: T65, R102, sec. 36, ♂ (S. Riechert). *Arizona.* Cochise Co.: Chiricahua Mts. (numerous records). Gila Co.: Miami, ♀. Santa Cruz Co.: Huachuca Mts. ♀ ♀ (Map 2).

Araneus mammatus (Archer)
Figures 72–85, 442; Map 2

Amamrotypus mammatus Archer, 1951, Amer. Mus. Novitates, No. 1487: 17, figs. 23, 24, ♀ [1 March 1951]. Female holotype from White House Canyon, Santa Rita Mountains, Arizona, in the American Museum of Natural History, examined.

Conaranea gertschi Archer, 1951, Amer. Mus. Novitates, No. 1502: 7, fig. 33, ♂ (not Figs. 17, 30, ♀) [5 April 1951]. Male holotype from Coconino Co. [General Springs, Mogollon Rim, 10 mi. east of Baker Butte, 12 mi. east of Pine, Giles Co.*], Arizona, in the American Museum of Natural History, examined. NEW SYNONYMY.

Note. The female paratypes of *Conaranea gertschi* are *Araneus arizonensis* (Banks).

Description. Female carapace brown with whitish hairs. Sternum light brown. Legs light brown, indistinctly banded with darker brown. Dorsum of abdomen brown with a pair of marks anterior to humps and a folium posteriorily (Figs. 79, 85). Venter with white pigment between epigynum and spinnerets and surrounding spinnerets. Center of pigment spot gray. Carapace hairy with a deep longitudinal groove. The legs are heavy, armed with macrosetae. The abdomen has large dorsal humps. Total length 8 mm. Carapace 4.0 mm long, 3.3 mm wide. First femur, 5.0 mm; patella and tibia, 5.8 mm; metatarsus, 3.0 mm; tarsus, 1.2 mm. Second patella and tibia, 5.5 mm; third, 3.0 mm; fourth, 4.3 mm.

Male is colored and marked like female. The abdomen is longer than wide, with large humps. Total length 5.8 mm. Carapace 3.3 mm long, 2.9 mm wide. First femur, 4.0 mm; patella and tibia, 4.5 mm; metatarsus, 3.0 mm; tarsus, 1.1 mm. Second patella and tibia, 3.9 mm; third, 2.2 mm; fourth, 3.6 mm.

Variation. Other females measured 7.8 mm total length, carapace 3.5 mm long, 2.7 mm wide.

Note. Males and females have not been collected together, but the massive scape of the female's epigynum is matched by a relatively large median apophysis. Also the abdominal color patterns of male and female match. I believe Archer's match to be incorrect.

Diagnosis. Female *Araneus mammatus* has the epigynal openings anterodorsal in the base and invisible in ventral view (Figs. 72, 73). It differs from the two California species (*A. bispinosus* and *A. montereyensis*) by having the base on each side with a longitudinal dark band (Figs. 73, 76) and having the abdomen longer than wide with distinct dorsal markings (Fig. 79). The abdomen of the California species is wider than long. Male *Araneus mammatus* differ from related species by the short embolus of the palpus (Figs. 83, 84), small terminal apophysis (Fig. 82), the single tip on the lower prong of the median apophysis (Figs. 80, 81), and the distinct conductor (Fig. 81).

Records. Arizona. Cochise Co.: Upper Cave Cr. and Southwestern Research Station, Chiricahua Mts., ♀ (Map 2).

Araneus bispinosus (Keyserling)
Figures 86–106; Map 3

Epeira bispinosa Keyserling, 1885, Verhandl. Zool. Bot. Ges. Wien, 34: 531, pl. 13, fig. 30, ♀. Female holotype from San Diego, California, in the Museum of Comparative Zoology, examined.

Epeira pacifica McCook, 1894, American Spiders, 3: 180, pl. 11, fig. 15, ♀. Female lectotype here designated, one female, one male, paralectotypes, in poor condition from San Diego, California, in the Academy of Natural Sciences, Philadelphia, examined; not male paralectotype. First

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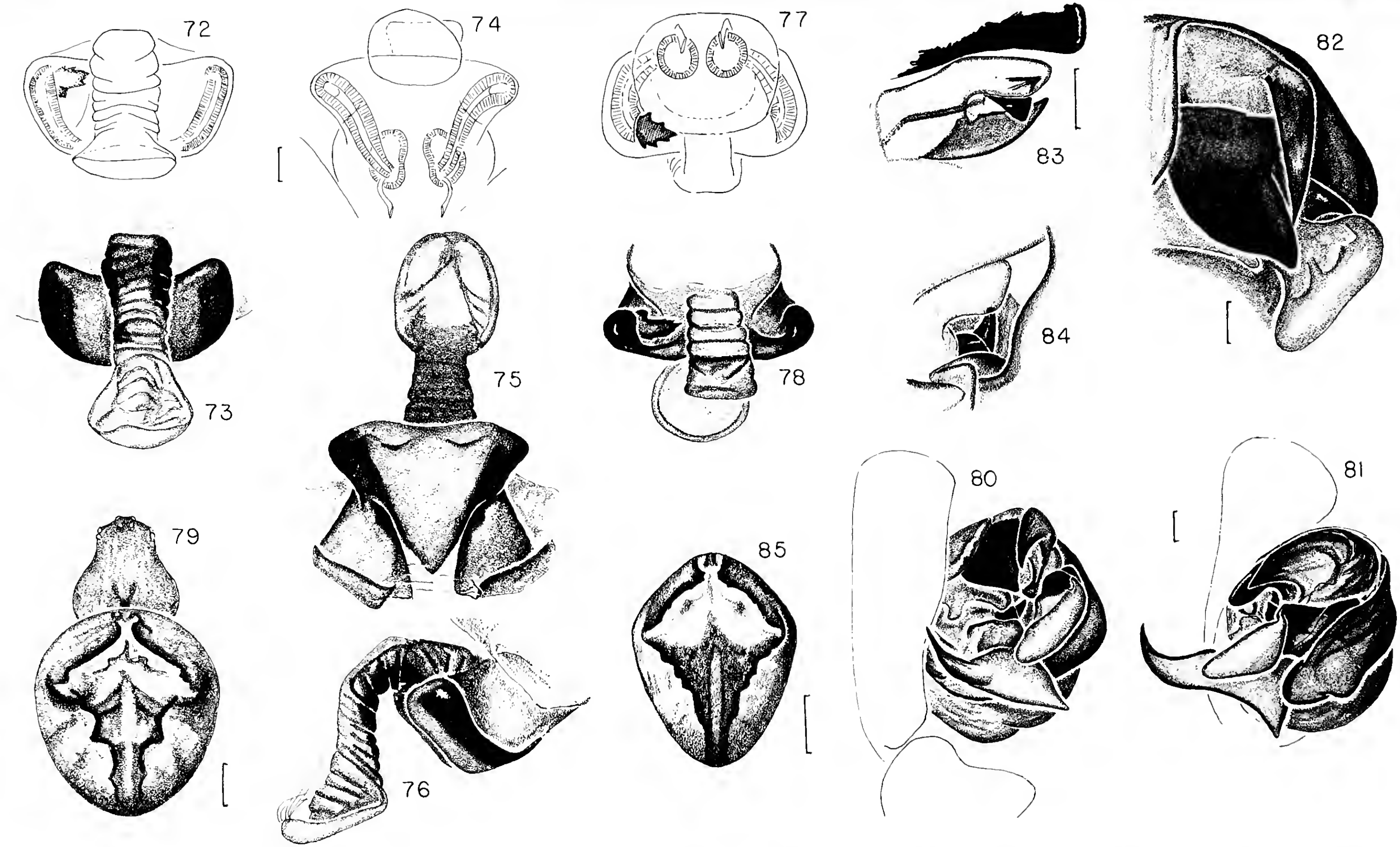
[*] I. J. Cantrall, the collector, personal communication.



Figures 72–85. *Araneus mammatus* (Archer). 72–78. Epigynum. 72. Ventral, cleared. 73. Ventral. 74. Posterior, cleared. 75. Posterior. 76. Lateral. 77. Anterior, cleared. 78. Anterior. 79. Female. 80–84. Left palpus. 80. Mesal. 81. Ventral. 82. Terminal apophysis. 83–84. Embolus, mesal. 85. Male abdomen.
(Size indicators 0.1 mm, for Figs. 79, 85, 1 mm)

synonymized by Banks, 1910, Bull. U.S. Natl. Mus. 72: 41.

Epeira excelsa Banks, 1896, J. New York Entomol. Soc., 4: 90. Female holotype from Palo Alto, California, in the Museum of Comparative Zoology, examined. First synonymized by Banks, 1910, Bull. U.S. Natl. Mus. 72: 41.

Note. One specimen of the Chamberlin collection of this species was marked as *A. bonsallae*. Specimens of this collection marked *Araneus bispinosus* all belonged to *A. montereyensis*.

Description. Female. Carapace, sternum, legs brown. Dorsum of abdomen with a dark folium and anterior dark (Fig. 94). Venter black between epigynum and spinnerets, with a white longitudinal band on each side. Spinnerets dark. Anterior median eyes three diameters apart. Abdomen is triangular, wider than long with a slight hump anteriorily on each side (Figs. 94, 95). Total length 4.1–6.8 mm. Carapace 1.6–3.0 mm long, 1.5–2.5 mm wide.

Male coloration as in female. Abdomen with distinct lateral lobes. Total length 3.2–5.0 mm. Carapace 1.7–2.4 mm long, 1.5–2.1 mm wide.

Variation. The lobes of each side of the epigynum (Fig. 87) are quite variable, as is the length of the embolus.

Diagnosis. Female *Araneus bispinosus* is distinct from *A. montereyensis, A. mariposa* and *A. monica*, by having the openings of the epigynum toward the anterior, not visible from the venter (Figs. 86–93), and dark marks on their rim (Figs. 91, 92); *A. montereyensis* has the opening visible from the venter; in *A. mariposa* and *A. monica* the openings face dorsally. Also the female usually has a long, folded scape (Fig. 87); that of the other three species is short. Males of *A. bispinosus* differ from those of *A. montereyensis* by having a narrow terminal apophysis (Fig. 98) in the palpus and the conductor sclerotized laterally (Fig. 97), and from both *A. montereyensis* and *A. mariposa* by having a longer median apophysis (Figs. 96, 104–106).

Natural history. Numerous collections indicate that the animals were collected by sweeping chaparral, coastal sage or coastal sage-oak woodland. Males are mature in March to June, females from February to July.

Distribution. Central to Southern California (Map 3).

Araneus mariposa n. sp.

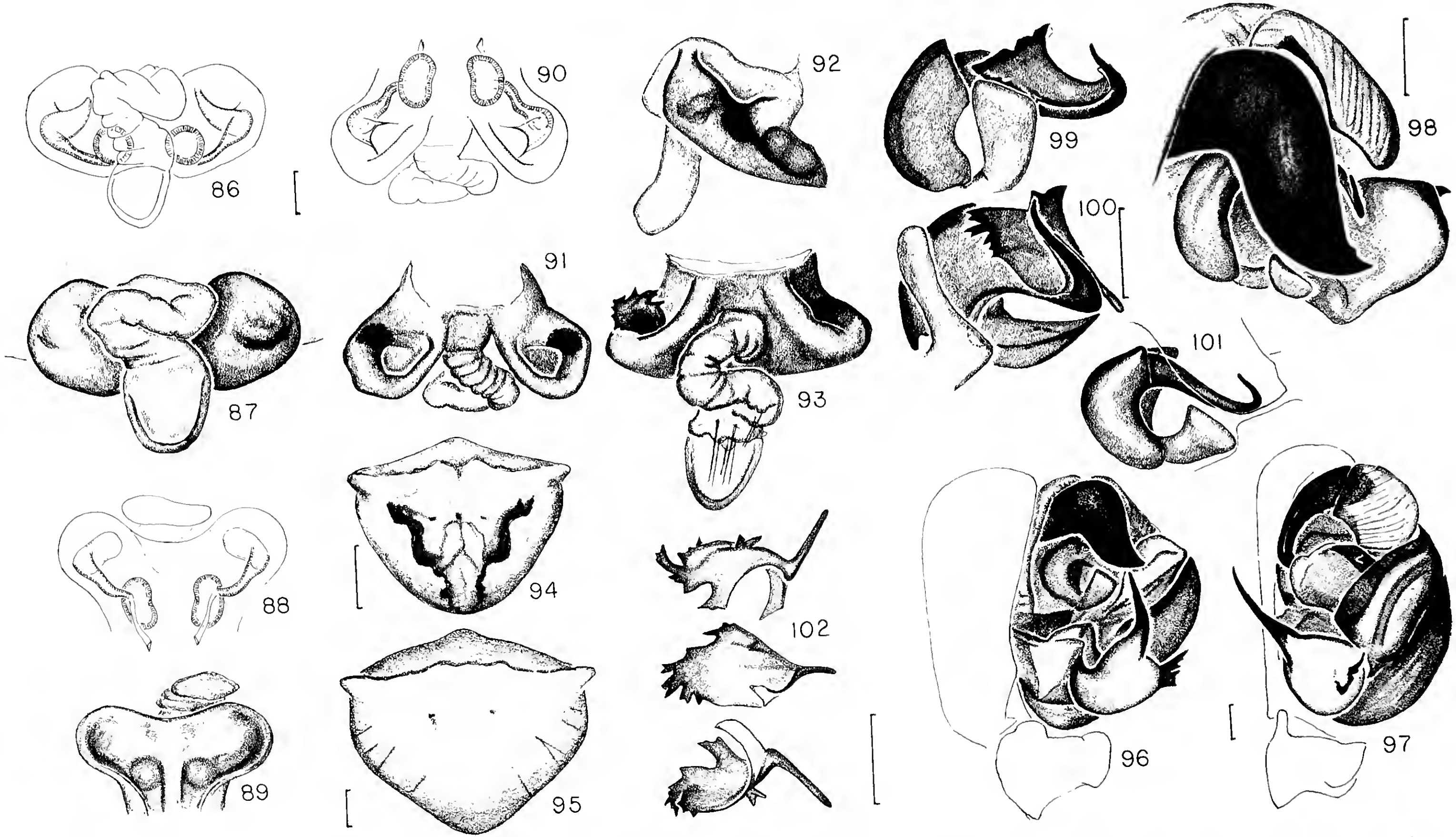
Figures 107, 122–137; Map 3

Type. Female holotype from Mt. Bullion, Mariposa County, California, in chaparral, 2 May 1959 (no. 187, R. X. Schick), is in the American Museum of Natural History. The specific name is a noun in apposition after the type locality.

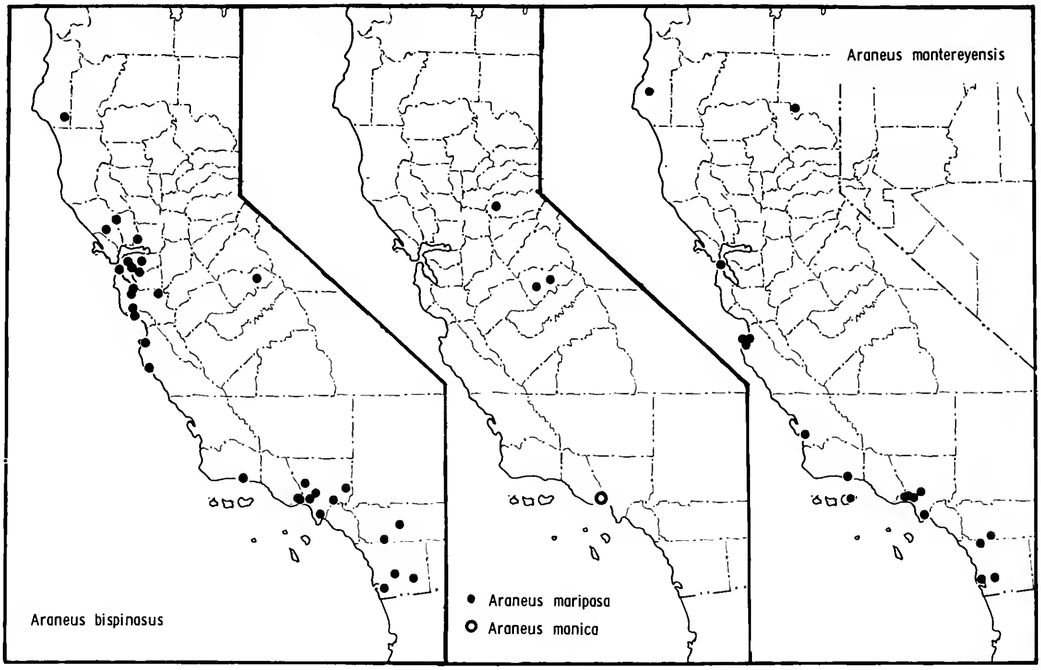
Description. Carapace yellow with white setae in head region. Sternum orange, legs orange-yellow. Dorsum of abdomen white with some transverse marks (Fig. 131). White pigment more dense anteriorly toward the humps. Sides with brownish streaks radiating from spinnerets. The venter has gray pigment between epigynum and spinnerets with a white longitudinal line on each side. Spinnerets surrounded by brown anteriorly and on sides. Anterior median eyes three diameters apart, four from laterals. Posterior 1.5 diameters apart, four diameters from laterals. The legs are quite heavy and hairy. Abdomen is triangular with lateral humps and with many hairs. Total length 7.0 mm. Carapace 3.0 mm long, 2.5 mm wide. First femur, 3.0 mm; patella and tibia, 3.7 mm; metatarsus, 2.3 mm; tarsus, 0.9 mm. Second patella and tibia, 3.4 mm; third, 1.8 mm; fourth, 2.9 mm.

Male coloration as in female, with more black pigment. Legs banded. Narrow longitudinal thoracic line is dark. Anterior median eyes two diameters apart, two from laterals. Posterior median eyes are 1.5 diameters apart, three from laterals. Abdomen triangular with two anterior humps. Neither legs nor coxae modified. Total length, 5.0 mm. Carapace 2.5 mm long, 2.3 mm wide. First femur, 3.6 mm; patella and tibia, 4.3 mm; metatarsus, 3.0 mm; tarsus, 1.0 mm. Second patella and tibia, 3.9 mm; third, 1.8 mm; fourth, 2.2 mm.

Diagnosis. Female of *Araneus mariposa*



Figures 86–102. *Araneus bispinosus* (Keyserling). 86–93. Epigynum. 86. Ventral, cleared. 87. Ventral. 88. Posterior, cleared. 89. Posterior. 90. Anterior, cleared. 91. Anterior. 92. Lateral. 93. Anterior with embolus cap. 94, 95. Female abdomen. 96–102. Left palpus. 96. Mesal. 97. Ventral. 98. Terminal apophysis. 99, 100. Virgin embolus with tip. 101. Embolus. 102. Embolus cap.
(Size indicators 0.1 mm, for abdomen 1 mm)



Map 3. Distributions of small California species of *Araneus.*

differs from *A. bispinosus* and *A. montereyensis* female in having the epigynal openings face dorsally (Figs. 126, 129, 130), from *bispinosus* by the short, straight scape (Fig. 123), and from *A. monica* by having the openings larger and bordered all around (Fig. 126). The median apophysis of the male (Fig. 107) is much shorter than that of *A. bispinosus.*

Records. California. Eldorado Co.: near Nashville, 25 April 1958, ♂ paratype, 25 April 1958, in Berlese sample of clay loam (R. O. Schuster and Smith). Mariposa Co.: El Portal, 2 May 1959, 2 ♂ paratypes (R. X. Schick) (Map 3).

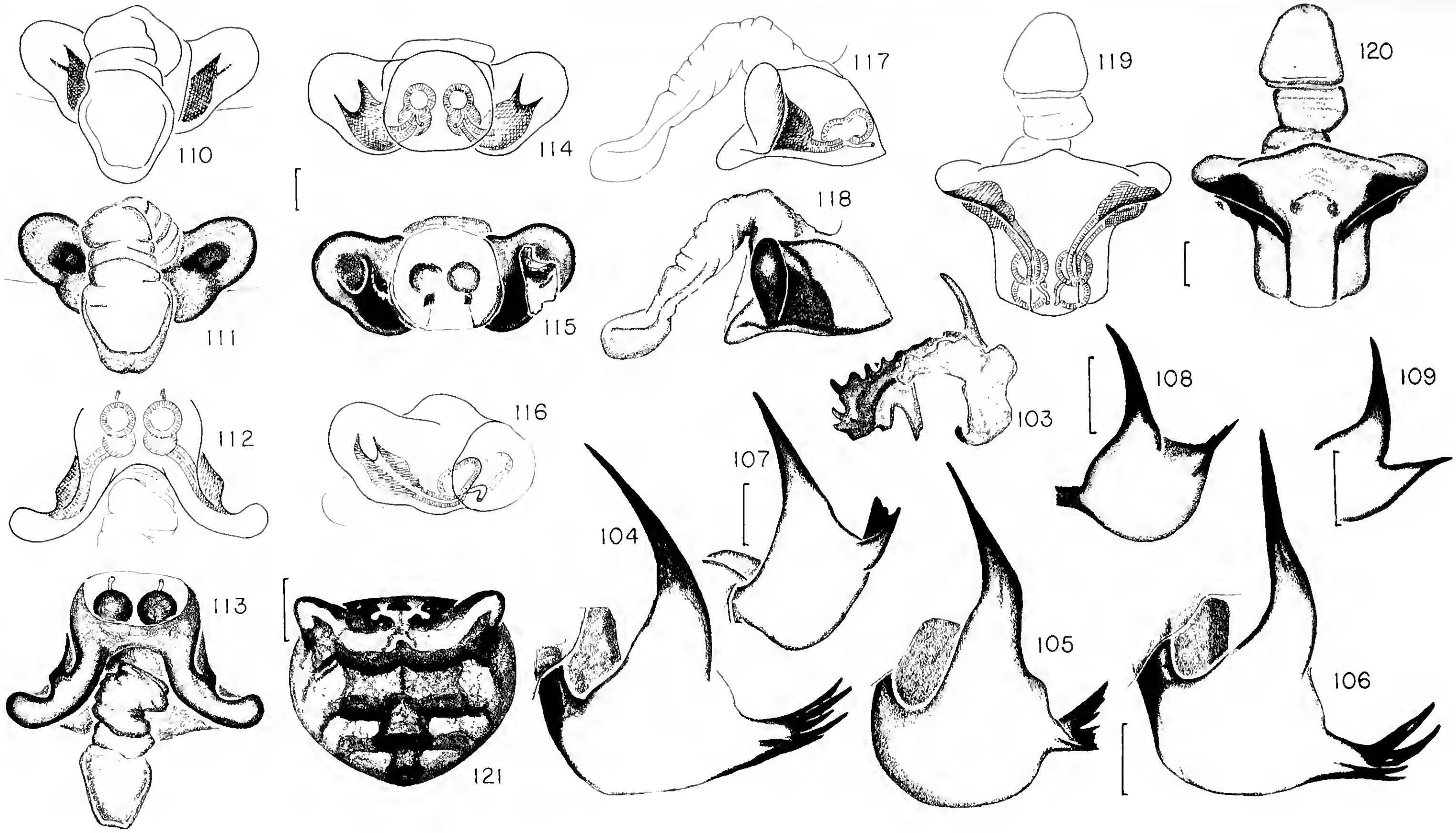
Araneus monica n. sp.

Figures 110–121; Map 3

Type. Female holotype from Santa Monica Mts., Los Angeles County, California, April 1953 (R. X. Schick) in the American Museum of Natural History. The name is a noun in apposition after the type locality.

Description. Female carapace yellowish brown with some gray. Posterior median eyes and lateral eyes on black spots. Sternum dark brown. Legs indistinctly banded. Dorsum of abdomen with transverse bars, which are shorter posteriorly with white on each side. Anterior of bars above pedicel is a white triangle, pointing to pedicel (Fig. 121). Black between epigynum and spinnerets, white on each side. Anterior median eyes 1.5 diameters apart, 1.5 from laterals. Posterior median eyes slightly more than one diameter apart, 2.5 from laterals. The abdomen is triangular with very distinct, long humps. Total length 5.5 mm. Carapace 2.3 mm long, 1.9 mm wide. First femur, 2.3 mm; patella and tibia, 2.7 mm; metatarsus, 1.8 mm; tarsus, 0.7 mm. Second patella and tibia, 2.6 mm; third, 1.6 mm; fourth, 2.2 mm.

Diagnosis. Araneus monica differs from the sympatric *A. bispinosus* and *A. montereyensis* by having the epigynal openings face dorsally (Figs. 114–118), and from *A.*



Figures 103–106. *Araneus bispinosus* (Keyserling), left palpus. 103. Embolus cap, different individual. 104–106. Median apophysis.
Figure 107. *Araneus mariposa* n. sp., median apophysis.
Figures 108–109. *Araneus montereyensis* (Archer), median apophysis.
Figures 110–121. *Araneus monica* n. sp. 110–120. Epigynum. 110. Ventral, cleared. 111. Ventral. 112. Anterior, cleared. 113. Anterior. 114. Dorsal, cleared. 115. Dorsal. 116. Dorsolateral, cleared. 117. Lateral, cleared. 118. Lateral. 119. Posterior, cleared. 120. Posterior. 121. Female abdomen.
(Size indicators 0.1 mm, for abdomen 1 mm)

bispinosus by having a shorter scape (Fig. 111). *Araneus monica* is distinct from *A. mariposa* in having the openings smaller and bordered only posteriorly and toward the median (Fig. 115).

Araneus montereyensis (Archer)

Figures 108, 109, 138–151; Map 3

Epeira pacifica,—McCook, 1894, American Spiders, 3: 180, pl. 11, fig. 16, ♂. Male paralectotype from San Diego, California, here designated in the Academy of Natural Sciences, Philadelphia; not lectotype.

Conaranea montereyensis Archer, 1951, Amer. Mus. Novitates, No. 1502: 8, figs. 3, 24, 25, ♀, ♂. Female holotype from Monterey, California, in the American Museum of Natural History, examined.

Note. In the Chamberlin collection specimens of this species were marked *A. bispinosus.*

Description. Female carapace light brown, head region black; black area often going to the thoracic depression (Fig. 144) and with black border. Sternum dark brown. Coxae light brown. Legs light brown, with narrow dark brown bands. Dorsum of abdomen black anteriorly and with dark folium; sides black, clearly delineated toward dorsum (Figs. 143–144). Venter black between epigynum and spinnerets, with a longitudinal white band on each side. Anterior median eyes 1.5 diameters apart, two diameters from laterals; posterior median eyes are slightly more than one diameter apart, 2.5 diameters from laterals. The abdomen is subtriangular with indistinct humps. Total length 3.2–5.5 mm. Carapace 1.8–2.0 mm long, 1.4–1.9 mm wide.

Male coloration like that of female. Thoracic depression is a shallow longitudinal pit. Anterior median eyes 1.5 diameters apart, 1.5 from laterals. Posterior median eyes 1.2 diameters apart, slightly more than two from laterals. Total length 3.5–3.6 mm. Carapace 1.8–2.0 mm long, 1.5–1.7 mm wide.

Variation. There is considerable variation in color. Sometimes the thorax is lighter. The anterior abdominal band is generally broken in middle. The distal branch of the median apophysis of the palpus may be a single tip (Fig. 109) or may have teeth (Fig. 108). This would place the specimens in different genera were we to follow Archer's system of generic classification.

Diagnosis. The females differ from those of *A. bispinosus* by having less distinct humps on the abdomen (Fig. 144), and from other *A. bispinosus* and other California species by having the opening of the epigynum show in ventral view. The scape is short (Figs. 138, 139) and not folded as in *A. bispinosus.* The wide terminal apophysis of the palpus (Fig. 147), the bottle-shaped conductor (Fig. 146), and the almost circular median apophysis (Figs. 108, 109, 145) readily separate *A. montereyensis* from other California species.

Natural history. Specimens have been collected on a eucalyptus tree, in upper branches of small trees (*Ceanothus* sp.) and in chaparral and coastal oak woodland. Males are mature from January to June, adult females have been collected until October. Some collections are with *A. bispinosus.*

Distribution. Central and Southern California (Map 3).

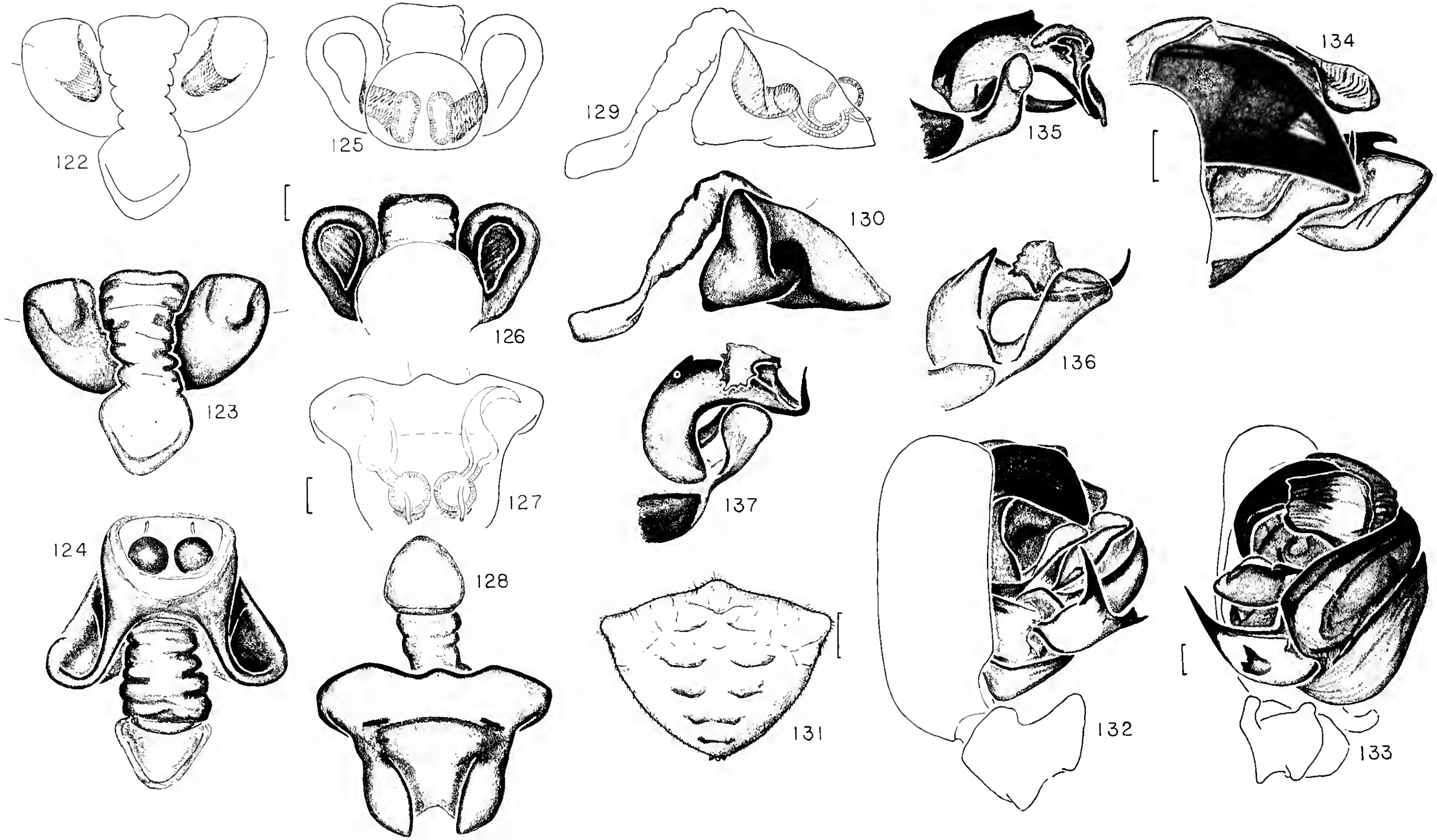
Araneus miniatus (Walckenaer)

Figures 158–171; Map 4

Epeira miniata Walckenaer, 1841, Histoire Naturelles des Insectes. Aptères, 2: 39. The types are Abbot's manuscript Spiders of Georgia, figs. 228–230, of which I here choose fig. 228 lectotype, in the British Museum, Natural History. Copies in the Museum of Comparative Zoology, examined. McCook, 1894, American Spiders, 3: 177, pl. 8, figs. 8, 9 [pl. 10, figs. 7, 8 as *E. reticulata*], ♀, ♂.

Epeira scutulata Hentz, 1850, J. Boston Natur. Hist. Soc., 6: 19, pl. 3, fig. 3, ♂. Male type from Alabama, destroyed. Emerton, 1902, Common Spiders, p. 178, fig. 415, ♀. Name first synonymized by McCook, 1894.

Larinia nigrofoliata Keyserling, 1883, Verhandl. Zool. Bot. Ges. Wien, 32: 653, pl. 21, fig. 5, ♂. Male holotype from "Summit Canyon, Utah" (however, marked "Col." or "Cal." not Utah on label, G. Marx collection) in the United States National Museum, stored in the American Museum of Natural History, examined. Collecting



Figures 122–137. *Araneus mariposa* n. sp. 122–130. Epigynum. 122. Ventral, cleared. 123. Ventral. 124. Anterior. 125. Dorsal, cleared. 126. Dorsal. 127. Posterior, cleared. 128. Posterior. 129. Lateral, cleared. 130. Lateral. 131. Female abdomen. 132–137. Left palpus. 132. Mesal. 133. Ventral. 134. Terminal apophysis. 135–137. Virgin embolus.

(Size indicators 0.1 mm, for abdomen 1 mm)

localities in error. 1893, Spinnen Amerikas, 4: 291, pl. 15, fig. 215, ♂. Roewer, 1942, Katalog der Araneae, 1: 772. Bonnet, 1957, Bibliographia Araneorum, 2: 2350. NEW SYNONYMY.

Epeira floridensis Banks, 1904, Proc. Acad. Natur. Sci. Philadelphia, 56: 129, pl. 7, fig. 5, ♀. Female holotype from Miami, Florida, in the Museum of Comparative Zoology, examined. NEW SYNONYMY.

Araneus miniatus,—Petrunkevitch, 1911, Bull. Amer. Mus. Natur. Hist., 29: 303. Bonnet, 1955, Bibliographia Araneorum, 2: 544.

Araneus floridensis,—Petrunkevitch, 1911, Bull. Amer. Mus. Natur. Hist., 29: 292. Bonnet, 1955, Bibliographia Araneorum, 2: 504.

Aranea miniata,—Comstock, 1912, Spider Book, p. 474, fig. 492, ♀. 1940, rev. ed., p. 488, fig. 492, ♀. Roewer, 1942, Katalog der Araneae, 1: 861. Kaston, 1948, Connecticut Geol. Natur. Hist. Surv., 70: 252, fig. 790, ♀.

Aranea floridensis,—Roewer, 1942, Katalog der Araneae, 1: 842.

Epeira guttulata,—Chamberlin and Ivie, 1944, Bull. Univ. Utah, biol. ser., 8(5): 99.

Conepeira partita,—Archer, 1951, Amer. Mus. Novitates, No. 1502: 13, fig. 63, ♀ (not ♂).

Conepeira floridensis,—Archer, 1951, Amer. Mus. Novitates, No. 1502: 14, figs. 38, 58, ♀, ♂.

Conepeira miniata,—Archer, 1951, Amer. Mus. Novitates, No. 1502: 15, figs. 36, 37, 61, ♀, ♂.

Conepeira dawsoni Archer, 1951, Amer. Mus. Novitates, No. 1502: 16, figs. 13, 39, 53, 59, ♀, ♂. Male holotype from Centreville, Wilkinson Co., Mississippi, in the American Museum of Natural History, examined. NEW SYNONYMY.

Note. Since this species has been called *miniatus* from the time of McCook (more than 50 years), I will keep the name, although the Abbot illustrations are not convincing. I chose fig. 228 of Abbot lectotype since the others do not have lateral humps. There are no specimens marked *Epeira reticulata* in the McCook collection. While the type of *Larinia nigrofoliata* has the characteristic pattern, that of *E. floridensis* Banks is bleached white. Banks, however, described the pattern to be "like *E. scutulata.*" The type locality of *L. nigrofoliata,* Marx collection, is almost certainly in error, regardless whether Utah, Colorado, or California. The two Chamberlin specimens from Georgia of this species had been misidentified as *Epeira guttulata* (Chamberlin and Ivie, 1944). Other specimens in the Chamberlin collection were marked *miniata* in 1942, *Araneus* sp. B, in 1933. The Figures 159, 163, 164 were prepared from the paratype of *Conepeira dawsoni* Archer. In collections *A. miniatus* and *A. partitus* had both been labeled *miniatus* or *scutulata.*

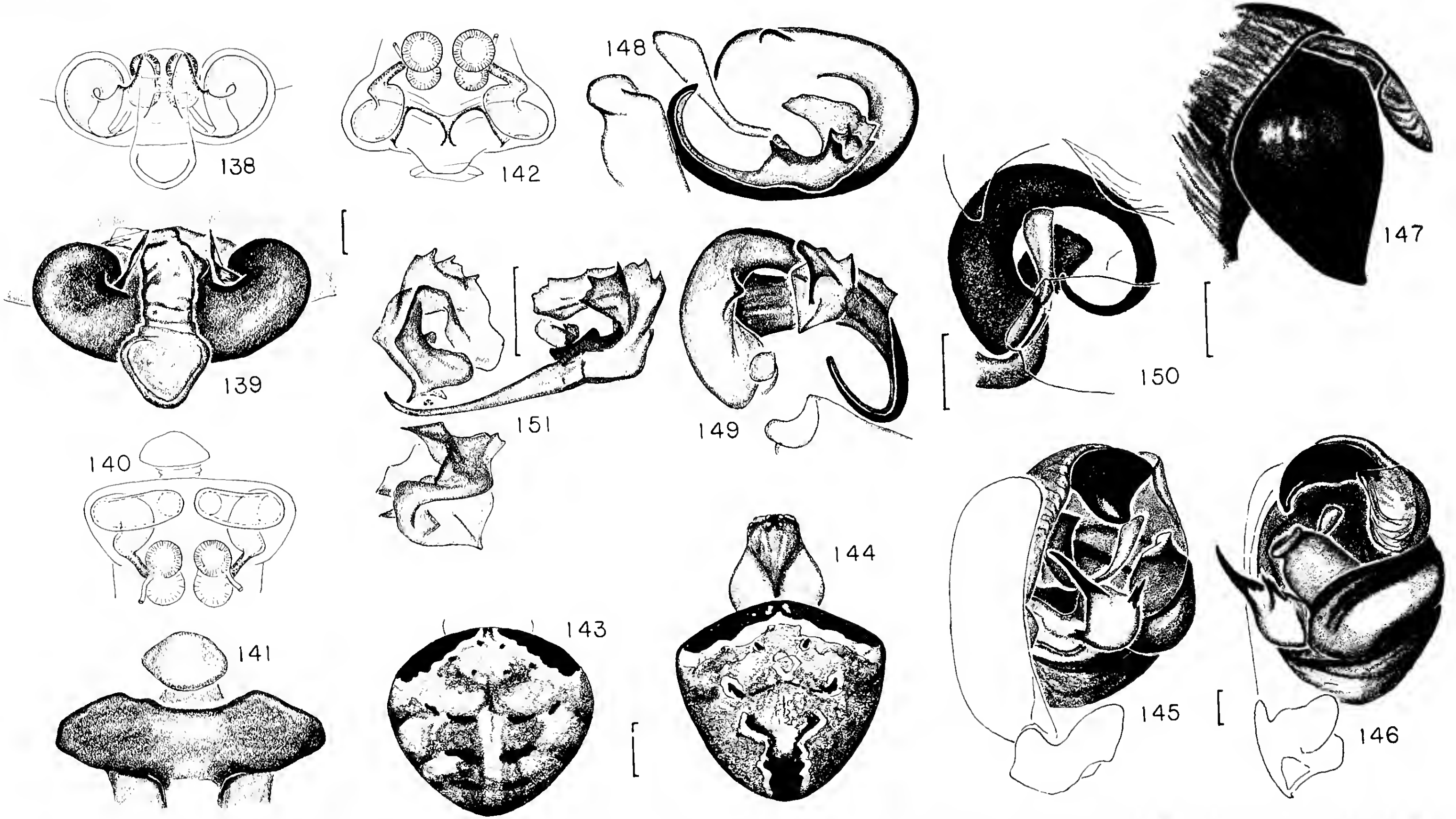
Description. Female carapace, sternum yellow. Legs yellowish, distal ends of articles darker. Dorsum of abdomen with transverse white band, three pairs of black spots posterior and between them a darker folium (Fig. 164). Anterior of white transverse band, the abdomen is darker spotted with some black spots around the outside. Sides of abdomen with some white pigment; venter with two pairs of white longitudinal pigment bands between epigynum and spinnerets, yellowish inbetween. The abdomen is wider than long (Fig. 164). Total length 3.0–4.7 mm. Carapace 1.4–1.9 mm long, 1.2–1.7 mm wide.

Male carapace, sternum, legs yellow. Dorsum of abdomen with pattern similar to that of female. Carapace with a shallow, longitudinal groove. The abdomen is triangular. Total length 2.5–3.7 mm. Carapace 1.4–1.9 mm long, 1.2–1.6 mm wide.

Note. The embolus cap that breaks off is heart-shaped (Figs. 161, 162, 171). The part hanging out of the epigynum is the part closest to the base of the embolus; the inserted part the one closest to the tip. The inserted part of the cap has a hook which fastens it into the epigynum and usually makes its removal difficult or impossible without breaking (Fig. 171). The hook on the cap is not visible in Figure 169 because the embolus was drawn through a cleared palpus. Normally in the contracted palpus the embolus is almost completely hidden (Figs. 165, 166).

Variation. Florida specimens are noticeably smaller and lighter than those from other parts of the range.

Diagnosis. *Araneus miniatus* and *A. partitus* differ from other eastern species of small *Araneus* by having the abdomen wider than long in the female (Fig. 164), as wide as long in the male, and dorsally marked with spots around the periphery. (*A. alboventris* has the abdomen wider than



Figures 138–151. *Araneus montereyensis* (Archer). 138–142. Epigynum. 138. Ventral, cleared. 139. Ventral. 140. Posterior, cleared. 141. Posterior. 142. Anterior, cleared. 143. Female abdomen. 144. Female. 145–150. Left palpus. 145. Mesal. 146. Ventral. 147. Terminal apophysis. 148–149. Virgin embolus. 150. Embolus. 151. Caps.

(Size indicators, 0.1 mm, for Figs. 143, 144, 1 mm) long, but with a central dorsal black patch.) The male, like those of *A. partitus* and *A. alboventris,* lacks two macrosetae on the cymbium. The female of *A. miniatus* differs from that of *A. partitus* by having a wrinkled scape (Figs. 159–162); the embolus of the *A. miniatus* male palpus is an evenly tapering pointed structure (Figs. 165, 169, 170), while that of *A. partitus* has almost parallel sides and is blunt at its tip, and that of *A. alboventris* is twisted.

Natural history. Specimens have been collected from citrus groves and water oak (*Quercus nigra*) forests in Florida. In Florida males are mature from January to August, and farther north, from March. Females are mature from March (Florida) to August.

Distribution. Eastern United States, from Woods Hole, Massachusetts, to northeastern Texas and Florida (Map 4).

Araneus partitus (Walckenaer)

Figures 177–191; Map 4

Epeira partita Walckenaer, 1841, Histoire Naturelles des Insectes. Aptères, 2: 46. The type is Abbot's manuscript Spiders of Georgia, fig. 40, in the British Museum, Natural History. Copies in the Museum of Comparative Zoology, examined.

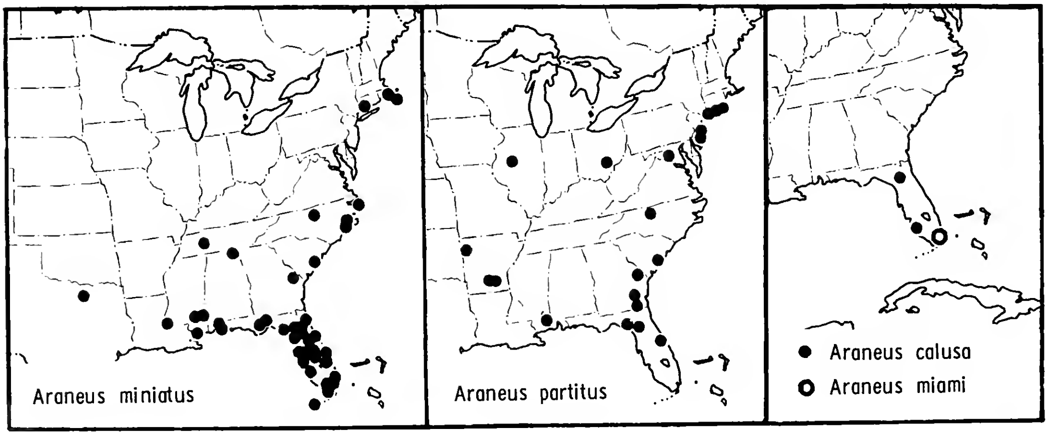
Epeira punctillata Keyserling, 1879, Verhandl. Zool. Bot. Ges. Wien, 29: 304, pl. 4, fig. 7, ♂. Male holotype from Peoria, Illinois, in the British Museum, Natural History, examined. NEW SYNONYMY.

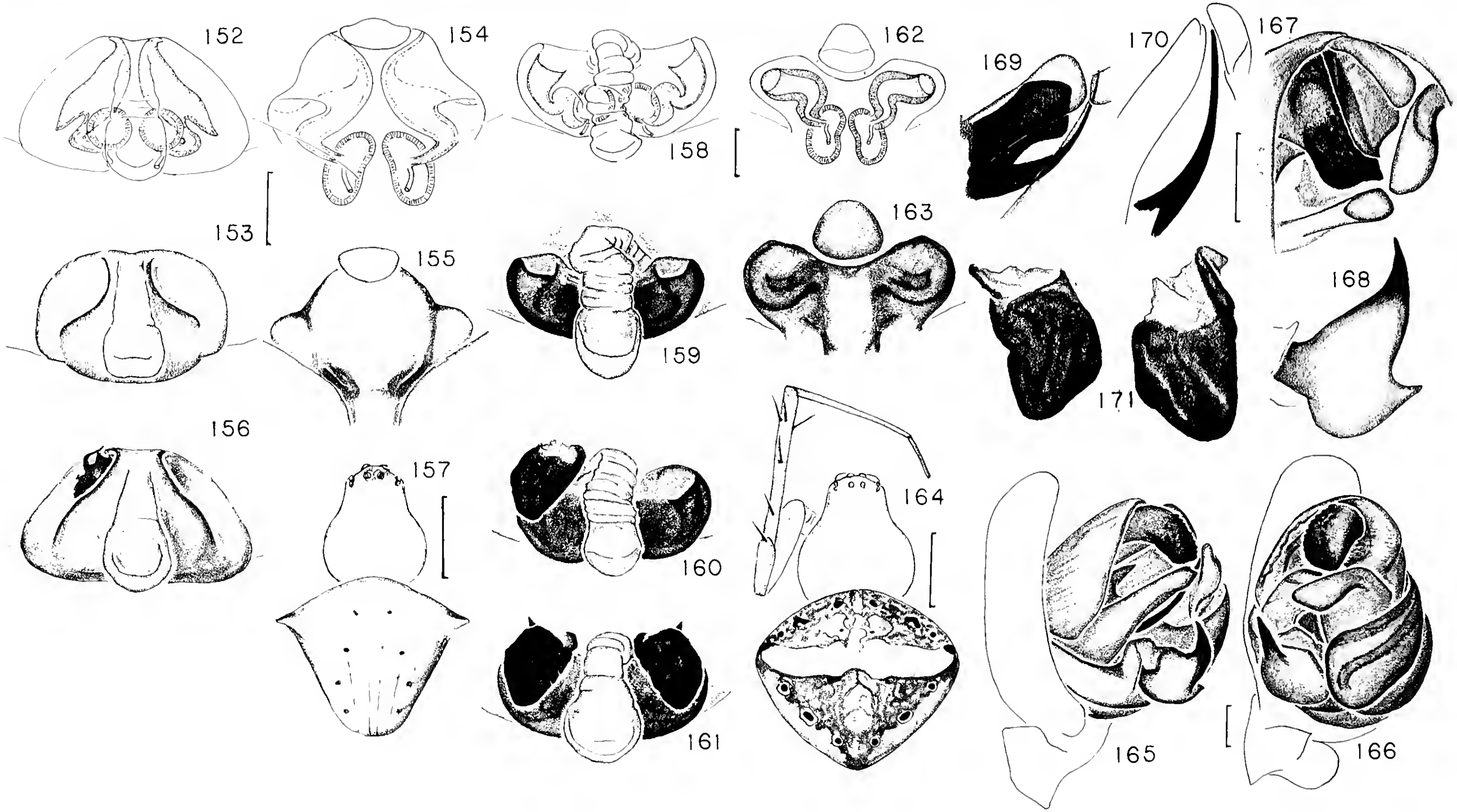
Conepeira partita,—Archer, 1951, Amer. Mus. Novitates, No. 1502: 13, fig. 34 [not 63, ♀].

Conepeira atlantis Archer, 1951, Amer. Mus. Novitates, No. 1502: 13, figs. 32, 35, ♂ [not fig. 60, ♀]. Male fragment from Lakehurst, New Jersey, 1 May 1912 (J. H. Emerton), under leaves, in the Museum of Comparative Zoology, examined. NEW SYNONYMY.

Note. Archer as first reviser decided that *A. partita* is a different species from *miniatus.* Archer designated a neotype, which is invalid, according to the International Code on Zoological Nomenclature, because the original type, Abbot's illustration, is still in existence. But then Archer gave the new name *atlantis* to the same species; the holotype is a male. The female labeled *A. partita* by Archer is *A. miniatus,* the female *A. atlantis* is also *A. miniatus.* The use of the Walckenaerian name does not upset usage of names, although Chamberlin and Ivie (1944) labeled *partitus* specimens as *A. miniatus;* previously Chamberlin specimens had been labeled *Araneus* sp. A in 1933. Also a Barrows specimen from Ohio had been labeled *miniatus.*

Description. Female carapace, legs, sternum yellowish white. Posterior median eyes on small black tubercles. Dorsum of abdomen with four pairs of black spots posteriorly, bordered by small light pairs anteriorly; there are black marks on humps. The area between the humps is white, pos-





Figures 152–157. *Araneus calusa* n. sp. 152–156. Epigynum. 152. Ventral, cleared. 153. Ventral. 154. Posterior, cleared. 155. Posterior. 156. Ventral with cap of embolus. 157. Female.

Figures 158–171. *Araneus miniatus* (Walckenaer). 158–163. Epigynum. 158. Ventral, cleared. 159. Ventral. 160, 161. Ventral with embolus caps. 162. Posterior, cleared. 163. Posterior. 164. Female. 165–171. Left palpus. 165. Mesal. 166. Ventral. 167. Terminal apophysis. 168 Median apophysis. 169. Virgin embolus. 170. Embolus. 171. Embolus cap.

(Size indicators 0.1 mm, for females 1 mm)

terior to it gray, and anterior to it also irregularly gray. The sides and venter of the abdomen are covered by white pigment spots. The abdomen is wider than long with lateral humps (Fig. 183). Total length 3.3–4.3 mm. Carapace 1.5–1.7 mm long, 1.2–1.4 mm wide.

Male coloration more or less like that of female with pairs of black spots on the dorsum (Fig. 191). The abdomen has slight humps, and is pointed behind. Total length 2.7–3.3 mm. Carapace 1.5–1.6 mm long, 1.2–1.4 mm wide. First femur, 2.2 mm; patella and tibia, 2.5 mm; metatarsus, 1.8 mm; tarsus, 0.7 mm. Second patella and tibia, 1.9 mm; third, 1.0 mm; fourth, 1.5 mm.

Diagnosis. Araneus miniatus, A. calusa and *A. partitus* are the only eastern species of small *Araneus* that have the abdomen wider than long in the female and the periphery of the dorsum spotted. The female differs from that of *A. miniatus* and all other small *Araneus* species by having a short, smooth (not wrinkled) scape attached to the middle of the venter of the base (Figs. 177, 179, 180). The male differs from all related eastern species, except *A. miniatus* and *A. alboventris,* by lacking two macrosetae on the cymbium, and from those also by the truncate shape of its embolus (Figs. 185, 189) and by the median apophysis having only one tip (Fig. 188).

Natural history. Nothing on collecting labels suggests differences in habits that distinguish *A. partitus* from *A. miniatus.* The males are also mature in spring.

Distribution. Long Island to Arkansas and Florida (Map 4).

Araneus calusa n. sp.

Figures 152–157; Map 4

Type. Female holotype from Koreshan State Park, Lee County, Florida, 2 February 1971, in few strands of silk on underside of palm leaf, live oak stand, *Vitis,* collected by Susan Riechert, in the Museum of Comparative Zoology. The name is a noun in apposition after a Florida Indian tribe.

Description. Female carapace yellowish white with yellow rings around posterior median eyes. Some black pigment behind lateral eyes. Red spots on first leg; second leg with few red spots on the base of macrosetae. Dorsum of abdomen with white pigment and indistinct, maculated orange lines and spots. A distinct red mark anterior on each lateral hump. A pair of red spots posteriorly on each side. Venter lacking white pigment. The abdomen is somewhat triangular with anterior lateral pointed humps (Fig. 157). Total length 2.9 mm. Carapace 1.4 mm long, 1.2 mm wide. First femur, 1.7 mm; patella and tibia, 2.0 mm; metatarsus, 1.4 mm; tarsus, 0.6 mm. Second patella and tibia, 1.5 mm; third, 0.5 mm; fourth, 1.3 mm.

Variation. Total length varies from 2.9 to 3.8 mm, carapace length from 1.8 to 1.4 mm, width from 1.4 to 1.2 mm.

Diagnosis. Araneus calusa differ from *A. miniatus* and *A. partitus* by having the openings of the epigynum behind a diagonal lip (Figs. 153, 156) rather than at the anterior of the base.

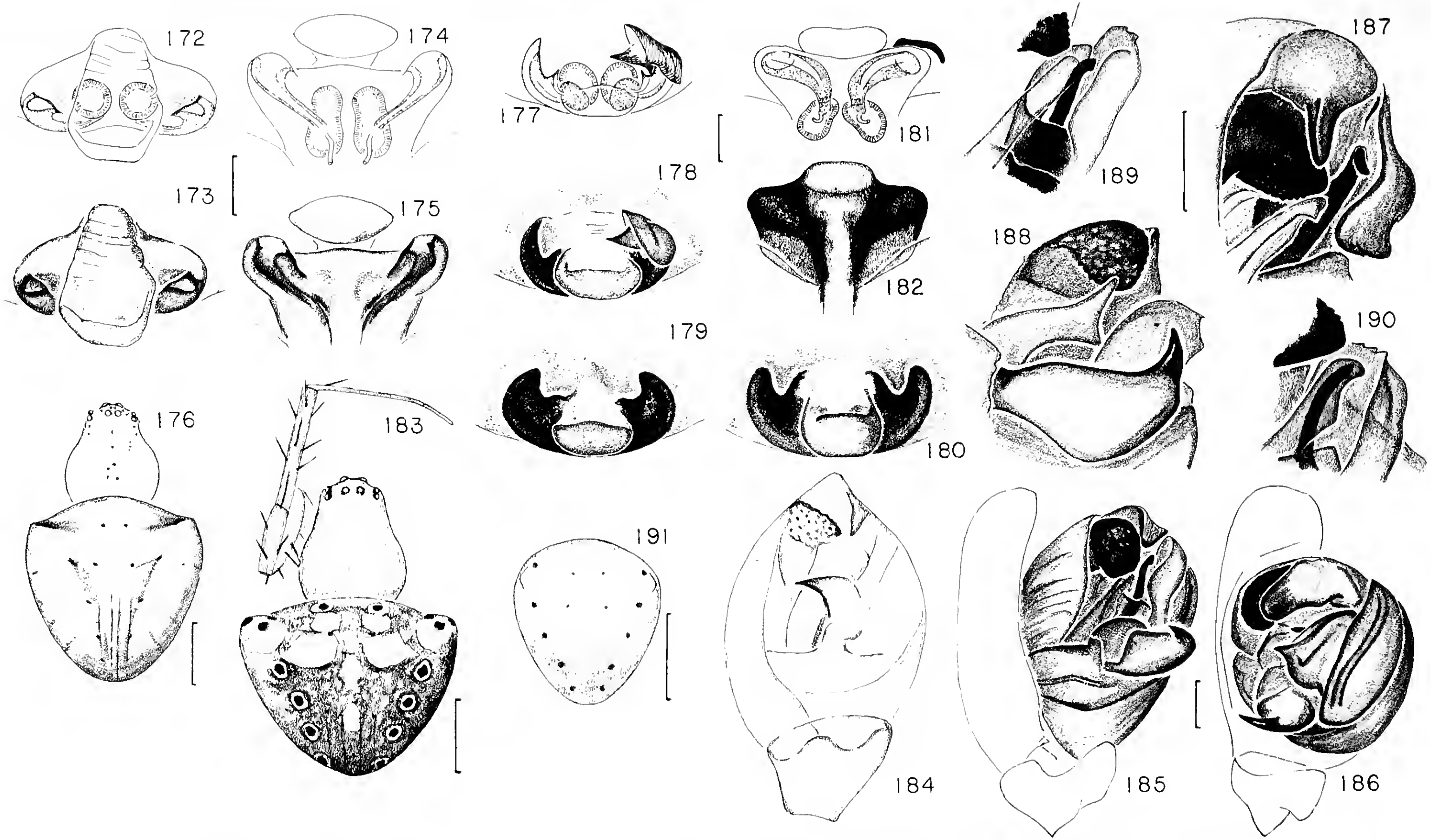
Records. Florida. Alachua Co., ♀ paratype, 24 June 1958 (H. A. Denmark, FSC); 6.2 mi. W of Newberry, 1941, ♀ paratype (H. K. Wallace, HKW) (Map 4).

Araneus miami n. sp.

Figures 172–176; Map 4

Type. Female holotype from Biscayne Bay, Florida (N. Banks Collection) in the Museum of Comparative Zoology. The name is a noun in apposition after the type locality.

Description. Female carapace yellow with scattered black spots. Sternum with scattered black spots. Legs yellowish with scattered black spots. Dorsum of abdomen dark anteriorly between humps, with a dark spot on anterior of each hump, and a brown folium posteriorly on dorsum. Folium is narrower behind than in front, with sides concave (Fig. 176). Sides white. Venter with a white median quadrangular patch, slightly darker on sides. The abdomen is subspherical, shield-shaped in dorsal view, with anteriorly directed humps. Total length 4.5 mm. Carapace 1.6 mm long,



Figures 172–176. *Araneus miami* n. sp. 172–175. Epigynum. 172. Ventral, cleared. 173. Ventral. 174. Posterior, cleared. 175. Posterior. 176. Female.
Figures 177–191. *Araneus partitus* (Walckenaer). 177–180. Epigynum. 177. Ventral, cleared. 178–180. Ventral. 181. Posterior, cleared. 182. Posterior. 183. Female. 184–190. Left palpus. 184. Before last molt. 185. Mesal. 186. Ventral. 187. Terminal apophysis. 188. Median apophysis. 189. Virgin embolus, cleared. 190. Embolus, cleared. 191. Male abdomen.
(Size indicators 0.1 mm, for Figs. 176, 183, 191, 1 mm)

1.4 mm wide. First femur, 2.5 mm. All other leg segments broken off.

Diagnosis. Araneus miami differs from other species of the *A. juniperi* group by the shape of the abdomen (Fig. 176) and by the epigynum (Figs. 173, 175) having a short scape and openings far apart with a diagonal rim.

Araneus alboventris (Emerton)

Plate 6; Figures 192–203, 443; Map 5

Epeira alboventris Emerton, 1884, Trans. Connecticut Acad. Sci., 6: 314, pl. 34, fig. 5, pl. 36, fig. 12, ♀. Female holotype from Peabody, Massachusetts, in the Museum of Comparative Zoology. Not *Epeira albiventer* Keyserling (= *Eustala albiventer*).

Araneus attestor Petrunkevitch, 1911, Bull. Amer. Mus. Natur. Hist., 29: 280. New name because *alboventris* erroneously thought preoccupied by Keyserling. Bonnet, 1955, Bibliographia Araneorum, 2: 440.

Aranea alboventris,—Roewer, 1941, Katalog der Araneae, 1: 859.

Epeira attestor,—Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 260, figs. 791–792, ♀.

Conepeira alboventris,—Archer, 1951, Amer. Mus. Novitates, No. 1502: 20, figs. 47, 71, ♀, ♂.

Note. According to the present International Code of Zoological Nomenclature (1961) *albiventer* and *alboventris* are not homonyms, and the original name for this species, *alboventris,* can be used.

Description. Female, when alive, with carapace, sternum, legs greenish yellow. Bright yellow rings around posterior median eyes. Abdomen dorsum with a black patch bordered by crimson red border on golden yellow background (Plate 6, Figs. 196, 197). Specimens in alcohol have prosoma yellowish, abdomen white with only a triangular dorsal black patch. The abdomen is subtriangular, as wide as long, almost circular. Total length 2.4–3.8 mm. Carapace 1.4–1.6 mm long, 1.1–1.3 mm wide.

Male coloration like that of female. Total length 1.5–2.5 mm. Carapace 1.3 mm long, 1.0 mm wide.

Diagnosis. Freshly collected *A. alboventris* can be recognized immediately by their unique red-bordered black patch on the golden yellow abdomen. Alcoholic specimens of *A. alboventris,* like those of *A. niveus* and *A. glyphicus,* have a median dorsal black patch on the abdomen, but differ by having the abdomen usually slightly wider than long or as wide as long. Females also differ by the short wide scape and the large lateral pocketlike openings in the base (Fig. 193). Males differ from almost all eastern species (except *A. tuscarora, A. miniatus* and *A. partitus*) by lacking the two macrosetae on the cymbium. They also differ from these two and from all other species by the coiled, tapering embolus (Figs. 202, 203), and very thin long basal tooth of the conductor (Figs. 199, 201). *Araneus alboventris* differs from *A. tuscarora* in having a black spot on the abdomen and in the position of the lateral openings of the epigynum, farther apart anteriorly than posteriorly (Fig. 193).

Natural history. One female was collected under leaf of a shrub in the center of a meadow in Vermont. No web was nearby. The female had probably oviposited.

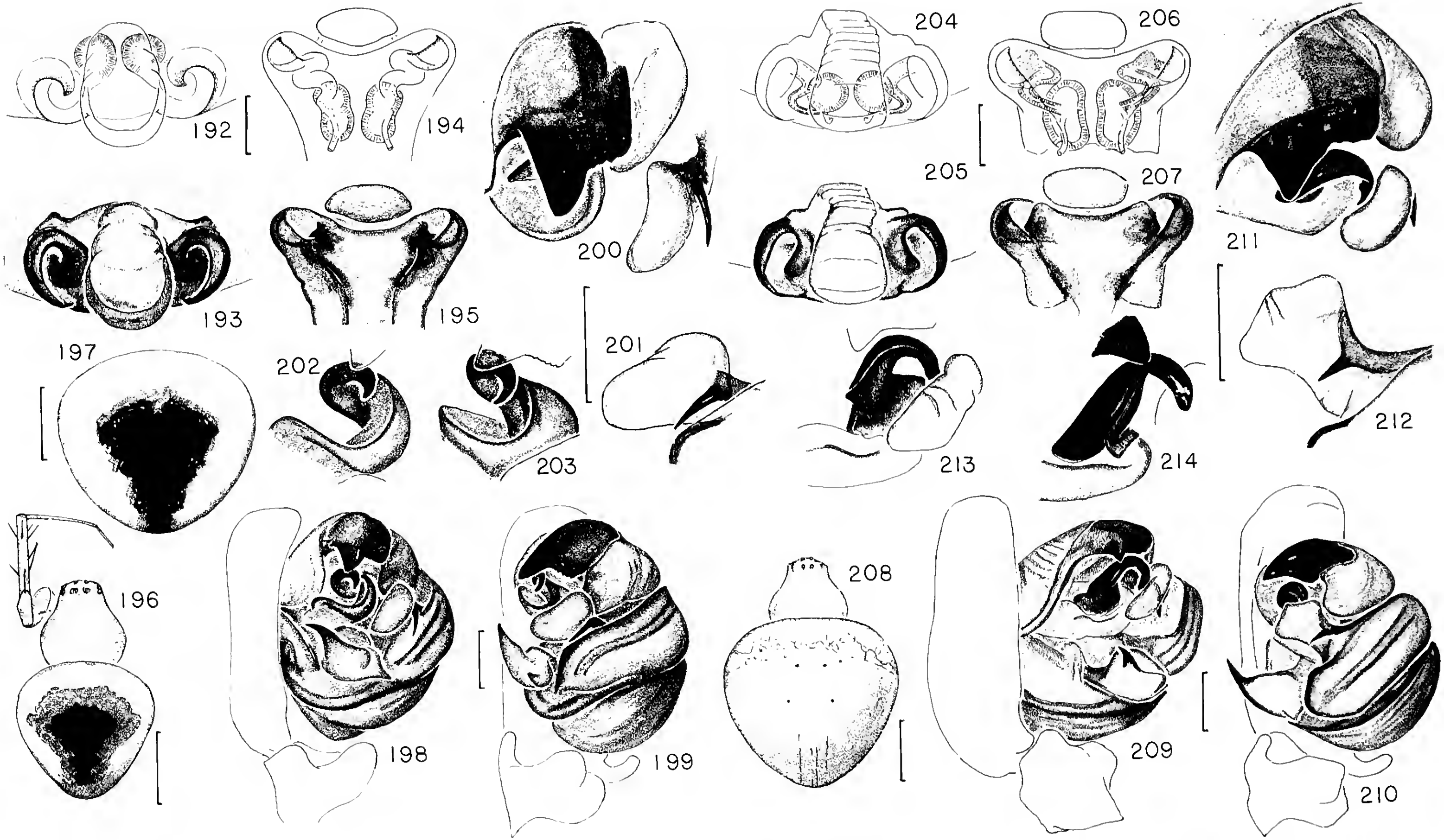
Distribution. New England to Georgia (Map 5). After completion of this paper a female was received from jack pine (*Pinus banksiana*) 1 mi. north of Oylen, Wadena Co., Minnesota, 25 June 1972 (B. Cutler) which lacked the black spot and had a narrower scape. It may belong to a different species.

Araneus tuscarora n. sp.

Figures 204–214, 444; Map 5

Type. Female holotype from broomsedge field, 1.1 miles south of Durham on North Carolina route 55, Durham Co., North Carolina, 8 September 1964 (J. W. Berry), in the Museum of Comparative Zoology. The name is a noun in apposition after a Carolina Indian tribe.

Description. In alcohol, female carapace yellowish brown. Legs, sternum yellowish brown, legs with distal segments darker. Dorsum of abdomen yellowish brown with an anterior transverse band consisting of tiny white spots, posterior with some scattered tiny white spots (Fig. 208). Venter with white spots anterior to pedicel. Sec-



Figures 192–203. *Araneus alboventris* (Emerton). 192–195. Epigynum. 192. Ventral, cleared. 193. Ventral. 194. Posterior, cleared. 195. Posterior. 196. Female. 197. Female abdomen, color washed out. 198–203. Left palpus. 198. Mesal. 199. Ventral. 200. Terminal apophysis. 201. Conductor. 202, 203. Embolus.

Figures 204–214. *Araneus tuscarora* n. sp. 204–207. Epigynum. 204. Ventral, cleared. 205. Ventral. 206. Posterior, cleared. 207. Posterior. 208. Female. 209–214. Palpus. 209. Mesal. 210. Ventral. 211. Terminal apophysis. 212. Conductor. 213, 214. Virgin embolus.

(Size indicators 0.1 mm, for Figs. 196, 197, 208, 1 mm)

ondary eyes 0.8 diameters of anterior median eyes. Anterior median eyes their diameter apart, their diameter from laterals. Posterior median eyes 1.5 diameters apart, 2.5 diameters from laterals. Abdomen is triangular with posterior overhanging spinnerets. Total length 3.7 mm. Carapace 1.36 mm long, 1.18 mm wide. First femur, 1.18 mm; patella and tibia, 1.46 mm; metatarsus, 1.01 mm; tarsus, 0.50 mm. Second patella and tibia, 1.25 mm; third, 0.82 mm; fourth, 1.20 mm.

Male carapace, sternum, legs yellowish orange-brown. Dorsum of abdomen orange-brown without white pigment. Secondary eyes 0.8 diameters of anterior medians. Anterior median eyes 1.5 diameters apart, 1.2 diameters from laterals. Posterior median eyes 1.2 diameters apart, 2 diameters from laterals. The abdomen is triangular but somewhat narrower than that of female. There are no setae on the cymbium of the palpus. Only one strong and one weak seta are on the palpal patella. Total length 2.9 mm. Carapace 1.32 mm long, 1.18 mm wide. First femur 1.37 mm; patella and tibia, 1.62 mm; metatarsus, 1.19 mm; tarsus, 0.52 mm. Second patella and tibia, 1.49 mm; third, 0.83 mm; fourth, 1.21 mm.

Diagnosis. Araneus tuscarora differs from *A. alboventris* by lacking a red-bordered black spot on the dorsum of the abdomen (Fig. 208). In ventral view the openings on each side of the scape of the epigynum are closer together anteriorly than posteriorly (Fig. 205), the reverse in *A. alboventris.* The internal ducts of the female differ (Figs. 204, 206) and the palpus has a different embolus (Figs. 213, 214).

Records. North Carolina. Durham Co.: Durham, Chapel Hill Blvd., east of county line; broomsedge field, sweeping, 7 June 1963, ♂ paratype (J. W. Berry, MCZ). Lee Co.: Sanford, 21 Aug. 1933, juv. (W. Ivie, AMNH). Montgomery Co.: 1.9 mi. W of Biscoe on route 27, 20 July 1953, ♂ paratype (R. Barnes, AMNH) (Map 5).

Araneus carroll n. sp.

Figures 215–220; Map 5

Type. Female holotype from Berryville, Carroll Co., Arkansas, June–October 1941 (O. C. Wilton) in the American Museum of Natural History. The specific name is a noun in apposition after the name of the type locality. Carroll County in turn is named after an early American patriot, Charles Carroll.

Note. This specimen had previously been labeled paratype of *Conepeira texana* Archer.

Description. Female holotype, carapace, sternum, legs yellowish. Dorsum of abdomen all white with indication of paired red spots and some pigment anteriorly in a transverse mark (Fig. 220). Sides and venter white. Total length 4.0 mm. Carapace 1.7 mm long, 1.5 mm wide. First femur, 2.3 mm; patella and tibia, 2.9 mm; metatarsus, 2.4 mm; tarsus, 0.8 mm. Second patella and tibia, 2.5 mm; third, 1.4 mm; fourth, 2.0 mm.

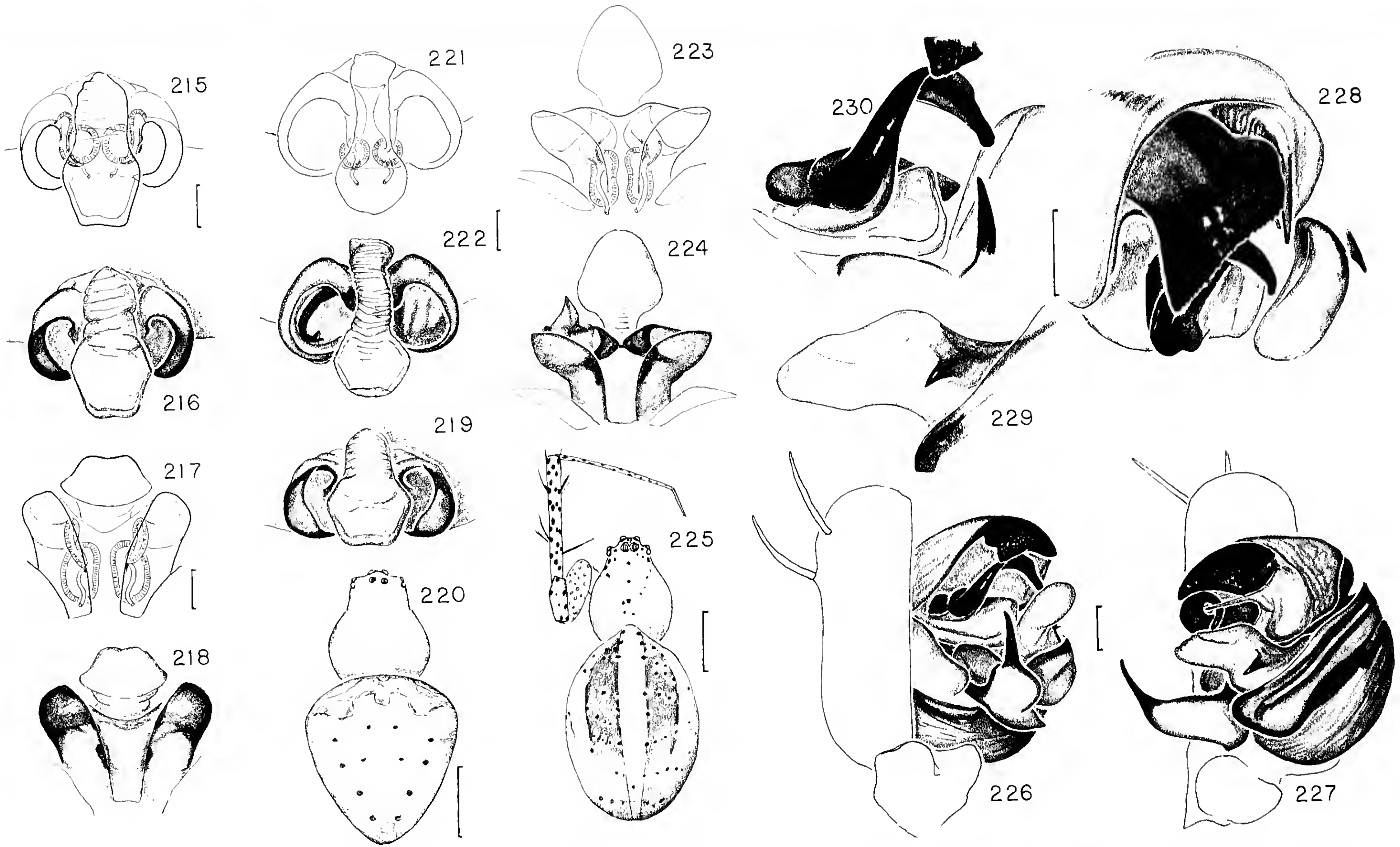
Diagnosis. The openings of the epigynum of *A. carroll* are most like those of *A. cingulatus* but the epigynum differs by having its base narrower and longer and having a much shorter scape (Fig. 216).

Araneus raui n. sp.

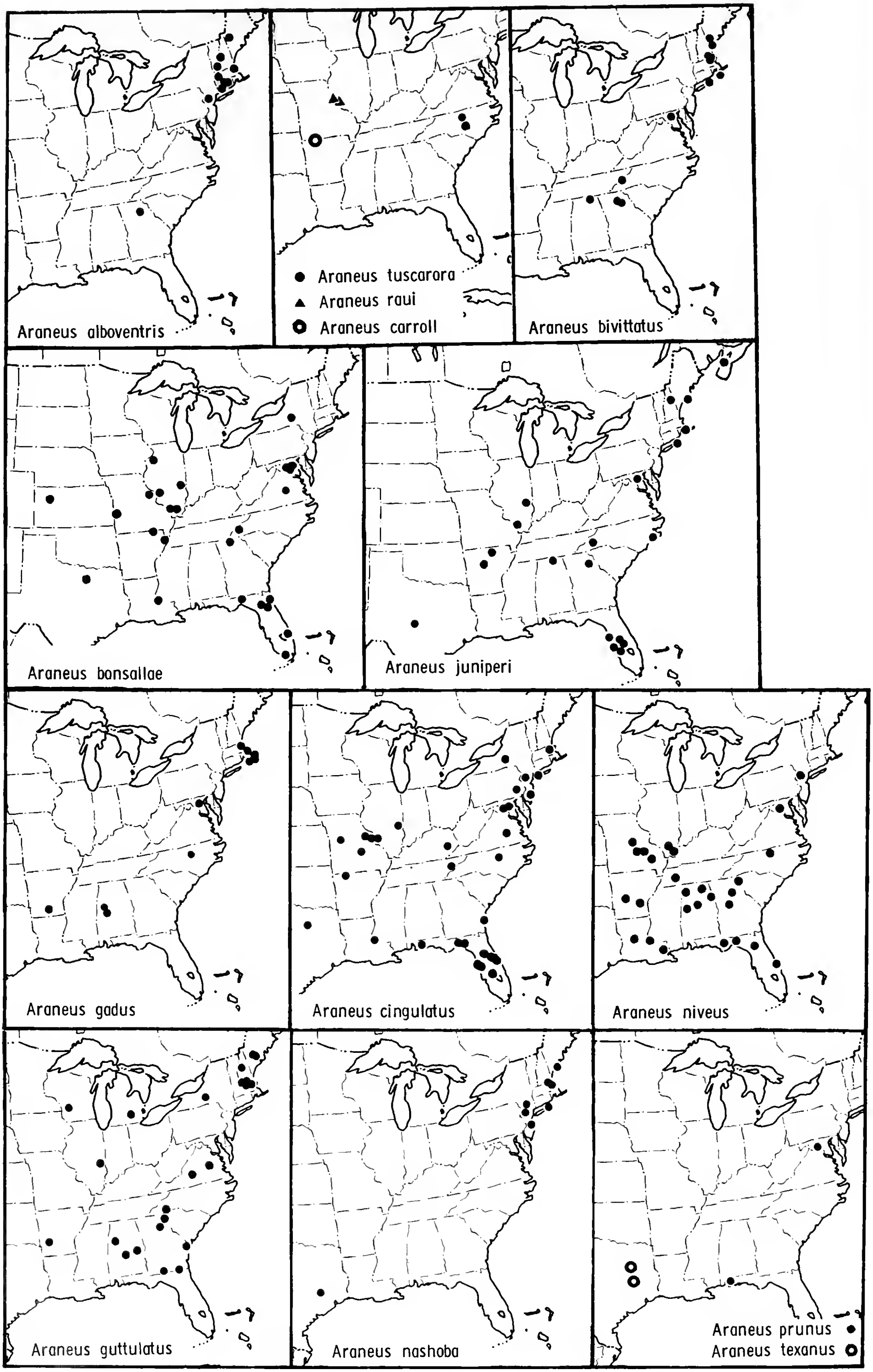
Figures 295–300; Map 5

Type. Female holotype from Wentzville, Saint Charles Co., Missouri, 9 July 1929 (P. Rau, no. 1617D), presumably from a wasp nest, in the Museum of Comparative Zoology. The species is named after the wasp specialist and collector, Philip Rau.

Description. Female, carapace, sternum, legs yellow. Dorsum of abdomen white. Venter with a distinct clear white patch. The dorsum probably had pairs of red spots but no pattern is visible on any of the specimens. Anterior and posterior median eyes subequal in size. Laterals 0.8 diameters of medians. Anterior median eyes 1.5 diameters apart, two diameters from laterals. Posterior median eyes slightly more than their diameter apart, slightly



Figures 215–220. *Araneus carroll* n. sp. 215–219. Epigynum. 215. Ventral, cleared. 216. Ventral. 217. Posterior, cleared. 218. Posterior. 219. Subventral. 220. Female.
Figures 221–230. *Araneus bivittatus* (Walckenaer). 221–224. Epigynum. 221. Ventral, cleared. 222. Ventral. 223. Posterior, cleared. 224. Posterior. 225. Female. 226–230. Left palpus. 226. Mesal. 227. Ventral. 228. Terminal apophysis. 229. Conductor. 230. Virgin embolus.
(Size indicators 0.1 mm, for females 1 mm).



Map 5. Distributions of relatives of *Araneus juniperi* (Emerton).

more than two diameters from laterals. Total length 5.4 mm. Carapace 2.3 mm long, 1.9 mm wide. First femur, 2.9 mm; patella and tibia, 3.4 mm; metatarsus, 2.6 mm; tarsus, 0.8 mm. Second patella and tibia, 2.9 mm; third, 1.6 mm; fourth, lost.

Diagnosis. This species differs from *Araneus carroll* in having a shorter scape and different openings in the epigynum (Figs. 296, 297).

Records. Missouri. Saint Charles Co.: Wentzville, 9 July 1929, 4 ♀ paratypes (P. Rau, no. 1617A, MCZ). Saint Louis Co.: Kirkwood, mud dauber, ♀ paratype (P. Rau, MCZ) (Map 5).

Araneus bivittatus (Walckenaer)

Plate 6; Figures 221–230, 445; Map 5

Epeira bivittata Walckenaer, 1841, Histoire Naturelle des Insectes. Aptères, 2: 78. The type is Abbot manuscript illustration no. 234 of his Drawings of the Insects of Georgia, in America, vol. 14, 1792, in the British Museum, Natural History; copies in the Museum of Comparative Zoology, examined.

Note. Abbot's comment on No. 234 is "taken 17th May several of these kind in a Dirt daubers Nest. This beautyfull [sic] Species I never met with by any other means." Abbot illustrated the species with red dorsal stripes but arranged the spots symmetrically. Despite the symmetrical spots, there is no *Araneus* other than this that has two distinct red longitudinal dorsal bands grading into green on each end, except indistinct bands reported in some southern specimens of *A. juniperi.* Abbot's illustration shows the abdomen spherical, rather than elongate as it is in most specimens.

Some specimens of this species in collections had been labeled *Conepeira marilandica,* others *C. bivittatus* by Archer.

Description. Female from Athens, Georgia, about one year in alcohol: Carapace yellow with some dark red spots, no black eye pigment. Sternum yellow with dark red spots. Legs dark yellow with dark red spots. Dorsum of abdomen with a white lanceolate cardiac band on each side of which is a wide crimson band. The crimson bands turn both posteriorly and anteriorly into green. The posterior and sides of abdomen are green, the posterior very dark green. There are some dark red spots, but the spots are not symmetrical in pairs. The venter has white pigment between epigy-

Plate 6. Top Fig. *Araneus alboventris* females from Massachusetts wasp trap. The abdomen has a crimson-bordered black patch on yellow. Bottom Fig. *Araneus bivittatus* female from Massachusetts. The abdomen has green bands separated by white. The bands are sometimes red.

num and spinnerets, but is greenish in color, darker green on sides. A female from Massachusetts had carapace and legs light reddish brown, the abdomen dorsum with two green longitudinal bands separated by a median brilliant white longitudinal band (Plate 6; Fig. 225). Toward the side, the green bands were also separated anteriorly by white from the greenish sides. The abdomen is oval, longer than wide, with a slight median hump anteriorly. Total length 3.6–5.0 mm. Carapace 1.7–2.2 mm long, 1.3–1.6 mm wide.

Male coloration like that of female. Total length 3.5–4.3 mm long. Carapace 1.6–2.0 mm long, 1.4–1.7 mm wide.

Diagnosis. *Araneus bivittatus* is the only species that has the abdomen longer than wide, widest in the middle, with a median anterior hump (Fig. 225) and two longitudinal dorsal red or green bands on the abdomen (Fig. 225). *Araneus juniperi* usually has the abdomen spherical. The large openings have a distinct rim (Fig. 222) similar to those of *A. guttulatus*, but the epigynum has a shorter scape. Unlike all other related species, *A. bivittatus* has the rim widest anteriorly. The male can be separated from that of *A. juniperi* by the heavier embolus (Fig. 230) and longer tooth on the conductor (Fig. 229), and from other species by the abdominal markings (Fig. 225).

Natural history. Most specimens came from wasp nests, but the species has also been found among oak leaves on Long Island and in pines on Martha's Vineyard, Massachusetts. All males and most females were collected in July.

In 1973, two female specimens were raised from penultimate instar to adult. One came from Dunstable, the other from Pepperell, Middlesex County, Massachusetts. When received, the spiders had green stripes on the abdomen which changed to red before molting to the adult. The adults had red stripes and also, unlike the Georgia specimens recently examined, paired red spots at the edge of the stripes.

Distribution. Maine to Mississippi (Map 5).

Araneus gadus n. sp.

Figures 231–247, 446; Map 5

Conepeira marilandica,—Archer, 1951, Amer. Mus. Novitates, No. 1502, figs. 11, 72, ♀. Not male holotype.

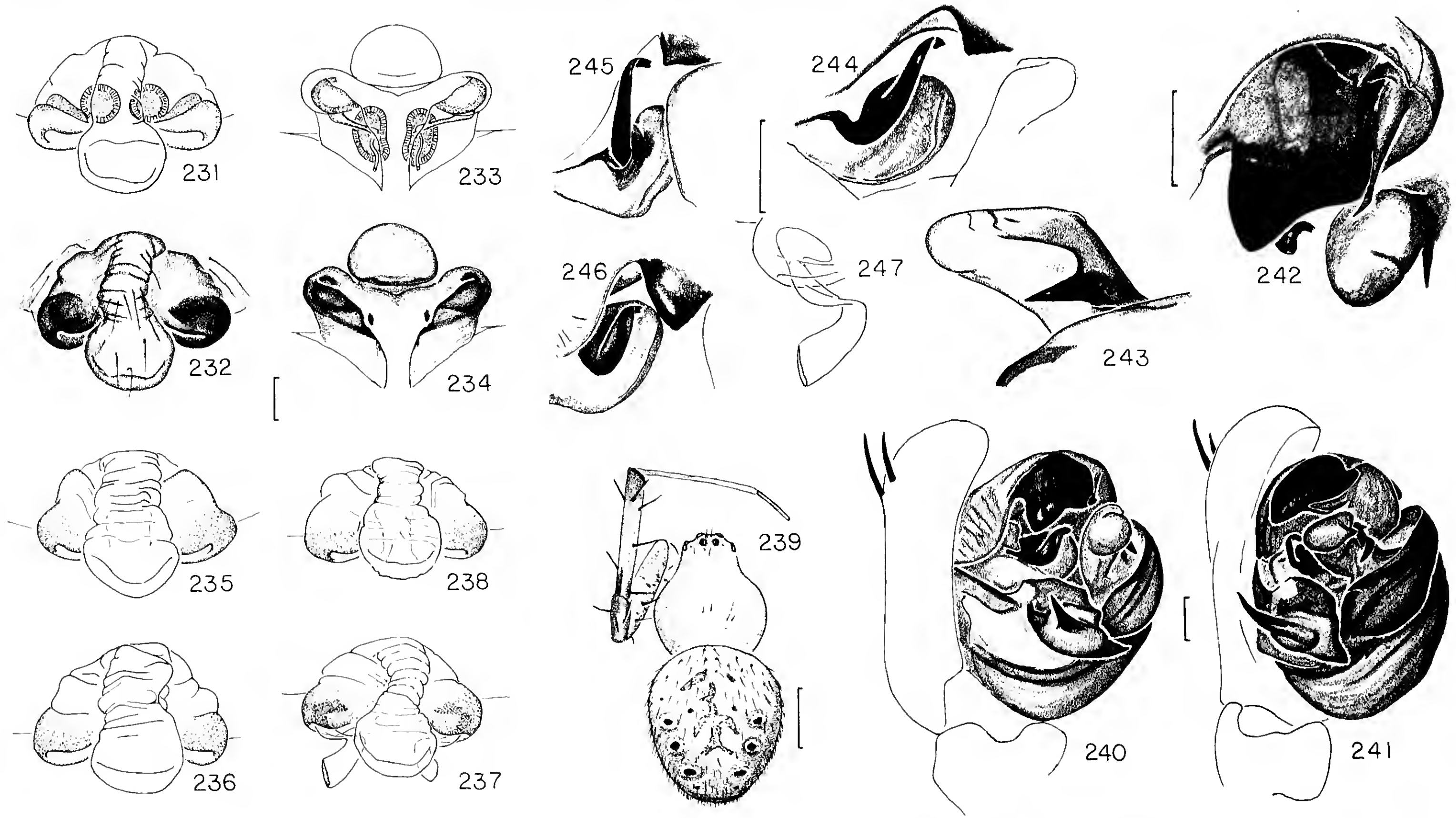
Type. Female holotype from South Chatham, Barnstable County, Cape Cod, Massachusetts, sweeping oak-pitch pine woods (*Pinus rigida*), 16 June 1971 (H. and F. Levi) in the Museum of Comparative Zoology.

Note. In collections specimens had been marked *Conepeira marilandica* and *Araniella displicata* by Archer. The female allotype of *Conepeira marilandica* is this species.

Description. Female a month in alcohol had carapace yellowish, sternum yellowish white. Legs yellowish with indistinct reddish rings. Dorsum of abdomen greenish white with a reddish cast posteriorly, some fine red dots anteriorly in light area, and four pairs of black spots posteriorly, each surrounded by a light ring (Fig. 239). Sides greenish, venter whitish. No depressions on carapace. The legs have strong macrosetae, some originating from red marks. Abdomen longer than wide, slightly pointed behind with many seta. Total length 4.2 mm. Carapace 2.0 mm long, 1.6 mm wide. First femur, 2.2 mm; patella and tibia, 2.9 mm; metatarsus, 2.1 mm; tarsus, 0.7 mm. Second patella and tibia, 2.3 mm; third, 1.2 mm.

Male coloration like that of female but legs not banded, distal ends of first and second legs reddish. Carapace with a median longitudinal thoracic line. The palpal patella has one strong and one weak seta. The abdomen is longer than wide, slightly pointed behind. Total length 4.2 mm. Carapace 2.0 mm long, 1.7 mm wide. First femur, 2.6 mm; patella and tibia, 2.9 mm; metatarsus, 2.3 mm; tarsus, 0.7 mm. Second patella and tibia, 2.6 mm; third, 1.5 mm; fourth, 2.1 mm.

Variation. Females vary in total length



Figures 231–247. *Araneus gadus* n. sp. 231–238. Epigynum. 231. Ventral, cleared. 232. Ventral. 233. Posterior, cleared. 234. Posterior. 235–238. Ventral (Cape Cod). 235. (Plymouth, Mass.). 236. (Martha's Vineyard). 237, 238. (Nantucket). 239. Female. 240–247. Left palpus. 240. Mesal. 241. Ventral. 242. Terminal apophysis. 243. Conductor. 244–246. Embolus. 247. Embolus cap in epigynum.
(Size indicators 0.1 mm, for female 1 mm)

from 4.0–6.0 mm, carapace 1.9–2.6 mm long, 1.4–2.0 mm wide. The smallest specimens came from Massachusetts, the largest from Alabama.

Diagnosis. Araneus gadus differs from all other small *Araneus* species by the paired black spots on the abdomen, each spot having a light halo (Fig. 239). The black spots with their light area do not wash out in alcohol. In addition females differ from *A. juniperi* by having a thinner shorter scape in the epigynum and the most anterior part of the opening being towards the median (Figs. 231–237). Males differ from *A. juniperi* by having a shorter embolus (Figs. 244, 245), and a very large basal tooth on the conductor (Figs. 241, 243). Even juveniles of this species can be recognized by the pattern.

Natural history. Of eleven collections available, six indicate that the specimens were collected in pines; only two came from a wasp nest. In Massachusetts *A. gadus* is limited to pitch pine (*Pinus rigida*), apparently not found on white pine (*Pinus strobus*). A female from Alabama, out of the range of pitch pine, came from "pine tops"; a juvenile from Arkansas, also outside the range of pitch pine, was collected "on pine." Males were collected in June in Massachusetts, females in June and July, juveniles in April and October.

Records. Massachusetts. Barnstable Co.: South Chatham, 12–18 June 1971, ♂, juv. paratypes. Dukes Co.: Martha's Vineyard, 15 July 1913, ♀ paratype. Middlesex Co.: Belmont, juv. ♀. Nantucket Co.: Nantucket, 1913, ♀ ♀ paratypes, 19 June 1929, ♀, ♂, paratypes; 28 October 1929, juv. Plymouth Co.: Plymouth, 24 July 1915, ♀ paratype. *North Carolina.* Durham Co.: Durham. *Maryland.* Prince Georges Co.: Berwyn, 21 July 1942, ♀ paratype. *Alabama.* Hale Co.: near Havana, ♀ paratype. Tuscaloosa Co.: 30 April 1952. *Arkansas.* Calhoun Co., 11 April 1964, juv. (Map 5).

Araneus juniperi (Emerton)

Figures 248–264, 447–452; Map 5

Epeira juniperi Emerton, 1884, Trans. Connecticut Acad. Sci., 6: 313, pl. 34, fig. 6, pl. 36, figs. 14–16, ♀, ♂. Female and male syntype from Peaks Island, Portland, Maine, in the Museum of Comparative Zoology, examined. Kaston, 1948, Bull. Connecticut Natur. Hist. Surv., 70: 261, fig. 830, ♀ [not fig. 811, ♂].

Singa floridana Banks, 1896. Trans. Amer. Entomol. Soc., 23: 69. Female holotype from Punta Gorda, Florida, in the Museum of Comparative Zoology, examined. NEW SYNONYMY.

Conepeira bivittata,—Archer, 1951, Amer. Mus. Novitates, No. 1502: 21, figs. 12, 49, 70, ♀, ♂. Not *Epeira bivittata* Walckenaer. Archer designated specimens as neotypes which are invalid since Abbot's drawings, the types, still exist.

Conepeira mumai Archer, 1951, Amer. Mus. Novitates, No. 1502: 22, fig. 51, ♂. Male holotype from Berwyn, Maryland, in the American Museum of Natural History, examined. Not ♀, and not paratypes. NEW SYNONYMY.

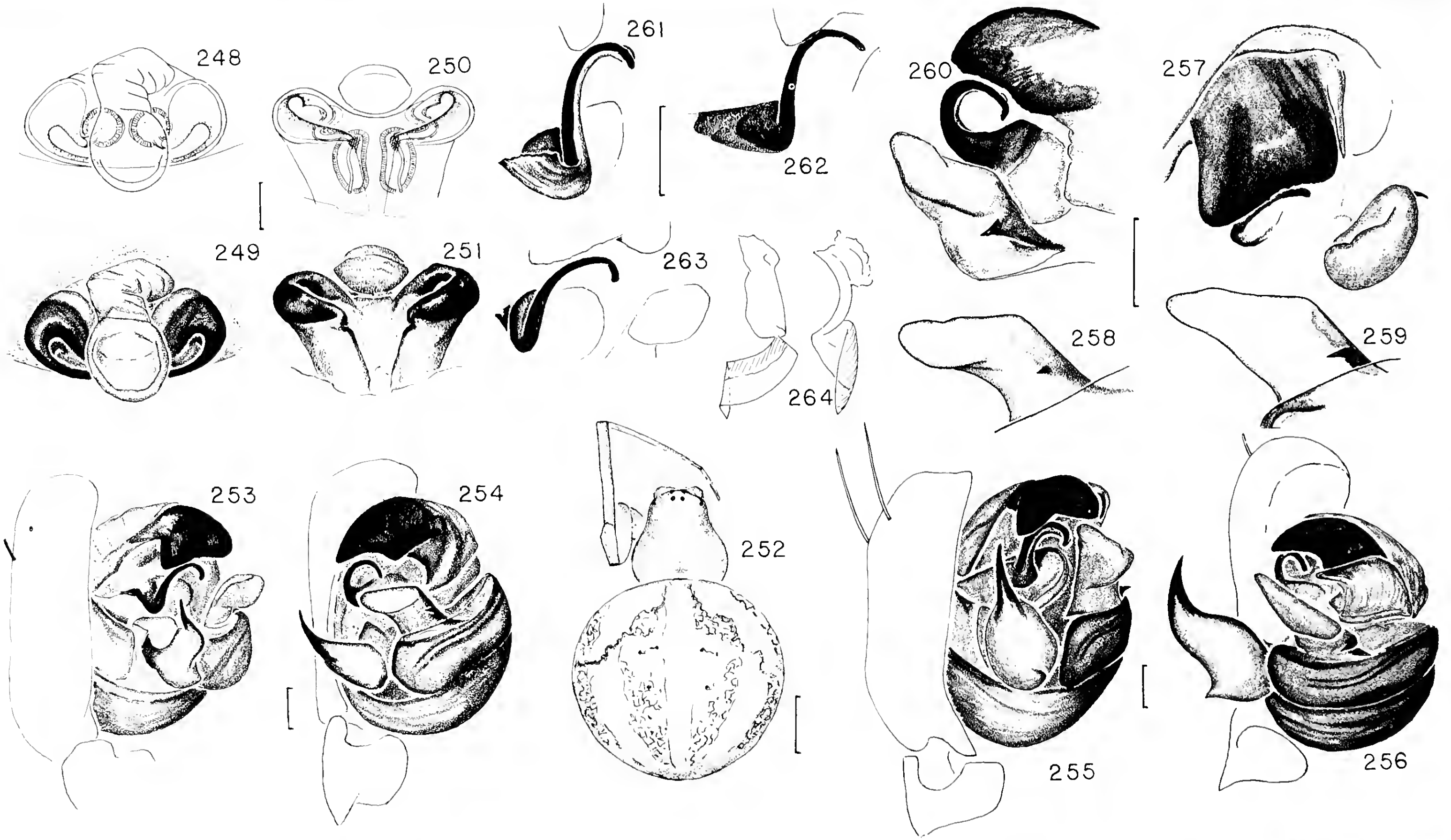
Conepeira sarasota Archer, 1951, Amer. Mus. Novitates, No. 1502: 23, fig. 74, ♀. Female holotype from south of Sarasota, Sarasota County, Florida, in the American Museum of Natural History, examined. NEW SYNONYMY.

Coneperia llano Archer, 1951, Amer. Mus. Novitates, No. 1502: 24, figs. 52, 55, ♀, ♂. Male holotype from Llano, Llano Co., Texas, in the American Museum of Natural History, examined. NEW SYNONYMY.

Note. In collections specimens have been marked *Conepeira juniperi, C. marilandica, C. mumai, C. innominata, C. sarasota* and *C. bivittata* by Archer. In older collections all related species were labeled *A. juniperi.* The illustrations (Figs. 249–254) are made from syntypes of *A. juniperi.*

Description. Female syntype. Carapace, sternum, legs yellowish. No black eye pigment, but white pigment circles around posterior median eyes. Abdomen dorsum with three longitudinal bands of dense white pigment (Fig. 252). Posterior median eyes slightly larger, laterals slightly smaller than anterior medians. The median ocular quadrangle as long as wide behind; narrower behind than in front. Abdomen subspherical. Total length 5.2 mm. Carapace 1.9 mm long, 1.5 mm wide. First femur, 2.4 mm; patella and tibia, 2.7 mm; metatarsus, 2.2 mm; tarsus, 0.7 mm. Second patella and tibia, 2.4 mm; third, 1.4 mm; fourth, 2.0 mm.

Male syntype with coloration as in female. Abdomen oval, longer than wide. Total length 3.8 mm. Carapace 1.8 mm



Figures 248–264. *Araneus juniperi* (Emerton). 248–251. Epigynum. 248. Ventral, cleared. 249. Ventral. 250. Posterior, cleared. 251. Posterior. 252. Female. 253, 254. Left palpus (Maine). 255, 256. Virgin palpus (Maryland). 253, 255. Mesal. 254, 256. Ventral. 257. Terminal apophysis. 258, 259. Conductor. 260, 261. Virgin embolus. 262, 263. Embolus. 264. Embolus cap.

(Size indicators 0.1 mm, for female 1 mm) long, 1.5 mm wide. First femur, 2.6 mm; patella and tibia, 2.9 mm; metatarsus, 2.6 mm; tarsus, 0.9 mm. Second patella and tibia, 2.7 mm; third, 1.4 mm; fourth, 2.2 mm.

Variation. Living specimens have two longitudinal green bands on the abdomen, but specimens may or may not have paired red spots on the abdomen (Fig. 252). To judge from Bank's description of *A. floridanus,* the bands may be red in the southern part of the range: "Cephalothorax greenish yellow, pars cephalica reddish, darkest on sides; mandibles with red lines. Legs greenish yellow; patellae, tibiae and metatarsus of anterior pairs with elongate red spots, less distinct on hind pairs; sternum and coxae greenish yellow. Abdomen greenish yellow with two prominent submedian red stripes reaching from base to tip, broadest at base and converging toward tip where they surround the spinnerets; three white stripes, one between the red and one on each side."

Total length of females 2.5–5.2 mm. Carapace 1.3–1.9 mm long, 1.1–1.8 mm wide. Total length of males 3.2–4.6 mm. Carapace 1.7–2.2 mm long, 1.4–1.8 mm wide. The smallest specimens come from the northern part of the range and Florida.

Diagnosis. Araneus juniperi differs from *A. bivittatus* by having the abdomen subspherical rather than oval, and the bands much less distinct, separated probably by lighter green rather than white (Fig. 252). *Araneus juniperi* differs from *A. gadus* and other small *Araneus* species by having slit-like openings on the posterior of the base of the epigynum (Fig. 249), the lateral edges of the slit extending most anteriorly. It differs from *A. cingulatus* by having a shorter scape and a median anterior extension of the base behind the scape. The male differs from other species by having a long, thin, curved embolus (Figs. 260–263), and the tooth on the base of the conductor is unusually small, hidden in the slightly sclerotized edge (Figs. 258–259).

Natural history. Most collections come from wasp nests. The types of *A. juniperi* were collected in junipers (*Juniperus* sp.). The only other females with a note on their collecting site came from a "cedar glade" in Arkansas. Since no cedars are found in Arkansas I assume that this is the local name for eastern red cedar (*Juniperus virginiana*).

Males are mature in February in Florida, in June in Arkansas, in August in New England.

Distribution. From Nova Scotia to Florida, west to Arkansas and Texas (Map 5).

Araneus bonsallae (McCook)
Figures 265–294, 453–454; Map 5

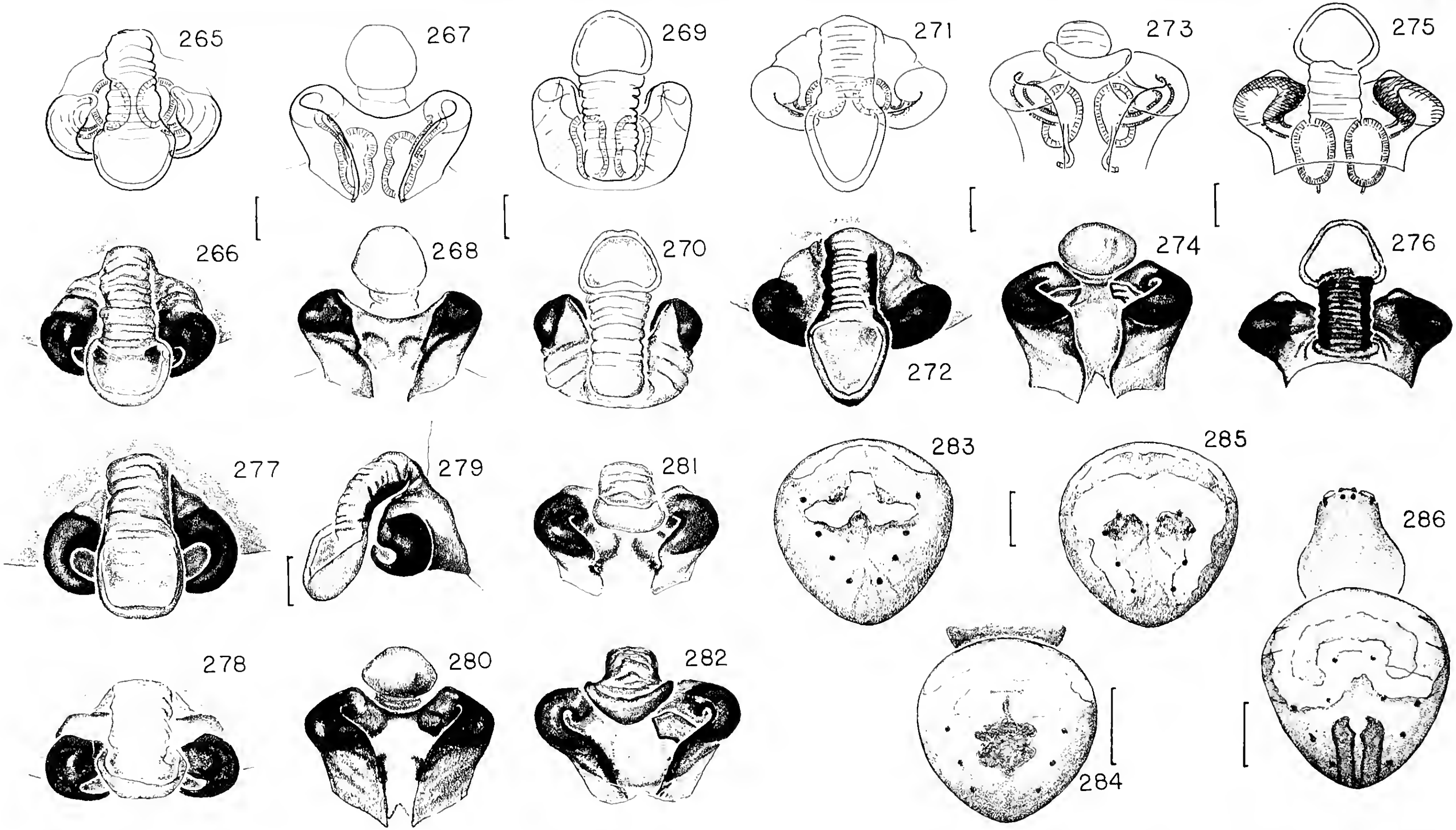
Epeira bonsallae McCook, 1894, American Spiders, 3: 179, pl. 8, fig. 10, ♀. Female holotype from California [sic] in very poor condition in the Academy of Natural Sciences, Philadelphia, examined and labeled as type.

Conepeira unica Archer, 1951. Amer. Mus. Novitates, No. 1502: 23, fig. 75, ♀. Female holotype from Centreville, Wilkinson Co., Mississippi, in the American Museum of Natural History, examined. NEW SYNONYMY.

Note. The statement on the label of *Epeira bonsallae* is "Ep. Bonsallae DC or Cala," District of Columbia or California. No doubt the published locality is in error and the locality of the type is District of Columbia.

Archer labeled specimens of this species *Conepeira innominata, mumai* (paratypes) and *C. unica.*

Description. Living female from Virginia has carapace, sternum a transparent green, rings around secondary eyes yellow. Legs green, distal articles reddish. Dorsum of abdomen green with paired red spots, a central black patch of irregular outline, anterior of black patch a transverse white mark having paired anterior median extensions covered in part by yellowish pigment. Between black patch and white mark is reddish and orange pigment; red in median, orange toward sides. Venter of abdomen green, underlain by white pigment, posterior to epigynum mostly white. The illustrations (Figs. 283–286) were made from specimens preserved in alcohol for at least one year. Total length 4.2–5.8 mm. Carapace 1.7–2.4 mm long, 1.5–1.8 mm wide.



Figures 265–286. *Araneus bonsallae* (McCook). 265–282. Epigynum. 265, 271. Ventral, cleared. 266, 272, 277. Ventral. 267, 273. Posterior, cleared. 268, 274, 280–282. Posterior and posteroventral. 269, 275. Anterior, cleared. 270, 276. Anterior. 279. Lateral. 265–270. (Illinois). 271–276, 279. Holotype of *Epeira bonsallae*. 277. (Mississippi). 278. (Kansas). 283–285. Female abdomen. 286. Female carapace and abdomen.
(Size indicators 0.1 mm, for Figs. 283–286, 1 mm)

Male coloration as in female. Total length 3.3–3.8 mm. Carapace 1.8–2.1 mm long, 1.5–1.7 mm wide.

Diagnosis. Araneus bonsallae has transverse markings on the anterior of the dorsum of the abdomen (Figs. 283–286) while the markings on *A. juniperi* are indistinct longitudinal bands. Females have the scape shorter and the openings of the epigynum smaller (Figs. 265–276) than in *A. juniperi*. While the openings of *A. bonsallae* are less than half the width of the base visible on each side of the scape, those of *A. juniperi* are more than half, and the lateral lip is narrower than the opening. The conductor tooth of the palpus of *A. bonsallae* is longer (Figs. 288, 291) than that of *A. juniperi*, and the median apophysis is smaller and has a distinct notch on the outside (Figs. 290, 453, 454).

Natural history. Most collections were made by wasps, other comments are "tree sweepings" in Texas and "under tree" in Illinois and in a car after driving through woods in Virginia.

Distribution. From New York State to Florida and west to Kansas and Texas (Map 5).

Araneus cingulatus (Walckenaer)

Plate 7; Figures 301–313, 455–462; Map 5

Epeira cingulata Walckenaer, 1841, Histoire Naturelles des Insectes. Aptères, 2: 40. The types are Abbot's manuscript Spiders of Georgia, figs. 232 and 365. I have chosen fig. 232 as lectotype since Walckenaer indicated that fig. 365 is probably only a variety of *E. cingulata*. Copies in the Museum of Comparative Zoology, examined. [Not *Aranea cingulata* Panzer, 1797 = *Salticus cingulata*].

Conepeira marilandica Archer, 1951, Amer. Mus. Novitates, No. 1502: 21; figs. 40, 50, ♂. Male holotype from Berwyn, Maryland, in the American Museum of Natural History, examined. Not ♀, not paratypes. NEW SYNONYMY.

Conepeira mumai,—Archer, 1951, Amer. Mus. Novitates, No. 1502: 22, fig. 73, ♀. Not male holotype, not paratypes.

Conepeira innominata Archer, 1951, Amer. Mus. Novitates, No. 1502: 24, fig. 62, ♂. Male holotype from MacDill Field, Tampa, Florida, in the American Museum of Natural History, examined. NEW SYNONYMY.

Conepeira ozarkensis Archer, 1951, Amer. Mus. Novitates, No. 1502: 25, fig. 76, ♀. Female holotype from Berryville, Carroll County, Arkansas, in the American Museum of Natural History, examined. NEW SYNONYMY.

Note. Abbot's figure 232 shows the characteristic color pattern. The use of Walckenaer's old name does not upset the use of any other name.

Archer labeled specimens of this species *mumai, ozarkensis, innominata* and *marilandica*.

Description. Living female from Massachusetts has carapace, sternum, legs light yellowish green with distal ends of first legs brownish. Dorsum of abdomen rich green, with pairs of relatively large dark red spots. The spots may have a yellowish halo and are in a longitudinal band of lighter green (or white)*; transverse area between anterior four red spots reddish (or white), anteriorly green enclosing some lighter green (or white) areas (Plate 7; Figs. 307, 308). There is no black pigment on the abdomen in any specimens examined. Total length 4.6–6.0 mm. Carapace 2.0–2.2 mm long, 1.6–1.8 mm wide.

Male coloration like that of female. Total length 2.7–3.5 mm. Carapace 1.3–1.9 mm long, 1.2–1.5 mm wide.

Variation. Florida specimens are noticeably smaller than others.

Diagnosis. Araneus cingulatus lacks the abdominal black patch of the related *A. niveus*. Fresh specimens from both Massachusetts and Virginia may have a transverse anterior brown patch enclosing two white spots side by side (Figs. 307, 308). The epigynum has a relatively long scape (Figs. 302, 305). The openings to the side of the scape have a diameter about equal to that of the lateral rim (Figs. 301–302, 305). The lateral rim has a distinct carina toward the anterior, making the opening appear larger than it is. The base to which the scape is attached has no median anterior extension. The terminal apophysis is pointed (Fig. 311), as in *A. niveus* males. The embolus in

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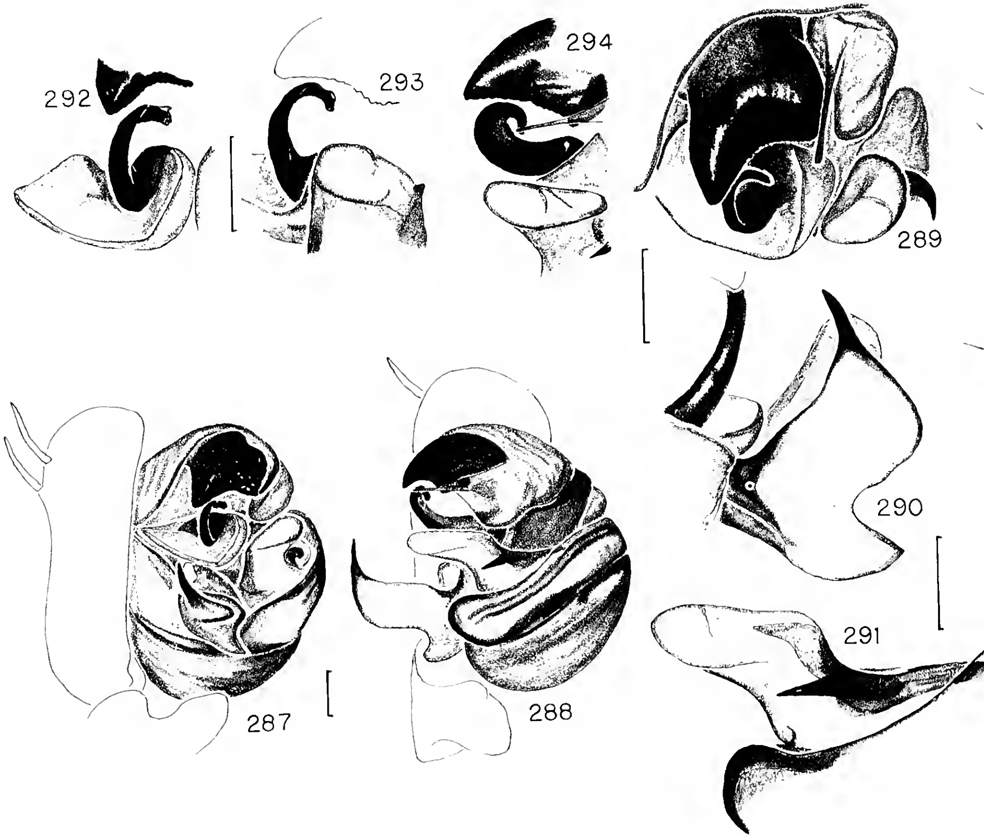
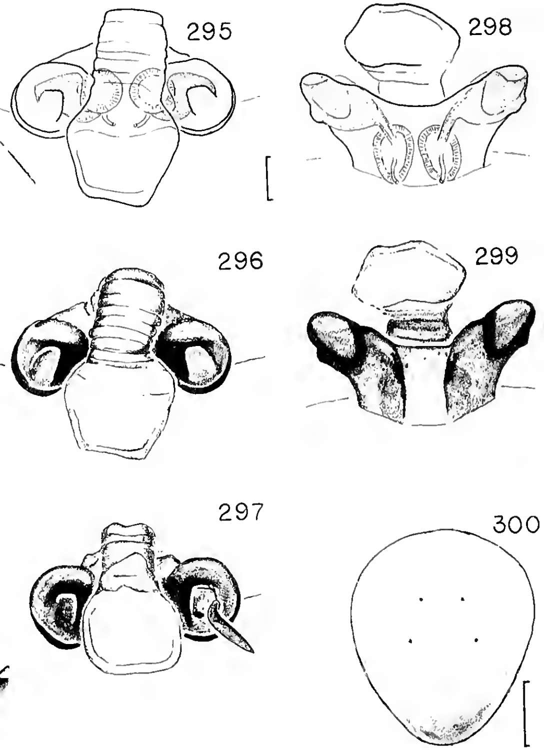
* Colors in brackets are of specimens in alcohol for a short period of time.





Figures 287–294. *Araneus bonsallae* (McCook). Left palpus. 287. Mesal. 288. Ventral. 289. Terminal apophysis. 290. Median apophysis. 291. Conductor. 292–294. Embolus.

Figures 295–300. *Araneus ravi* n. sp. 295–299. Epigynum. 295. Ventral, cleared. 296, 297. Ventral. 297. With embolus cap. 298. Posterior, cleared. 299. Posterior. 300. Bleached abdomen.

(Size indicators 0.1 mm, for abdomen 1 mm)

Plate 7. *Araneus cingulatus* female from Massachusetts wasp trap. The abdomen has crimson paired spots on green background; the area surrounding the anterior four white patches is reddish brown. The area surrounding the red spots is lighter green.

A. cingulatus is shorter than in *A. juniperi,* but longer than in *A. niveus* (Fig. 313).

Natural history. Most collections come from wasp nests; others are from an orange tree in Florida, tree sweepings in Texas, tall grass and low brush, one from upside down aluminum pot on the ground in Virginia, hanging on silk (determination from a color photograph only). Males are mature in September, March, and April in Florida, from May until July farther north. Females are found from May until September.

Distribution. From Massachusetts to Florida, west to Missouri and Texas (Map 5).

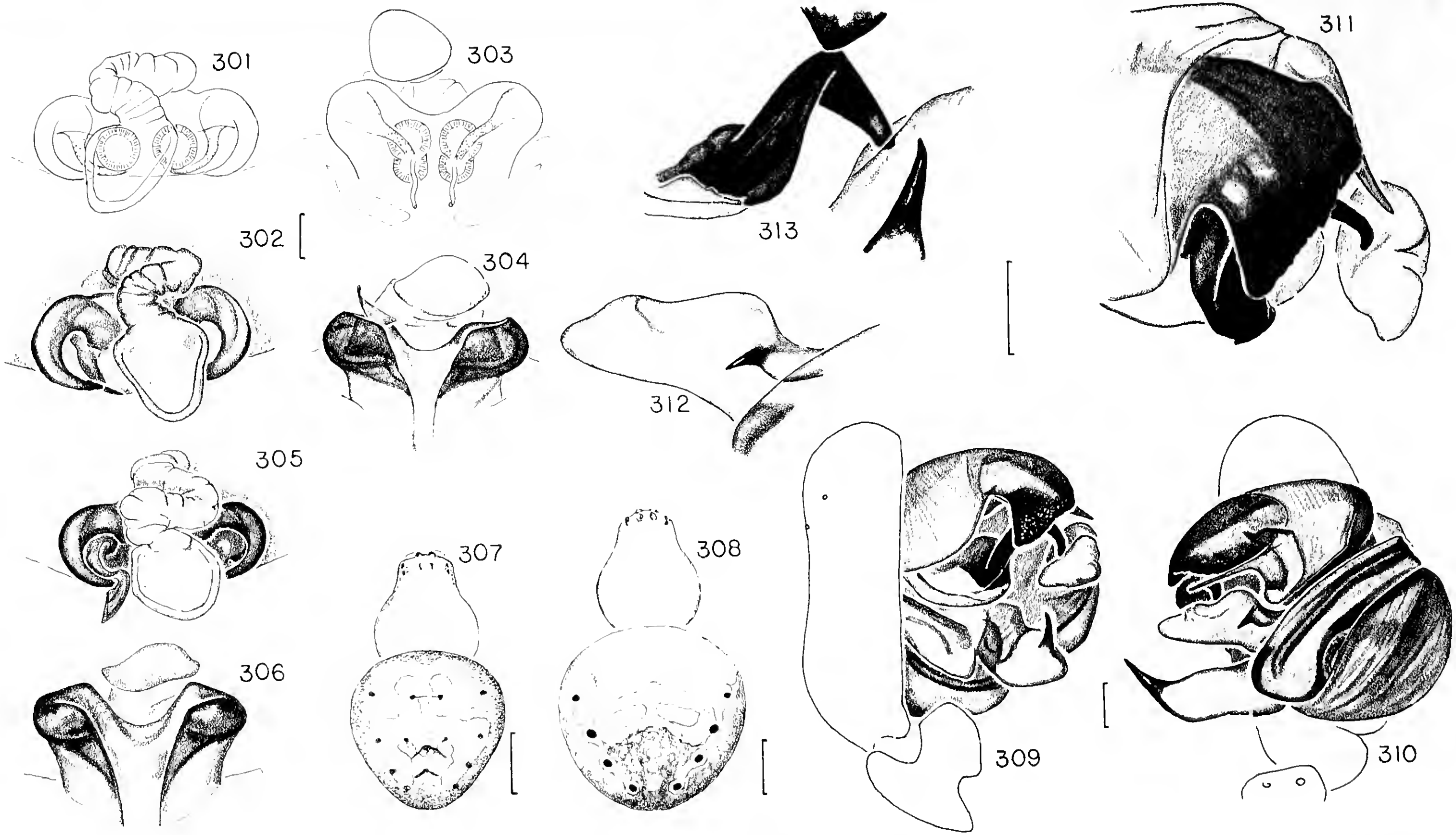
Araneus niveus (Hentz)

Figures 314–331, 463–469; Map 5

Epeira nivea Hentz, 1847, J. Boston Soc. Natur. Hist., 5: 474, pl. 31, fig. 9, ♀. Female holotype from Alabama destroyed (Hentz, 1875, The Spiders of the United States, Occ. Papers Boston Soc. Natur. Hist., 2: VII). I here designate the female holotype of *Conepeira nivosa* as neotype to stabilize the name (Art. 75, Intern. Code Zool. Nomencl.).

Conepeira nivosa Archer, 1951, Amer. Mus. Novitates, No. 1502: 18, figs. 45, 57, 68, ♀, ♂. Female holotype from Centreville, Wilkinson Co., Mississippi, in the American Museum of Natural History, examined. NEW SYNONYMY.

Note. Although Archer synonymized the name *Epeira nivea* with *Epeira guttulata,* it is probably better to apply the old name *nivea* to this widespread species, common in Alabama and with abdominal markings that match Hentz's illustration. However, *A. guttulatus* and *A. niveus* cannot readily be separated on color alone unless the specimens are fresh. In both species the large black patch on the dorsum is usually broken into an anterior transverse and a posterior triangular spot, but sometimes it is fused (Figs. 320–322). Hentz writes that the spider has a black spot on white. He pinned his specimens, so the color was not



Figures 301–313. *Araneus cingulatus* (Walckenaer). 301–306. Epigynum. 301. Ventral, cleared. 302. Ventral. 303. Posterior, cleared. 304. Posterior. 305. Ventral. 306. Posterior. 307, 308. Female. 307. Some color washed out in alcohol. 308. Freshly preserved individual. 309–313. Left palpus. 309. Mesal. 310. Ventral. 311. Terminal apophysis. 312. Conductor. 313. Embolus.
(Size indicators 0.1 mm, for females 1 mm)

washed out. This species has less color (green or red) on the abdomen than *guttulatus*. But I realize one can argue until doomsday the application of some of the old names whose types have disappeared. This adds neither to scientific knowledge nor to the stability of names.

Females in collections have been labeled by Archer *Conepeira nivosa, C. nivea, C. guttulata* and *C. alboventris;* males *C. nivosa, C. forata* and *C. guttulata.*

Description. Females that had been in alcohol for several months had carapace, sternum, and legs yellowish. The abdomen was white dorsally, green all around on the sides. Anteriorly was a transverse black band with its anterior edge reddish, posteriorly a triangular black mark and pairs of red spots (Fig. 320). The black marks do not fade in alcohol (Figs. 321–322). Total length of females 3.2–5.0 mm. Carapace 1.8–2.2 mm long, 1.4–1.8 mm wide.

Male coloration like that of female. Total length 2.9–4.3 mm. Carapace 1.4–2.0 mm long, 1.3–1.7 mm wide.

Diagnosis. Araneus niveus, unlike some related species, almost always has a median dorsal black patch on the abdomen (Figs. 320–321). Females differ from *A. guttulatus* by having narrower lateral margins of the depression of the epigynum; the margins cover small curved oval openings below. The shape of the openings is diagnostic (left in Figs. 315, 318). Also the scape of the epigynum is longer and the outline of the epigynum is square, while in *A. guttulatus* it is wider than long. The male would be difficult to separate from others were it not for the black abdominal patch almost always present. Although the palpus is much like that of the male of *A. niveus*, unlike all other males of this group (except *A. guttulatus*) it has the tooth of the conductor underneath or near the margin of the tegulum (Figs. 326–328). The long axis of the relatively small tooth is parallel to the long axis of the conductor. The palpus differs from that of *A. guttulatus* (which also has a black patch on the abdomen) in having the embolus at a 90° angle to the lamella and with a short tip (Figs. 329–331); that of *A. guttulatus* is about a 45° angle and has a longer tip.

Natural history. Specimens of this species came from bottomland pine and hardwood in North Carolina, from foliage of pecan trees in South Carolina and woods in Illinois as well as from wasp nests. Males are mature in June and July, females from June until September.

Distribution. New Jersey to Florida, west to Missouri and Arkansas (Map 5).

Araneus guttulatus (Walckenaer)

Plate 8; Figures 332–361, 470–474; Map 5

Epeira guttulata Walckenaer, 1841, Histoire Naturelles des Insectes. Aptères, 2: 78. The type is Abbot's manuscript drawing, fig. 233 in Drawings of the Insects of Georgia in America, vol. 14, 1792, in the British Museum, Natural History; copy in the Museum of Comparative Zoology, examined.

Epeira sanguinalis Hentz, 1847, J. Natur. Hist. Soc. Boston, 5: 476, pl. 31, fig. 15. Male holotype from Alabama destroyed. NEW SYNONYMY.

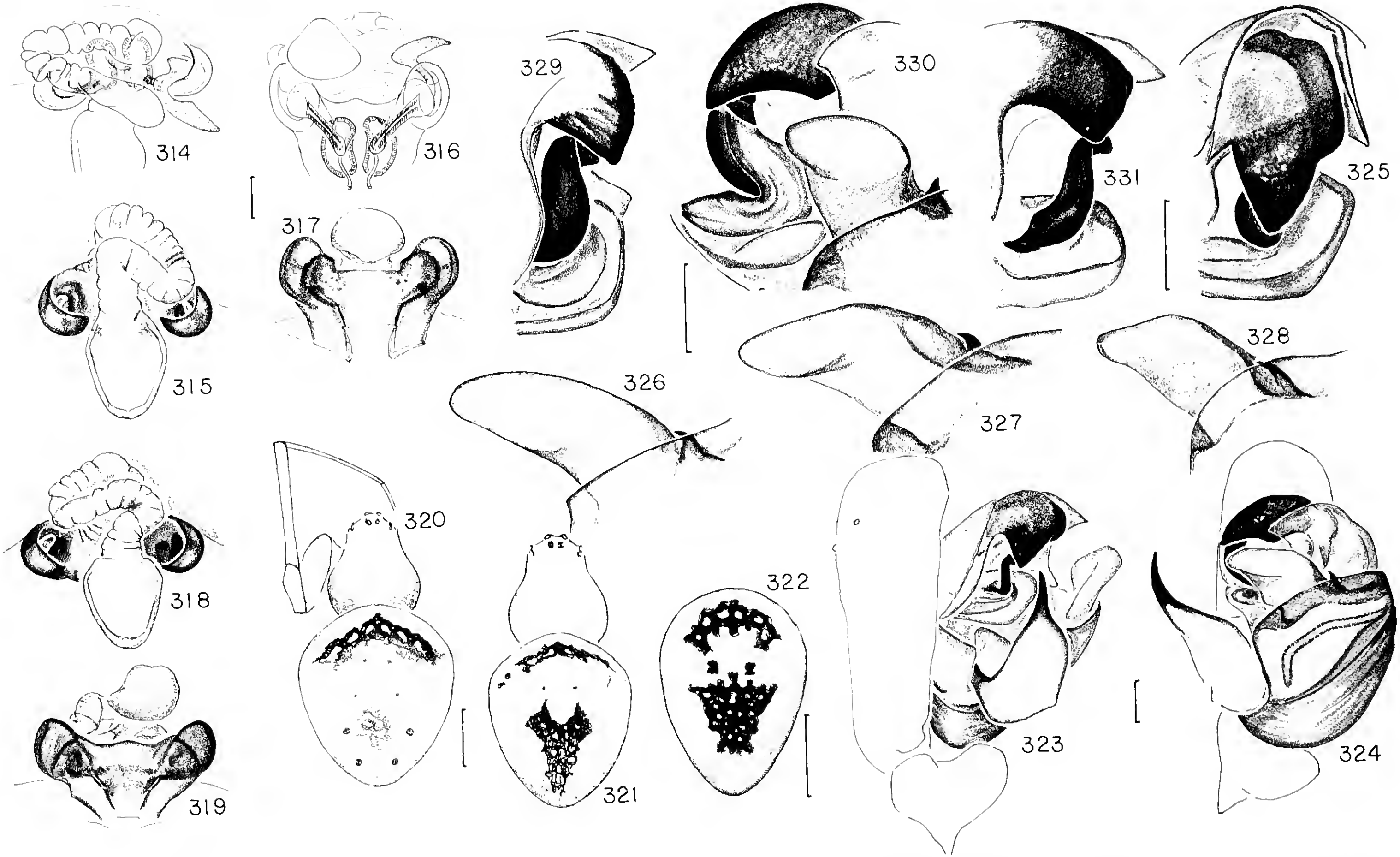
Epeira juniperi,—Emerton, 1909, Trans. Connecticut Acad. Sci., 14: 200, pl. 5, fig. 1, ♂.

Conepeira glyphica Archer, 1951, Amer. Mus. Novitates, No. 1502: 17, fig. 56, ♀. Female holotype from woods on Wildcat Mountain, Vernon Co., Wisconsin, in the American Museum of Natural History, examined. Levi, 1954, Amer. Midland Natur., 51: 450, figs. 33, 34, ♀. NEW SYNONYMY.

Note. Abbot's comment on fig. 233 is "Taken 20th May in a Dirt Daubers Nest. Very rare." The distribution of the spots on the abdomen of fig. 233 leaves little doubt that this is the species on hand.

Specimens in collections were labeled *Conepeira guttulata* and *C. marilandica* by Archer. Chamberlin and Ivie (1944) used the name *Epeira guttulata* for specimens of *A. miniatus.*

Description. Living female from Massachusetts: Carapace yellow-white, legs greenish yellow. Dorsum of abdomen with discrete pairs of crimson spots, and white patches surrounded by a red line that grades into orange areas; yellow around anterior of abdomen. Venter greenish yel-



Figures 314–331. *Araneus niveus* (Hentz). 314–319. Epigynum. 314. Ventral, cleared. 315. Ventral. 316. Posterior, cleared. 317. Posterior. 318. Ventral. 319. Posterior. 320, 321. Female. 322. Male. 323–331. Left palpus. 323. Mesal. 324. Ventral. 325. Terminal apophysis. 326–328. Conductor. 329, 330. Virgin embolus. 331. Embolus. (Size indicators 0.1 mm, for Figs. 320–322, 1 mm)

Plate 8. *Araneus guttulatus.* Top female specimens from Massachusetts wasp trap. Middle female from Virginia (photo A. Moreton). Bottom male from Massachusetts. The abdomen has white patches, paired red spots and between reddish to green areas, darkest red near border of white. The reddish area may enclose a black median patch posteriorly.

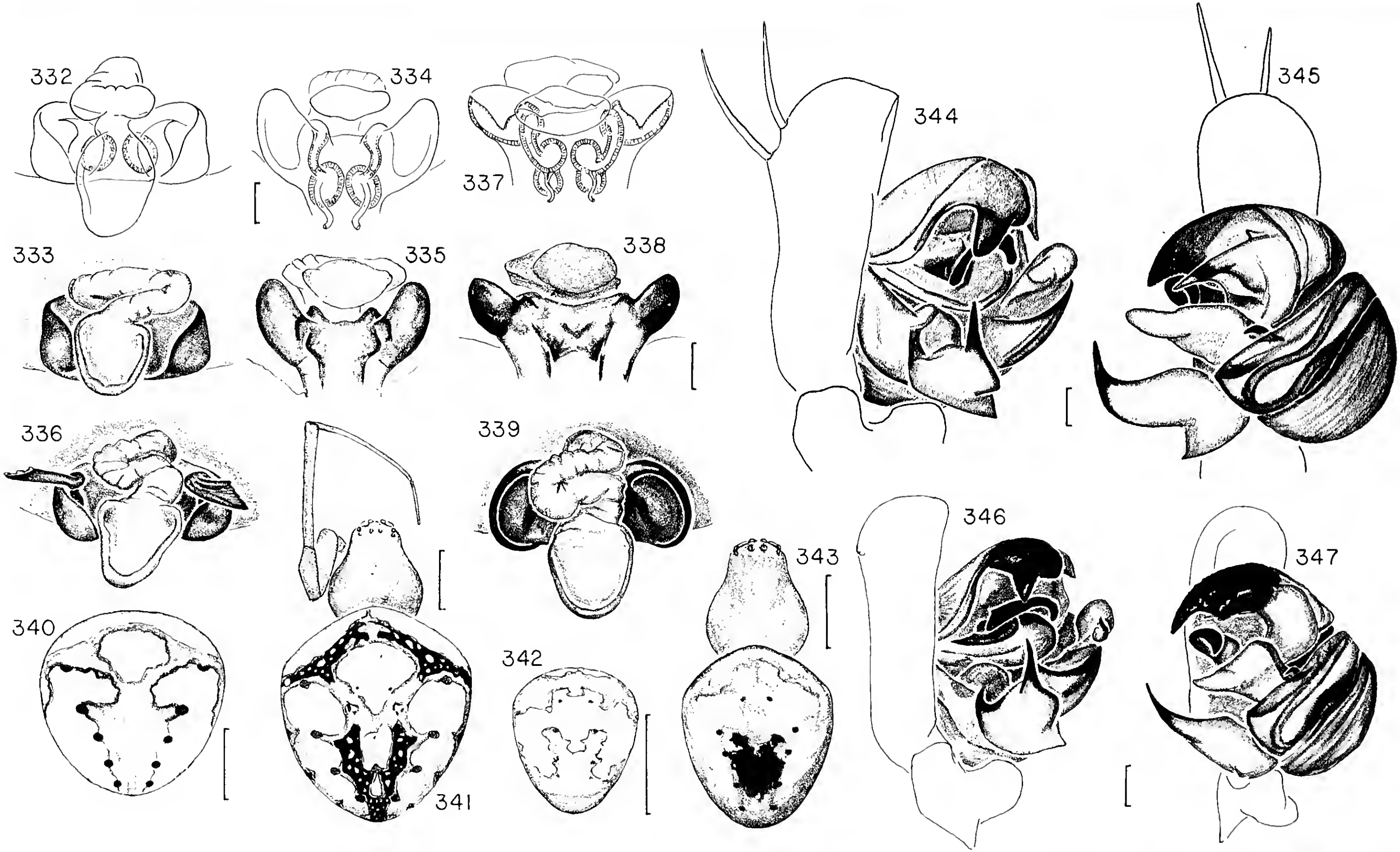
low. Recently collected females from Georgia have a triangular black patch posteriorly, a transverse anterior black band, white down each side to the side of paired red spots (Fig. 341), and a series of white spots in a median line, the most anterior largest, the most posterior smallest, the areas between green. The venter is whitish. Total length 3.8–6.0 mm. Carapace 1.3–2.3 mm long, 1.2–1.8 mm wide.

Male coloration like that of females. While New Hampshire males had no black mark on the abdomen, one from Massachusetts did. Total length 3.9–4.8 mm. Carapace 1.9–2.2 mm long, 1.7–1.9 mm wide.

Variation. Northern specimens have a narrower rim on the epigynum (Fig. 339). This and a slightly more different viewing angle (more anterior) made Archer believe the Wisconsin specimen to present a new species.

Diagnosis. Southeastern, heavily pigmented *Araneus guttulatus* can readily be recognized by their dorsal abdominal markings; others may have just a single median black patch, or just a white transverse band anteriorly, or a median longitudinal row of white spots, the most anterior largest, and two lateral white bands. The lateral bands have each lobe with a red spot; between these may be black pigment (Figs. 340–341). The openings of the epigynum are on each side of the long scape, the lips on each side are convex, projecting toward the scape (Figs. 333, 336), unlike those of *A. niveus.* The median margins of the large opening are below the scape (Figs. 332, 334, 337). The epigynum is wider than long. The male of *A. guttulatus,* unlike all other males of this group (except *A. niveus*), has the tooth of the conductor underneath or near the margin of the tegulum (Figs. 348–351). The palpus differs from that of *A. niveus* in having the embolus at a 45° angle to the lamella and in having a longer tip (Figs. 352–361); that of *A. niveus* is at a 90° angle and has a short tip.

Natural history. Most specimens in collections came from wasp nests, but individual females were found in Okefenokee



Figures 332–347. *Araneus guttulatus* (Walckenaer). 332–339. Epigynum. 332–336. (Georgia). 337–339. (Wisconsin). 332. Ventral, cleared. 333, 339. Ventral. 334, 337. Posterior, cleared. 335, 338. Posterior. 336. Ventral with embolus caps. 340. Female abdomen (Massachusetts). 341. Female (Georgia). 342. Male abdomen (New Hampshire). 343. Female (Wisconsin). 344–347. Left palpus. 344, 345. (Georgia). 346, 347 (New Hampshire). 344, 346. Mesal. 345, 347. Ventral.
(Size indicators 0.1 mm, for Figs. 340–343, 1 mm)

Swamp, Georgia, and in nest of fall web worm (*Hyphantria cunea*, Arctiidae) in Maine. Wallace's collection from Michigan came from woods along edge of swamp, sweeping birch-maple swamp, along edge of swamp, and sweeping bog. A female collected in Virginia came from underside of an oak leaf. A male was collected from foliage of pecan trees in South Carolina.

Distribution. New England to Wisconsin, south to southern Georgia and Arkansas. The northernmost locality is "Labrador, Oct. 1900, Britcher coll. 3222." This may refer either to Labrador Pond, a collecting site in Onondago Co., New York, or to the Canadian province (Map 5).

Araneus texanus (Archer)

Figures 362–374; Map 5

Conepeira texana Archer, 1951, Amer. Mus. Novitates, No. 1502: 20. Male holotype from Mexia, Texas, in the American Museum of Natural History, examined.

Note. The holotype was first thought to be the male of *A. guttulatus*. When the male of *A. guttulatus* was found together with the female, doubt was thrown on the match based on coloration. Subsequently a female was found, also from northern Texas, with *A. guttulatus* coloration but a different epigynum. It is likely but not certain that male and female belong together.

Description. Female in alcohol: Carapace, sternum, legs yellowish white. Dorsum of abdomen white but with faint pigment as in *A. guttulatus* (Fig. 374). Sides and venter white. Total length 4.5 mm. Carapace 1.9 mm long, 1.4 mm wide. First femur, 2.3 mm; patella and tibia, 2.9 mm; metatarsus, 2.2 mm; tarsus, 0.7 mm. Second patella and tibia, 2.4 mm; third, 1.2 mm; fourth, 1.8 mm.

Male holotype. Carapace, sternum, legs yellowish white. Dorsum of abdomen with white pigment, indications of a semicircular anterior gray patch, and a posterior median round black patch. The venter is not marked. The abdomen is triangular, much narrower than wide. Total length 3.8 mm. Carapace 1.9 mm long, 1.7 mm wide. First femur, 2.7 mm; patella and tibia, 3.2 mm; metatarsus, 2.6 mm; tarsus, 0.7 mm. Second patella and tibia, 2.7 mm; third, 1.2 mm; fourth, 1.9 mm.

Diagnosis. The embolus (Fig. 370), conductor spine (Fig. 373) and median apophysis (Fig. 372) of the palpus differ in shape from those of *A. guttulatus*. In *A. texanus*, the epigynum has a short scape (Fig. 363), in *A. guttulatus*, a long one; the openings in the base are shaped differently than in *A. guttulatus*.

Record. Texas. Brazos Co. ♀ (N. Banks, MCZ) (Map 5).

Araneus nashoba n. sp.

Plates 4, 9; Figures 380–397; Map 5

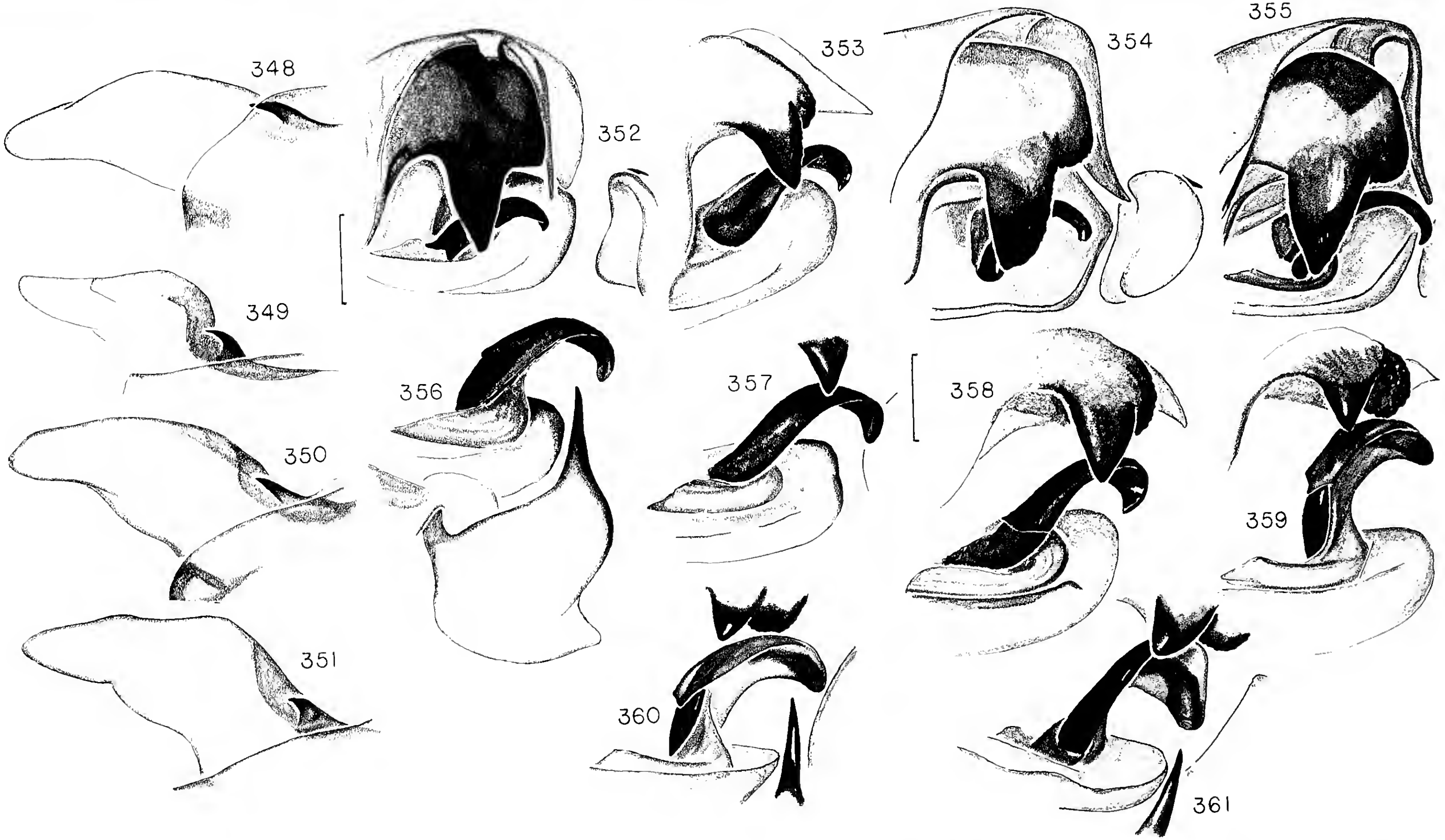
Conepeira juniperi,—Archer, 1951, Amer. Mus. Novitates, 1502: 25, figs. 54, 78, ♀, ♂. Not *Araneus juniperi* (Emerton).

Type. Male holotype and female paratype, June 1971, from Pepperell, Middlesex County, Massachusetts, in the Museum of Comparative Zoology. The specific name is a noun in apposition, after the Nashoba region of Massachusetts.

Description. Living female from Massachusetts: Carapace, sternum, legs green. Abdomen yellow-green, enclosing some white spots anteriorly. Posteriorly with four pairs of dark red spots (Plate 9; Fig. 386). The abdomen is almost circular, slightly wider anteriorly. Total length 3.6 mm. Carapace 1.8 mm long, 1.4 mm wide. First femur, 2.2 mm; patella and tibia, 2.5 mm; metatarsus, 1.8 mm; tarsus, 0.7 mm. Second patella and tibia, 2.2 mm; third, 1.0 mm; fourth, 1.7 mm.

Male from Massachusetts: Coloration like that of female but legs with wide red bands (Plate 9). The palpus has a patella with one weak and one strong macroseta. The abdomen is egg-shaped, longer than wide. Total length 3.0 mm. Carapace 1.3 mm long, 1.2 mm wide. First femur, 2.1 mm; patella and tibia, 2.3 mm; metatarsus, 2.0 mm; tarsus, 0.7 mm. Second patella and tibia, 2.0 mm; third, 1.1 mm; fourth, 1.6 mm.

Diagnosis. Araneus nashoba females differ from *A. juniperi* females by having a



Figures 348–361. *Araneus guttulatus* (Walckenaer), left palpus. 348–351. Conductor. 348. (Alabama). 349. (New Hampshire). 350, 351. (Georgia). 352–355. Terminal apophysis. 352. (New Hampshire). 353, 354. (Alabama). 355. (Georgia). 356–361. Embolus, some virgin. 356, 357. (New Hampshire). 358. (Arkansas). 359, 360. (Georgia). 361. (Alabama).
(Size indicators 0.1 mm)

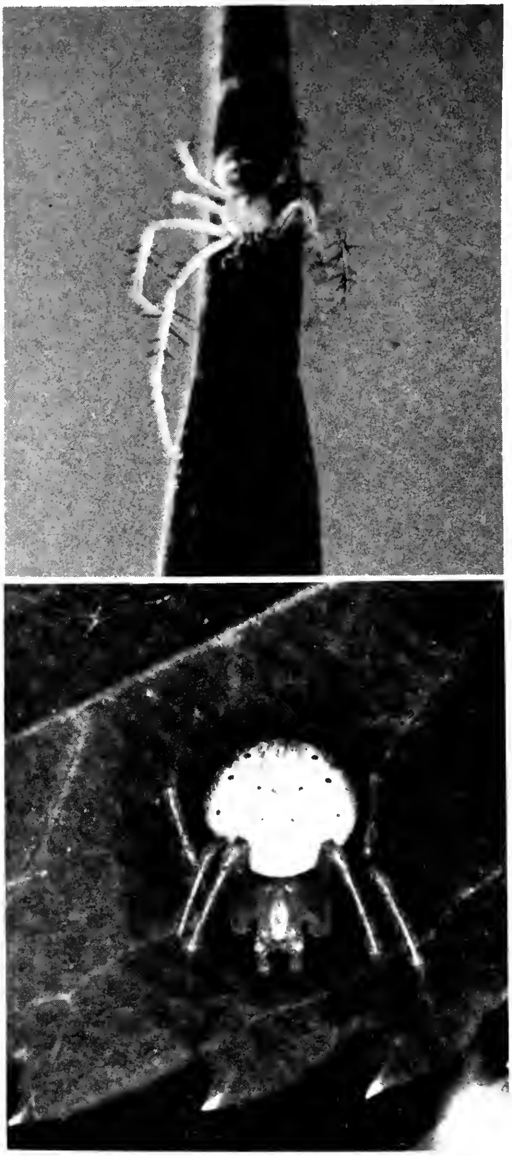


Plate 9. *Araneus nashoba* from Massachusetts. Top, male. Bottom, female. The abdomen has paired red spots on light green background; there are four indistinct anterior white patches.

slightly longer scape (Figs. 381–384) and by having the openings large and flaring, bordered only medially (Figs. 380–385). The males differ by having a distinct short projecting embolus, curved at the tip, paralleling the embolus lamella (Figs. 391–394). The conductor's basal tooth is longer than that of *A. juniperi* (Fig. 390) and the abdominal coloration differs by having some dorsal white pigment spots (Fig. 386) and paired red spots; freshly preserved *A. juniperi* tend to have indistinct longitudinal bands of darker green. The epigynum of *A. nashoba* has proportions different from those of *A. prunus.*

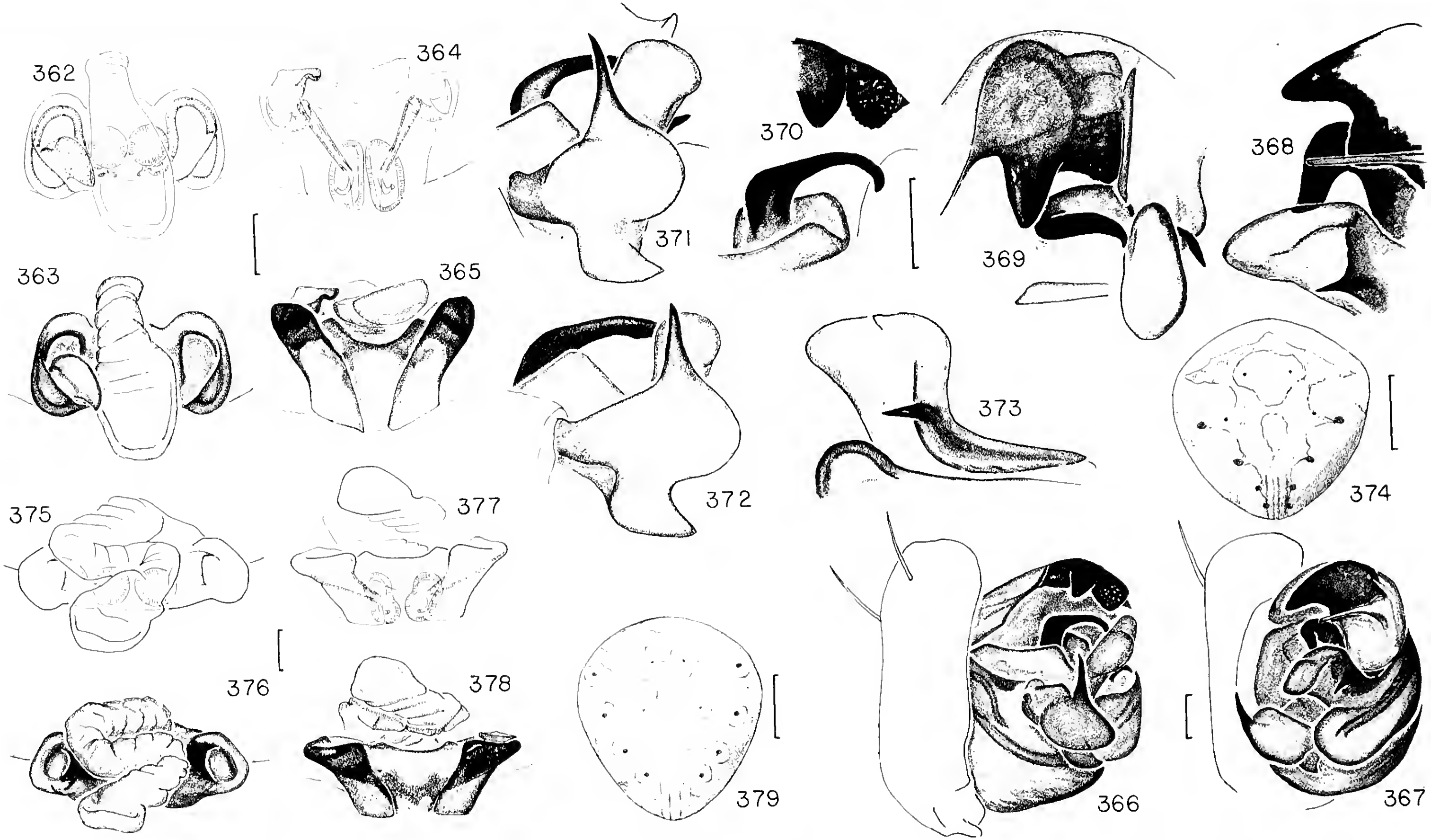
Natural history. Female paratypes were collected in a web under leaves of staghorn sumac (*Rhus typhina*) about 1.7 m above the ground on the edge of woods, and under *Forsythia* leaves (Plate 4). The male holotype was collected traversing a car, parked in the shade. Another female was collected on shrubs in a clearing for power lines in woods. Others were collected by wasps. Males have been collected in June and July, females until August. An eggsac was made out of yellow-green woolly silk, about 8 mm in diameter and contained about 25 agglutinated light green eggs.

Records. Maine. Cumberland Co.: Peaks Island, Portland, 12 July 1909, ♂ paratype (J. H. Emerton). *Massachusetts.* Middlesex Co.: Dunstable, 7 June 1971, juv., mature ♂ in July, paratype (P. Miliotis); Concord Field Station, Bedford, Aug. 1972, ♀ paratype (H. E. Evans); Pepperell, July 1967, ♀ paratype; August 1970, ♀ paratype; June 1971, ♂ paratype; July 1972, ♂ paratype (all H., L., and F. Levi). *New York.* Orange Co.: Cuddebackville, 10 July 1967, ♂ paratype. Suffolk Co.: Riverhead, 26 July 1950, ♂ paratype (R. Latham). *New Jersey.* Bergen Co.: Ramsey, July 1944, ♀ paratype (W. J. Gertsch). Ocean Co.: Lakehurst, ♀ ♀ paratypes. *Texas.* Fayette Co.: Carmine, 7 April 1966, ♀ (L. Pinter) (Map 5).

Araneus prunus n. sp.

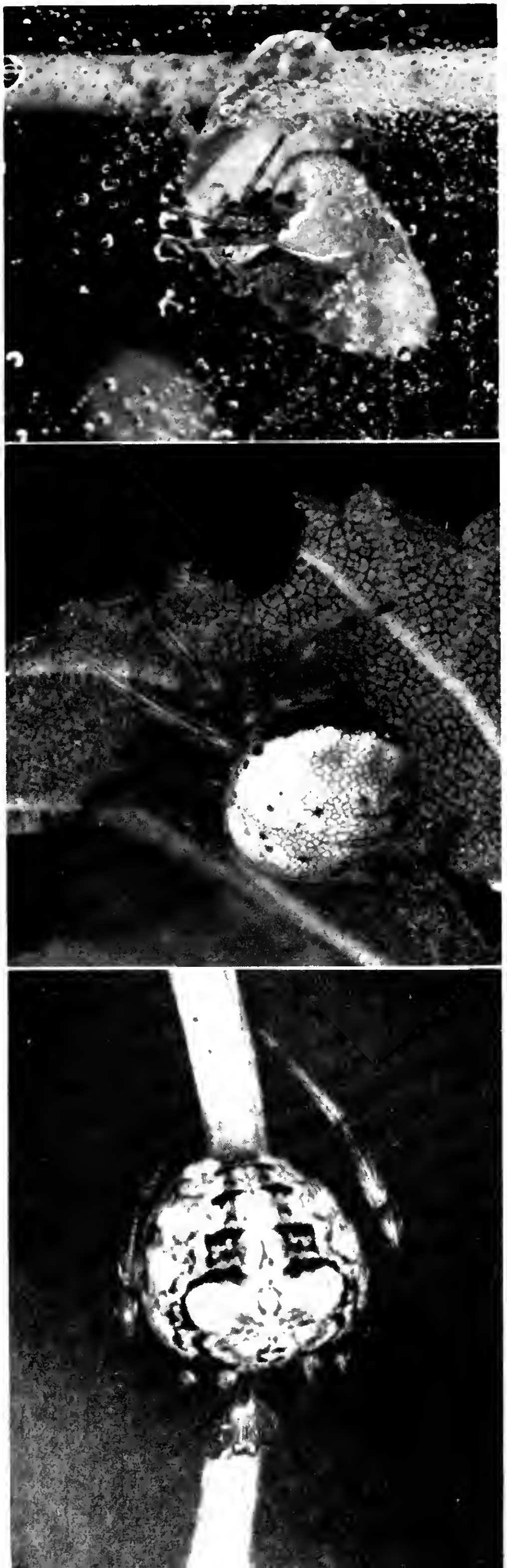
Figures 375–379; Map 5

Type. Female holotype from Plummers Island in Potomac River, Montgomery County, Maryland, few miles northwest of Washington, D.C., in wasp nest (K. V. Krombein), 23 July 1956; in the American



Figures 362–374. *Araneus texanus* (Archer). 362–365. Epigynum. 362. Ventral, cleared. 363. Ventral. 364. Posterior, cleared. 365. Posterior. 366–373. Left palpus. 366. Mesal. 367. Ventral. 368. Terminal apophysis, embolus and conductor, sublateral. 369. Terminal apophysis. 370. Embolus. 371, 372. Median apophysis. 373. Conductor. 374. Female abdomen.

Figures 375–379. *Araneus prunus* n. sp. 375–378. Epigynum. 375. Ventral, cleared. 376. Ventral. 377. Posterior, cleared. 378. Posterior. 379. Female abdomen. (Size indicators 0.1 mm, for abdomens 1 mm)



Museum of Natural History. The specific name is a noun in apposition after the genus of plum trees.

Note. Specimens of this species had been labeled *Conepeira marilandica* by Archer.

Description. Carapace, sternum, legs yellowish white. Dorsum of abdomen with faint indication of green with white spots, and of paired red spots (Fig. 379). Anterior and posterior median eyes subequal in size, lateral eyes 0.8 diameters of medians. Anterior median eyes 1.5 diameters apart, two diameters from laterals. Posterior median eyes slightly more than a diameter apart, three diameters from laterals. Total length 5.3 mm. Carapace 2.2 mm long, 1.8 mm wide. First femur, 2.6 mm; patella and tibia, 3.0 mm; metatarsus, 2.3 mm; tarsus, 0.8 mm. Second patella and tibia, 2.6 mm; third, 1.4 mm; fourth, 2.2 mm.

Diagnosis. The epigynum differs from that of *Araneus nashoba* in having a much longer scape and in having the openings of the epigynum wider apart (Figs. 375–378).

Record. Alabama. Baldwin Co.: Silverhill, July 1945, 7 ♀ paratypes (G. Nelson, MCZ).

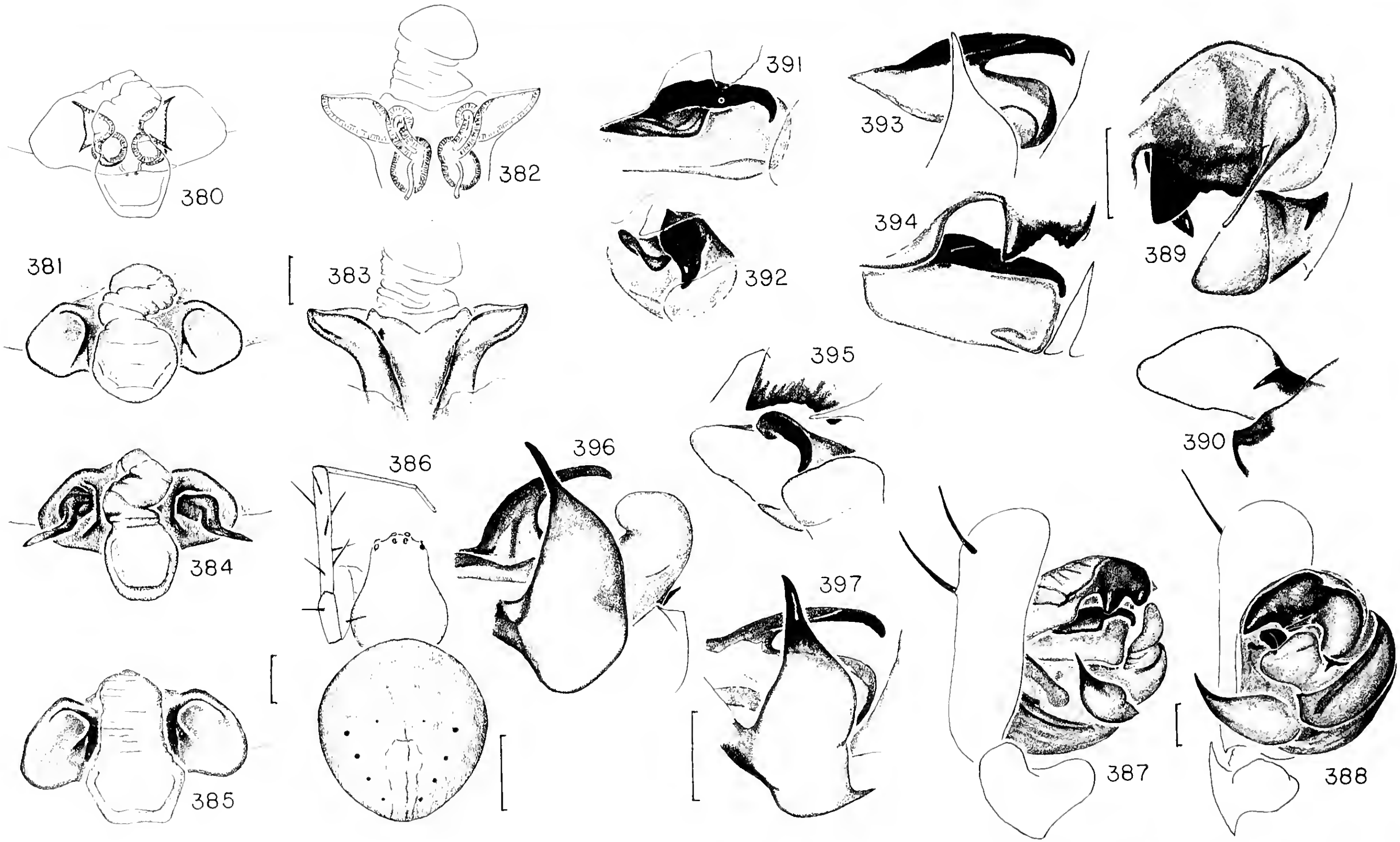
Araneus detrimentosus (O. P.-Cambridge)
Plate 10; Figures 398–414; Map 6

Epeira detrimentosa O. P.-Cambridge, 1889. Biologia Centrali-Americana, Araneidea, 1: 26, pl. 6, fig. 8, ♀. Female lectotype here designated from between Petab and Chicoyoito and Chilasco, Guatemala, in the British Museum, Natural History, examined. Keyserling, 1892, Spinnen Amerikas, 4: 137, pl. 7, fig. 101, ♀. Banks, 1898, Proc. California Acad. Sci., (3) 1(7): 253, pl. 15, fig. 7, ♀. Banks, 1910, Bull. U.S. Natl. Mus., 72: 41.

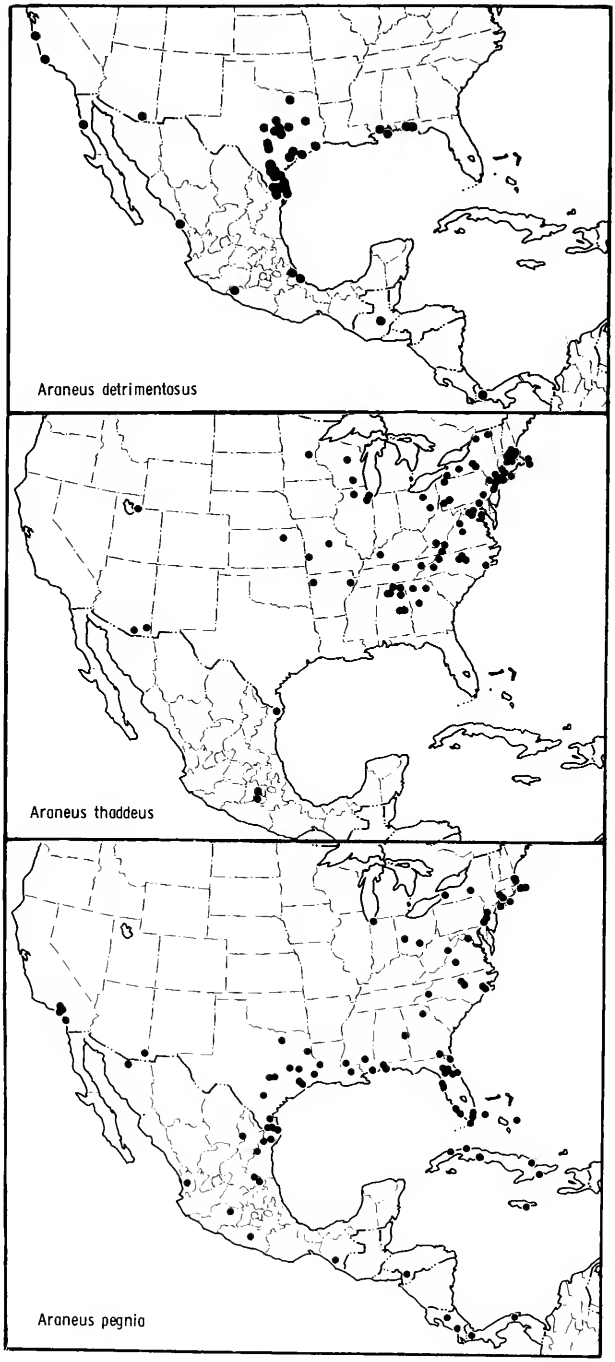
Epeira nigrohumeralis O. P.-Cambridge, 1893, Biologia Centrali-Americana, Araneidea, 1: 111, pl. 15, fig. 3, ♀. Female holotype from Venta de Zopilote, 2800 ft., Mexico, in the British Museum, Natural History, examined. First synonymized by F. O. P.-Cambridge, 1904.

Epeira tranquilla Keyserling, 1893, Spinnen Amerikas, 4: 224, pl. 11, fig. 166, ♀. Female holotype from Washington, D.C., Marx collection, probably erroneous locality, in the U.S. National Museum, examined. First synonymized by Banks, 1898.

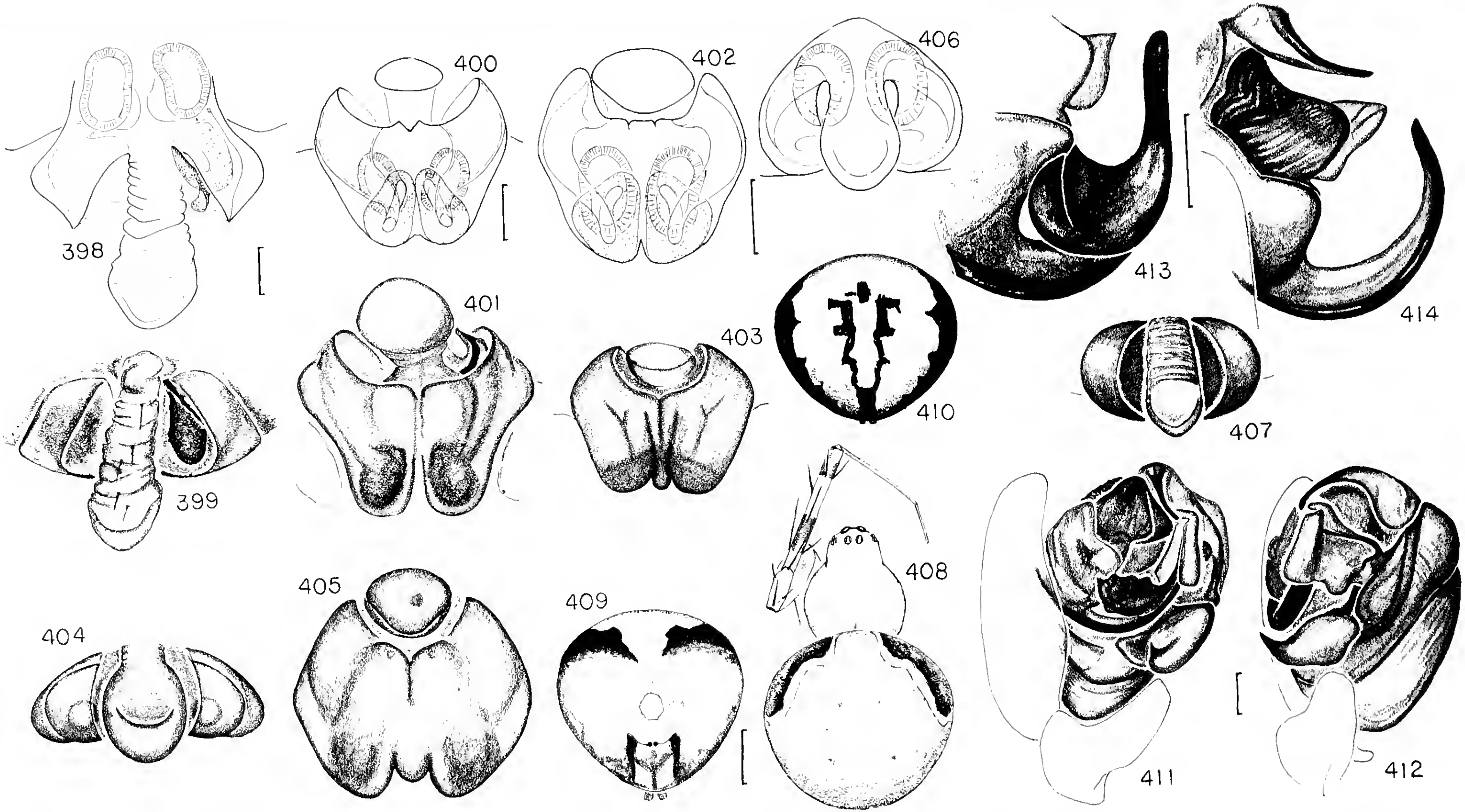
Plate 10. Top Fig. *Araneus detrimentosus* female from Mississippi (photo. A. Moreton). Middle Fig. *Araneus thaddeus* female from Massachusetts. Bottom Fig. *Araneus*



Figures 380–397. *Araneus nashoba* n. sp. 380–385. Epigynum. 380. Ventral, cleared. 381. Ventral. 382. Posterior, cleared. 383. Posterior. 384. Ventral, with embolus caps. 385. Ventral (Texas). 386. Female with first leg. 387–397. Left palpus. 387. Mesal. 388. Ventral. 389. Terminal apophysis. 390. Conductor. 391–392. Virgin embolus. 393–395. Embolus. 396, 397. Median apophysis. 396. (Ramsey, New Jersey). 397. (Lakehurst, New Jersey).
(Size indicotors 0.1 mm, for female 1 mm)



Map 6. Distributions of *Araneus detrimentosus* (O.P.-Cambridge), *A. thaddeus* (Hentz), and *A. pegnia* (Walckenaer).



Figures 398–414. *Araneus detrimentosus* (O.P.-Cambridge). 398–407. Epigynum. 398. Anterior, cleared. 399, 404, 407. Ventral. 400, 402. Posterior, cleared. 401, 403, 405. Posterior. 406. Ventral, cleared. 398, 401. (Texas). 402, 406. (Mazatlan). 403, 407. Holotype of *Epeira linteata*. 404–405. Syntype of *Epeira detrimentosa* (Guatemala). 408. Female with left first leg only. 409, 410. Female abdomen of holotype of *Epeira linteata*. 409. Ventral. 410. Posterior. 411–414. Left palpus. 411. Mesal. 412. Ventral. 413. Virgin embolus. 414. Embolus.

(Size indicators 0.1 mm, for Figs. 408–410, 1 mm)

Epeira tranquilla McCook, 1894, American Spiders, 3: 162, pl. 6, fig. 3, ♀. Female holotype from Bladensburg, D.C., Marx collections, probably erroneous locality. First synonymized by Banks, 1910.

Epeira linteata McCook, 1894, American Spiders, 3: 176, pl. 8, figs. 5, 6, ♀, ♂. Female syntype from North Carolina, in the Academy of Natural Sciences, Philadelphia, examined. NEW SYNONYMY.

Aranea detrimentosa,—F. O. P.-Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 515, pl. 49, fig. 18, ♀. Roewer, 1942, Katalog der Araneae, 1: 858.

Cambridgepeira detrimentosa,—Archer, 1951, Amer. Mus. Novitates, No. 1502: 2, figs. 8, 9, 10, ♀, ♂.

Araneus detrimentosus,—Bonnet, 1955, Bibliographia Araneorum, 2: 486.

Note. I am not sure if the specimens from Texas and southern United States are the same species as the type specimens of O. P.-Cambridge (Figs. 404, 405) even though I have examined the types on three different occasions. The male described by O. P.-Cambridge may be mismatched. But since it belongs to the same species group there is a possibility that I am confusing females of two species. No consistent differences could be found between Central American females and those from Texas other than size. The Guatemalan males have a short, straight embolus and spines on both ends of the median apophysis. No other males could be found in collections from Mexico and Central America. Figures 403, 407, 410 were prepared from the type of *Epeira linteata.*

Description. Female from Texas: Carapace, sternum light brown. Legs with dark bands. Dorsum of abdomen bright green in fresh specimen, underlain by white, a white band anteriorly on each side, and a reddish brown anterior lateral border (Plate 10; Figs. 408–410). Sides light brown. Venter light brown with four white, indistinct patches. Carapace with some white setae. The abdomen is wider than long. Total length 5.3 mm. Carapace 2.3 mm long, 2.0 mm wide. First femur, 2.9 mm; patella and tibia, 3.3 mm; metatarsus, 2.1 mm; tarsus, 1.0 mm. Second patella and tibia, 2.7 mm; third, 1.5 mm; fourth, 2.2 mm. Females range from 4.0–6.0 mm total length, carapace 1.9–2.7 mm long, 1.6–2.2 mm wide.

Male from Texas: Coloration like that of female. The palpus has two patellar setae. The first coxa has a hook on its edge. The first and second tibiae have strong macrosetae but are not noticeably modified. Total length 3.8 mm. Carapace 2.0 mm long, 1.7 mm wide. First femur, 2.7 mm; patella and tibia, 3.2 mm; metatarsus, 1.8 mm; tarsus, 1.0 mm. Second patella and tibia, 2.3 mm; third, 1.3 mm; fourth, 1.7 mm. Males vary from 2.5 to 4.2 mm total length, carapace 1.6 to 1.9 mm long, 1.3 to 1.6 mm wide.

Variation. Female specimens are usually bright green; sometimes the abdomen is white, sometimes with brown marks (from notes in vials and color photographs). Some have more black pigment on dorsum of abdomen than others.

Diagnosis. This species has been confused with *A. thaddeus.* The posterior view of the epigynum has a ventral concavity, the dorsum a notch (Figs. 400–403); the embolus is large and readily seen in mesal view (Figs. 411, 413, 414), very different from that of *A. thaddeus.*

Note. This species is related to *Araneus marmoreus* and *A. diadematus*, but differs by the abdominal markings (Figs. 408, 409).

Archer (1951) made the species the type of his new genus *Cambridgepeira.* Besides this species, Archer placed in *Cambridgepeira* the species *Epeira lathyrina* Holmberg and *E. uniformis* Keyserling. I have not seen specimens of *E. lathyrina.* The type of *E. uniformis* is a larger species of *Araneus,* not closely related to *A. detrimentosus.*

Natural history. Females have been collected from March until October, males July until October, in May from Baja California. Males are uncommon in collections. Specimens have been collected in mustard field, Lompoc, Santa Barbara County, California; shrubs on beach Destin, Florida. B. Vogel collected Texas specimens having "webs on mesquite [*Prosopis juliflora*], most on defoliated bushes, Travis County," "On juniper [*Juniperus*] or rock elm [*Ulmus* sp.]. Spins small flat shelter," Williamson County. Another collection came from under reeds along lagoon; hillsides at El Rosario, Baja California (W. J. Gertsch and V. Roth).

"It spins an orb web, about the size you would expect for a small spider, no bigger than your hand in all and the actual area covered by the spiral [is] probably around 3″. The shelter is small, hardly bigger than the huddled up spider, and slightly concave, a small plate set at a 45 degree angle to horizontal. I have usually found the green [*Araneus detrimentosus*] in a rock elm or juniper. They are only found in small-leafed bushes and trees about eye level." (personal communication, B. Vogel).

Distribution. Along the Gulf coast of northern Florida, Texas to Panama; Pacific Coast from Big Sur, California, to Boquete, Panama. A record from Trelease Woods, Urbana, Illinois, is probably mislabeled by a collector who also collected near Dallas, Texas, and so probably are various old specimens in the Marx and McCook collections, but not a female from Huachuca Mts., Arizona, 19 July 1936 (Knull, AMNH) (Map 6).

Araneus thaddeus (Hentz) Lattice Spider
Plates 10, 11; Figures 4, 415–425; Map 6

Epeira thaddeus Hentz, 1847, J. Boston Natur. Hist. Soc., 5: 473, pl. 31, fig. 6, ♀. Female type from Alabama, destroyed. Emerton, 1884, Trans. Connecticut Acad. Sci., 6: 309, pl. 33, fig. 9, ♀. McCook, 1889, 1890, American Spiders, 1: 348, 303–305; 2: 90, 331. McCook, 1894, American Spiders, 3: 169, pl. 7, figs. 3–5, ♀, ♂. Emerton, 1902, Common Spiders, p. 170, fig. 401, ♀. Emerton, 1909, Trans. Connecticut Acad. Sci., 14: 200, pl. 5, fig. 2, ♂. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 259, figs. 807–809; 826–827, ♀, ♂.

Epeira meropes Keyserling, 1865, Verh. Zool. Bot. Gesell. Wien, 15: 825, pl. 19, figs. 6, 7, ♂. Male holotype from the Spanish Colony, New Granada

Plate 11. Web of a penultimate instar of *Araneus thaddeus* male from Massachusetts in high-bush blueberries (*Vaccinium* sp.) about 1.8 m above ground. Retreat in curled-up leaf outside of photograph. The web was dusted with corn starch.

[Colombia, Panama], in the British Museum, Natural History. Keyserling, 1892, Spinnen Amerikas, 4: 139, pl. 7, fig. 102, ♂. NEW SYNONYMY.

Epeira baltimorensis Keyserling, 1879, Verhandl. Zool. Bot. Gesell. Wien, 29: 305, pl. 4, fig. 8, ♀. Female holotype from Baltimore, Maryland, in the British Museum, Natural History, examined. First synonymized by McCook, 1894.

Araneus thaddeus,—Petrunkevitch, 1911, Bull. Amer. Mus. Natur. Hist., 29: 319. Bonnet, 1955, Bibliographia Araneorum, 2: 610.

Aranea thaddeus,—Comstock, 1912, Spider Book, p. 490, figs. 519–522, ♀, web. Comstock, 1940, Spider Book, rev. ed., p. 504, figs. 519–523, ♀, web. Roewer, 1942, Katalog der Araneae, vol. 1, p. 863.

Neosconella thaddeus,—Archer, 1951, Amer. Mus. Novitates, No. 1487: 38.

Neosconella montana Archer, 1951, Amer. Mus. Novitates, No. 1487: 39, fig. 41, ♂. Male holotype from Santa Rita Mountains, Arizona, in the American Museum of Natural History, examined. NEW SYNONYMY. (Not *Epeira montana, Aranea montana* and *Araneus montanus* of other authors.)

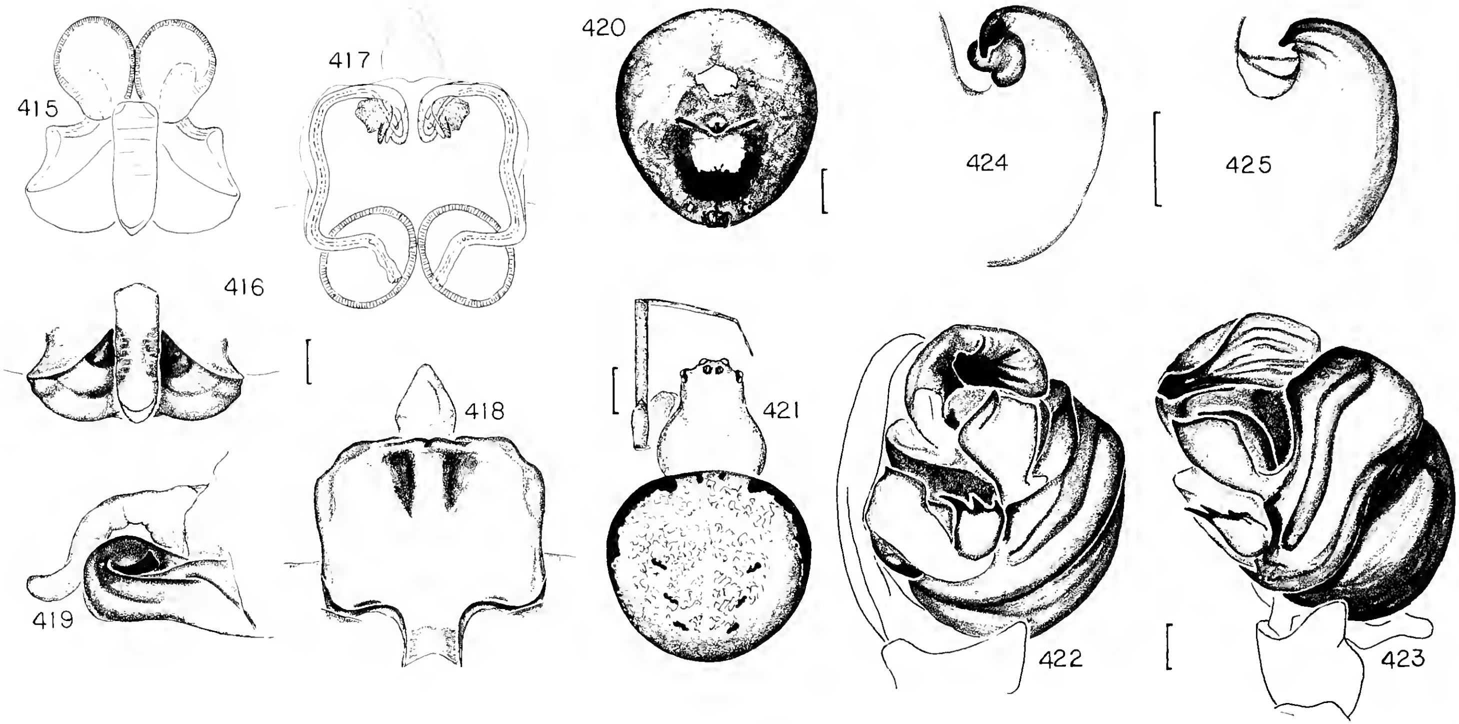
Description. Female from Georgia: Carapace, sternum, legs golden yellow. Distal articles of legs with some bands. Dorsum of abdomen whitish with five pairs of dark brown spots, which are farther apart anteriorly than posteriorly. Sides of abdomen blackish brown with a distinct border toward dorsum, fading toward venter (Figs. 420, 421). Venter with a transverse white mark behind epigynum; in front of spinnerets, a transverse brown mark which is extended anteriorly on each side (Fig. 420). Sides of venter white. The abdomen is wider than long as seen from above. Total length 6.2 mm. Carapace 2.5 mm long, 2.2 mm wide. First femur, 3.0 mm; patella and tibia, 3.8 mm; metatarsus, 2.7 mm; tarsus, 1.0 mm. Second patella and tibia, 3.0 mm; third, 1.7 mm; fourth, 2.2 mm.

Male from Georgia: Coloration like that of female, except carapace slightly darker in the mid-line and almost no dark pigment on abdomen; the lateral bands are indistinct. There is a hook on the first coxa and a groove on the second femur. The second tibia is slightly curved and is armed with macrosetae. The abdomen seems longer than wide. Total length 4.7 mm. Carapace 2.9 mm long, 2.2 mm wide. First femur, 4.3 mm; patella and tibia, 5.4 mm; metatarsus, 4.1 mm; tarsus, 1.2 mm. Second patella and tibia, 3.7 mm; third, 2.0 mm; fourth, 2.9 mm.

Variation. Females vary from 5.9 to 8.0 mm total length, carapace from 2.4 to 3.0 mm long, 2.1 to 2.8 mm wide. Males vary from 3.7 to 5.7 mm total length, carapace 2.2 to 2.9 mm long, 1.8 to 2.2 mm wide. Sometimes females lack black pigment; males usually do. According to the literature (Comstock, 1912, 1940) the abdomen varies from yellowish to purple and pink in color. Males collected had a green spot under each femur.

Diagnosis. Females of *A. thaddeus* have been confused with those of *A. detrimentosus;* males with *A. pegnia,* judging by labels in vials. *Araneus thaddeus* differs by having, on the venter of the abdomen, a white transverse bar anteriorly and a black transverse bar posteriorly (Fig. 420). Females of *A. thaddeus* differ from those of *A. pegnia* by the dorsal pattern (Fig. 421) and by the rectangular posterior view of the epigynum (Fig. 418). The coloration of males of *A. thaddeus* and *A. pegnia* is similar, but *A. pegnia* has a median apophysis with two apically directed teeth; *A. thaddeus* has three teeth of variable size. Males cannot be separated by color pattern.

Natural history. The retreat of the spider has lattice-like walls with smaller and larger openings, giving the spider the common name lattice spider. Sometimes there are free sectors in the web as in *Zygiella* (Comstock, 1912, 1940). I have never seen this. Comstock pictured the orb web. There is a signal line from the center to the retreat. The webs are small, the catching area probably less than 15–20 cm in diameter. The species is common along the edge of woods in New England among abundant foliage such as high-bush blueberry (*Vaccinium* sp.), at the height of about 1.7 m above the ground. Males are mature from late summer to early fall, females from late summer to early winter.



Figures 415–425. *Araneus thaddeus* (Hentz). 415–419. Epigynum. 415. Ventral, cleared. 416. Ventral. 417. Posterior, cleared, with two embolus caps. 418. Posterior. 419. Lateral, with embolus cap. 420. Female abdomen, ventral. 421. Female with first left leg. 422–425. Left palpus. 422. Mesal. 423. Ventral. 424. Virgin embolus, with conductor hiding embolus removed. 425. Embolus, with conductor hiding embolus removed.

(Size indicators 0.1 mm, for Figs. 420, 421, 1 mm)

The eggs are found in a curled-up leaf, covered by a lattice-like webbing; probably they are not usually suspended on a thread as shown by McCook (1890). Some specimens come from mud dauber nests of *Trypargilum* sp. in Georgia. Life history information is found in McCook, 1889, 1890.

Distribution. A Japanese record of this species (Peelle and Saito, 1932, J. Fac. Sci. Hokkaido Univ. Zool., (6) 2(2): 93, fig. 6), is not *A. thaddeus,* judging by the illustration. *Araneus thaddeus* is common in the eastern United States, but it has not been collected in Florida and is rare on the Gulf coast. In the west it is much less common, but has been found in Mill Creek Canyon, Salt Lake City, two males from the Southwest Research Station at Chihuahua Mountains, Arizona, a male from Santa Rita Mountains, Arizona. There is a specimen from N25: W97 (W. Ivie), others from Distrito Federal, Mexico, Cuernavaca, Morelos and from the former Spanish Colony of New Grenada in the Keyserling Collection. The distribution is complementary to that of the similar *A. detrimentosus* (Map 6).

Araneus pegnia (Walckenaer)
Plate 10; Figures 5, 426–438; Map 6

Epeira pegnia Walckenaer, 1841, Histoire Naturelle des Insectes. Aptères, 2: 80. Type is Abbot, Georgia Spiders manuscript, figs. 484, 375, 389, of which I here designate fig. 484 lectotype, in the British Museum, Natural History, copy in the Museum of Comparative Zoology, examined. McCook, 1894, American Spiders, 3: 170, pl. 7, figs. 8, 9, ♀, ♂. Kaston, 1948, Connecticut Geol. Natur. Hist. Surv., 70: 260, figs. 810, 828–829, 2050, ♀, ♂, web.

Epeira tytera Walckenaer, 1841, Histoire Naturelle des Insectes. Aptères, 2: 81. The type is Abbot, Georgia spiders manuscript, fig. 374, in the British Museum, Natural History, copy in Museum of Comparative Zoology, examined. First synonymized by McCook, 1894.

Epeira globosa Keyserling, 1865, Verh. Zool. Bot. Ges. Wien, 15: 820, pl. 18, figs. 19–21, ♀. Two female syntypes from the Spanish Colony New Grenada [Colombia and Panama] in the British Museum, Natural History, examined. McCook, 1878, Proc. Acad. Natur. Sci. Philadelphia, p. 134, fig. 4, 5, ♀, web. Keyserling, 1892, Spinnen Amerikas, 4: 159, pl. 8, fig. 117, ♀. Emerton, 1902, Common Spiders, p. 173, figs. 406, 407, ♀, web. First synonymized by McCook, 1894.

Epeira triaranea McCook, 1876, Proc. Acad. Natur. Sci. Philadelphia, p. 200. Eight female syntypes from Mt. Pleasant, New Jersey, in the Academy of Natural Sciences, Philadelphia, examined. McCook, 1889, American Spiders, 1: 136–142, 305, 340. McCook, 1890 American Spiders, 2: 89–90, 195, 208, 222, 231–239. Emerton, 1884, Trans. Connecticut Acad. Sci., 6: 315, pl. 34, fig. 9, pl. 36, figs. 6, 7, ♀, ♂. First synonymized by McCook, 1894.

Epeira solersioides O. P.-Cambridge, 1889, Biologia Centrali-Americana, Araneidea, 1: 25, pl. 7, fig. 15, ♂. Male holotype from Bugaba, Panama, in the British Museum, Natural History, examined. NEW SYNONYMY.

Neosconella solersioides,—F. O. P.-Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 475, pl. 44, fig. 4, ♂.

Araneus pegnia,—Petrunkevitch, 1911, Bull. Amer. Mus. Natur. Hist., 29: 308. Bonnet, 1955, Bibliographia Araneorum, 2: 564.

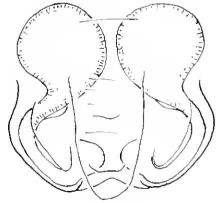
Araneus solersioides,—Petrunkevitch, 1911, Bull. Amer. Mus. Natur. Hist., 29: 316.

Aranea pegnia,—Comstock, 1912, Spider Book, p. 494, fig. 526, ♀; 1940, Spider Book, rev. ed., p. 508, fig. 526, ♀. Roewer, 1942, Katalog der Araneae, 1: 858.

Neosconella pegnia,—Archer, 1951, Amer. Mus. Novitates, No. 1487: 38, fig. 42, ♂.

Neosconella sollersioides,—Bonnet, 1955, Bibliographia Araneorum, 2: 3062.

Description. Female from North Carolina: Carapace yellow-brown. Sternum, legs yellow-brown. Legs sometimes banded. Dorsum of abdomen with anterior dorsal white mark, wider than long, framed by black lines that are widest at their posterior transverse borders (Plate 10; Fig. 433). Behind the transverse black lines are three to four pairs of black transverse lines, the posterior ones just round spots (Fig. 433). Black streaks on the sides run from anterior toward the spinnerets. Venter has a white transverse mark behind epigynum, and a black transverse mark near spinnerets. Living specimens have some red pigment above the dorsal white mark and some green on sides and posteriorly on dorsum. The abdomen is oval, wider than long as seen from the dorsum. Total length 6.1 mm. Carapace 2.7 mm long, 2.2 mm wide. First femur, 3.2 mm; patella and tibia, 3.6 mm; metatarsus, 2.6; tarsus, 1.0 mm. Second pa-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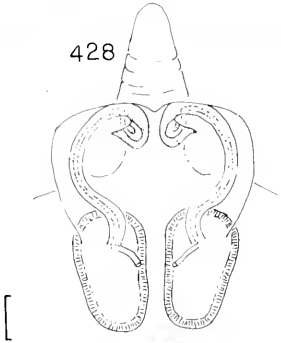
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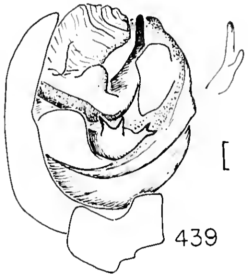
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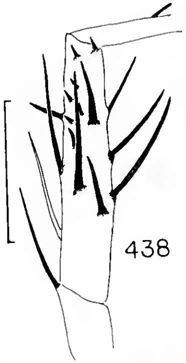
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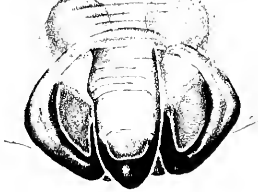
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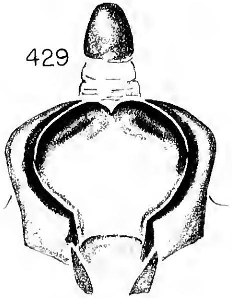
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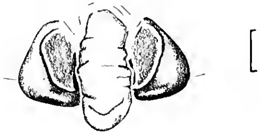
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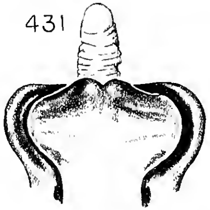
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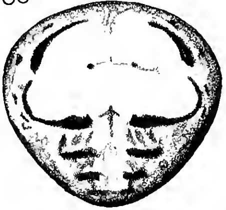
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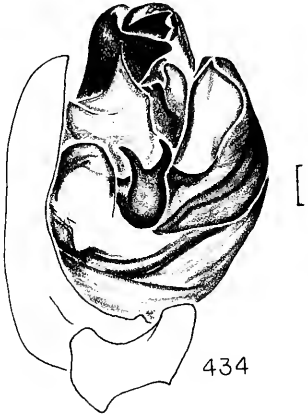
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Figures 426–438. *Araneus pegnia* (Walckenaer). 426–431. Epigynum. 426. Ventral, cleared. 427. Ventral. 428. Posterior, cleared. 429. Posterior. 430. Ventral. 431. Posterior. 432. Female abdomen, ventral. 433. Female abdomen, dorsal. 434–437. Left palpus. 434. Mesal. 435. Ventral. 436. Virgin embolus, conductor pulled aside. 437. Embolus, conductor pulled aside. 438. Left second tibia, prolateral.

Figure 439. *Neosconella styligera* O. P.-Cambridge, palpus, mesal.

(Size indicators 0.1 mm, for Figs. 432, 433, 438, 1 mm)

tella and tibia, 2.9 mm; third, 1.6 mm; fourth, 2.5 mm.

Male from North Carolina: Coloration as in female, but abdominal black spots much less distinct or absent, and only three pairs of tiny black spots remaining on the posterior of the abdomen. Thoracic depression a longitudinal line. The height of the clypeus equals the radius of the anterior median eyes. The first coxa has a hook on its distal margin. All legs are armed with macrosetae. The second tibia is thicker than other tibiae its entire length and armed with strong macrosetae, particularly on the anterior side (Fig. 438). Abdomen is wider than long. Total length 5.3 mm. Carapace 2.7 mm long, 2.3 mm wide. First femur, 3.8 mm; patella and tibia, 4.7 mm; metatarsus, 3.0 mm; tarsus, 0.9 mm. Second patella and tibia, 2.9 mm; third, 1.7 mm; fourth, 2.5 mm.

Variation. Females vary from 3.5 to 8.2 mm total length, carapace 1.6 to 3.0 mm long, 1.4 to 2.5 mm wide. Males vary from 2.5 to 4.9 mm total length, carapace 1.5 to 3.3 mm long, 1.3 to 2.2 mm wide. The smallest individuals all came from Jamaica. Some females lack black pigment, most males do. The amount of red pigment on the dorsum of the abdomen is variable, but washes out rapidly in alcohol.

Diagnosis. The pattern of the female abdomen is diagnostic (Fig. 433). *Araneus pegnia* females differ from *A. thaddeus* females by having the epigynum in posterior view rounded on each side, containing curved dark sclerotization (Figs. 428–431). The male median apophysis has only two apically directed prongs (Fig. 434), while *A. thaddeus* has three variable teeth. Males cannot be separated by color pattern. There are several similar species in Mexico and Central America, with the males having the median apophysis similar, but the embolus different and few macrosetae on the second tibia.

Natural history. The species has been found in bogs in New England and river bottom in Costa Rica, wetter sites than for *A. thaddeus*. Many specimens came from mud dauber wasp nests. The web is pictured by Emerton (1902). Additional life history information and illustrations are found in McCook, 1889, 1890.

Distribution. From Massachusetts to Porter County, Indiana, common in the southeastern United States; in the southern United States, west to the Los Angeles area, south to Panama; Bahamas, Cuba and Jamaica (Map 6).

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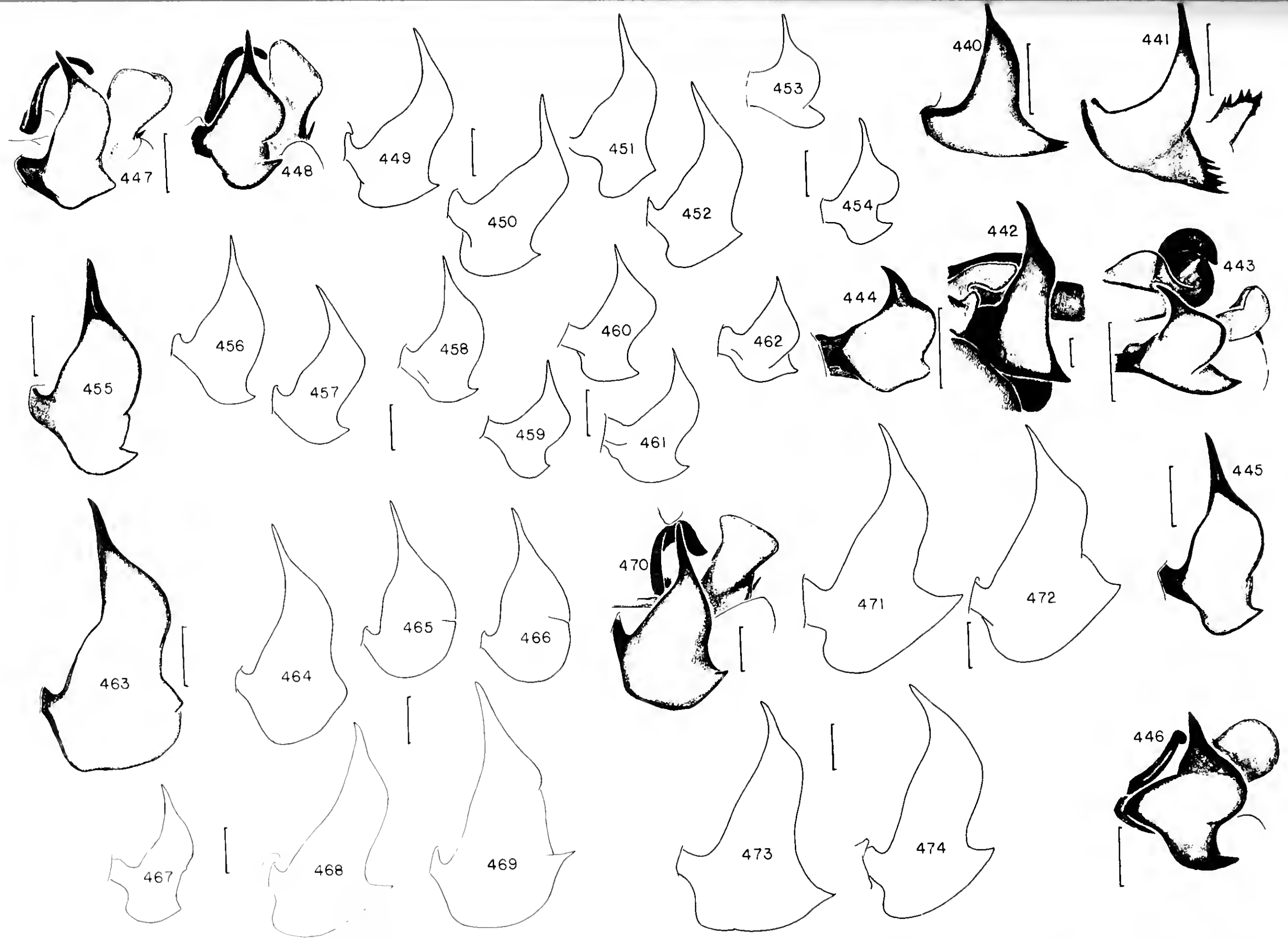

Figures 440–474. Median apophysis of left palpus. 440. *A. allani.* 441. *A. chiricahua.* 442. *A. mammatus.* 443. *A. alboventris.* 444. *A. tuscarora.* 445. *A. bivittatus.* 446. *A. gadus.* 447–452. *A. juniperi.* 447. (Maine). 448. (Gainesville, Florida). 449. (Georgia). 450. (Alabama). 451. (DeSoto Co., Florida). 452. (Maryland). 453–454. *A. bonsallae.* 453. (Kansas). 454. (Florida). 455–462. *A. cingulatus.* 455–458. (Berwyn, Maryland). 459. (Pinellas Co., Florida). 460. (Lake Co., Florida). 461. (Seminole Co., Florida). 462. (Brevard Co., Florida). 463–469. *A. niveus.* 463, 464. (Louisiana). 465, 466. (New Jersey). 467. (Liberty Co., Florida). 468. (Missouri). 469. (Alabama). 470–474. *A. guttulatus.* 470. (Alabama). 471, 472. (Arkansas). 473. (Georgia). 474. (Alabama).

(Size indicators 0.1 mm)

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